Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 9. The Subfamily Dirimiinae, subfam. nov.

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ABSTRACT:

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A new Subfamily Dirimiinae of the Family Kumpanophyllidae Fomichev, 1953 is introduced on the basis of *Dirimia* gen. nov., which is represented by six new named species and three species left in open nomenclature. The new species are *Dirimia multiplexa*, *D. similis*, *D. recessia*, *D. composita*, *D. extrema*, *D. nana*, *Dirimia* sp. 1, *Dirimia* sp. 2 and *Dirimia* sp. 3. The progressing atrophy of the columnotheca, leading to its total reduction in extreme species, and the occurrence of an axial structure instead of a compact pseudocolumella established in these species are accepted as differences exceeding the genus level. All specimens assigned to this subfamily were derived from the same Limestone F_1 of the Donets Basin, and mostly from the same locality. The reasons for their split into a relatively large number of species are: 1) an increased radiation typical for faunal turnover times; 2) a delay in the appearance of differentiated skeletal characters relative to the appearance of genetic differences large enough to characterise different species; 3) a bias in preservation of fossil remnants by comparison to living populations, amplified by biases in the collections available for study by comparison to the total number of specimens fossilised.

Key words: Rugosa (Anthozoa); Taxonomy; Middle Bashkirian; Donets Basin; Ukraine.

INTRODUCTION

The present paper belongs to a series of papers devoted to Bashkirian rugose corals from the Donets Basin, Ukraine (Text-figs 1, 2), published by the senior author either alone or with co-authors (see below). The Bashkirian is a crucial interval for the evolution of Pennsylvanian Rugosa following the collapse of the rugose coral fauna near the end of the Mississippian. The rugosans collected from the Donets Basin appear to be among the most diversified Bashkirian rugose coral faunas described so far. A new collection from the Limestone F_1 bed developed by the junior author supplements those collections from previous studies (Fedorowski 2009a, b,

2017a, b, 2019, in press; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013). Additionally, analysis of this new collection made it possible to correct misleading conclusions resulting from the scarcity of material available in an earlier study (see discussion on the subfamily below).

Most of the specimens described here were derived from a single, 1.5–2.0 m thick bed of bafflestone (Text-fig. 3). However, several corallites were collected from other sites, in some instances geographically distant. Those occurrences allow for us to suggest the possibility that some species migrated to and from the top of the main bioherm in question.

Descriptions of major septa can be problematic in situations where a septum strongly increases in

Text-fig. 1. General map of Ukraine showing the approximate position of the study area (after Fedorowski 2009a, supplemented with geographical names in Ukrainian)
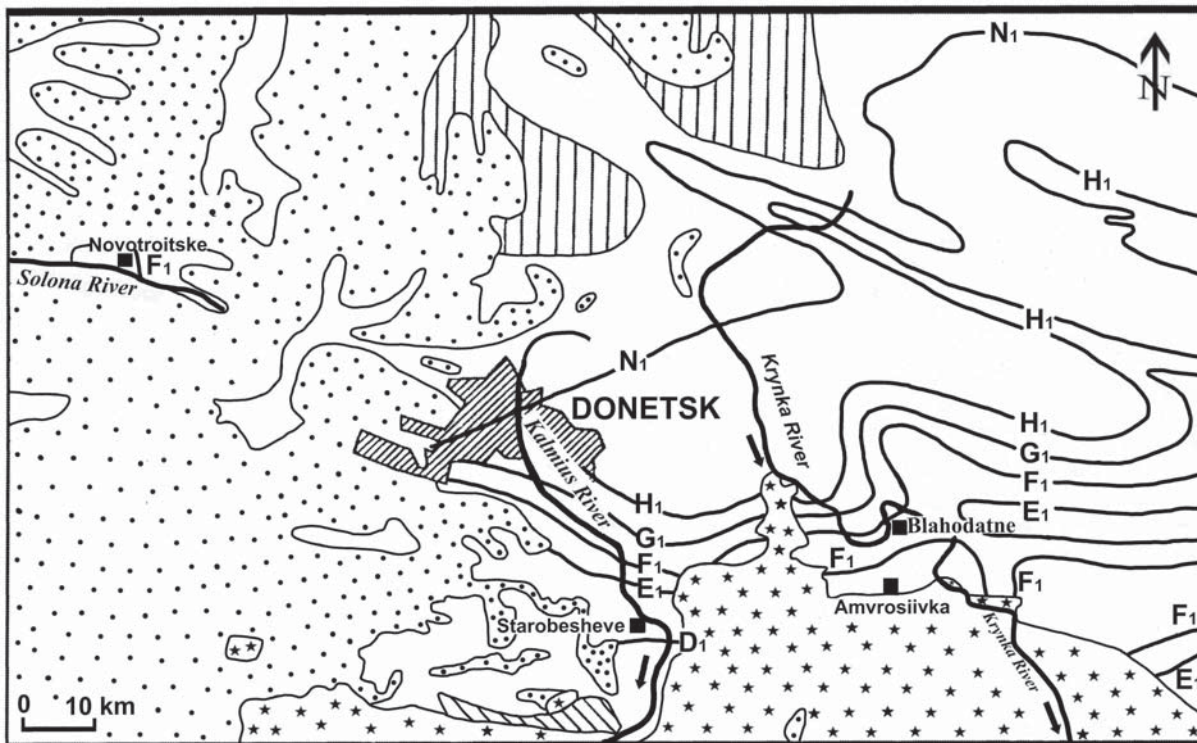
Text-fig. 2. Location of individual limestones D_1 to N_1 in the vicinity of Donetsk. Carboniferous deposits left in white (after Fedorowski 2009a, with geographical names in Ukrainian)
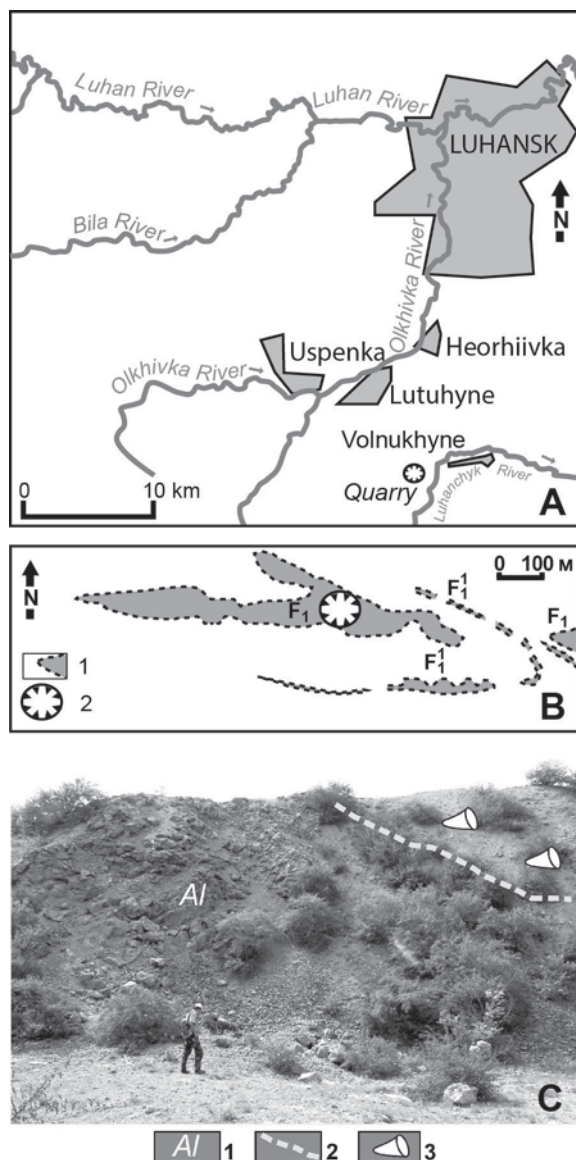
Text-fig. 3. Details of the type locality of the species described in this paper: A – Map of the Luhanchik and Olkhovka River areas, showing the location of the quarry near Volnukhine Village, B – extension of the Limestone F_1 near Volnukhine Village: 1 – limestone, 2 – quarry. C – the Volnukhine bioherm and position of the rugose coral bearing limestone: 1 – algal bafflestone, 2 – upper limit of the bioherm, 3 – argillaceous limestone with red algae and corals

length between sequential transverse sections. These rapid changes commonly result from the amplexoid character of septa (see Hill 1981, p. F16, fig. 79.1C). In the species described herein, the amplexoid character of major septa varies from weak to strong. This variety is mentioned in the descriptions of species,

but is omitted from Table 1, where only the shortest sectors of amplexoid major septa, terminated on sections of tabulae, are indicated.

The corals described in this paper are housed in the Institute of Geology, Adam Mickiewicz University in Poznań, Poland (collection UAM-Tc.Don.1) and in the Taras Shevchenko National University of Kyiv, Ukraine (collection TSNUK 3P267/F).

MATERIAL AND METHODS

Most of the studied specimens were collected by the junior author during his field investigations. Eight corallites were collected by V. Dernov from Limestone F_1 of Makedonovka Village (Luhansk region) and subsequently offered to the junior author for study. The remaining specimens belong to the large collection gathered by the late Dr. N.P. Vassilyuk, former Professor Emeritus of Donetsk Polytechnic, Ukraine, who passed away in March 2019. Years ago, she offered her collection to the senior author for study and housing. Several specimens are slightly corroded and/or eroded, but early growth stages and/ or incomplete calices remain in some. Diagenetic alterations – such as recrystallisation, dolomitic replacement, calcitic veins, and/or slight compression – are present in all specimens, often rendering their inner morphology unclear and destroying the septal microstructure. The few corallites that were most acutely affected were not investigated in detail.

Following Hudson (1936) and Fedorowski (1997), only the cardinal and the counter major septa derived from the axial septum are considered protosepta. The term 'primary septa' refers here to the innermost parts of the septa, created within the septal pockets prior to secretion of the sclerenchymal sheets.

In the present study, repetitions of the higher-ranked names in the diagnoses of the lower-ranked taxa mean that the main diagnostic characters of a higher level taxon all occur in the lower-ranked taxa. This approach reduces redundancy in diagnoses, limiting them to the distinguishing characters of the subfamily, genus, or species being described.

Traditional thin sectioning and peeling methods were applied in all instances. A cutting machine equipped with a 0.03 mm titanium cutting wire, used by the senior author for decades, allowed for very precise thin sectioning. Specimens with characters inadequately demonstrated in the images, but important for documenting morphotypes and/or variants of skeletal structure, are illustrated as drawings based on highly enlarged images.

Species	Major septa	Minor septa	Cardinal septum	Columnotheca	Axial structure early	Axial structure late	Peripheral tabularium	Dissepimentarium	n:d value
multiplexa	1/2 to 2/3 corallite radius	1/2 to 2/3 major septa	connection with median lamella long lasting	incomplete at one side or interrupted	narrow, simple with few septal lamellae	complex lamellae numerous, scattered	tabellae bubble-like, some flat	2-4 rows lonsdaleoid, none to frequent	holotype 20:7.5 mm paratypes 17:6-21:8.5 mm
similis	1/3 to 1/2 corallite radius	1/2 to 2/3 major septa	long, meets median lamella in some	almost complete, tabellae steep	narrow, simple, with few septal lamellae	loose lamellae scattered	tabellae loose, mostly flat	1-3 rows lonsdaleoid, sporadic	holotype 18:5 mm paratypes 16:6-19:5.8 mm
recessia	1/3 to 1/2 corallite radius	2/3 to 3/4 major septa	equal to major septa in mature growth stage	wide, almost complete, tabellae convex	narrow, simple with few septal lamellae	reduced to rare, short tabellae or absent	tabellae loose, spaced regularly	2-4 rows lonsdaleoid, absent from most	holotype 18:7.8 mm paratypes 19:6-21:8 mm
composita	thick, 1/3 corallite radius	1/2 to 2/3 major septa	equal to major septa in mature growth stage	absent	strong, compact	lamellae numerous, irregular, scattered	tabellae differentiated, several anastomose	1-2 rows lonsdaleoid, sporadic	holotype 17:9 mm
nana	2/3 to 3/4 corallite radius	septal crests, rare longer	commonly meets median lamella	short fragments, mostly absent	only axial septum	simple, very narrow	very narrow or absent	single incomplete row, rare lonsdaleoid	holotype 14:3 mm paratypes 15:4-16:3 mm
extrema	most meet axial structure	septal crests, rare longer	meets median lamella	absent	median lamella and margins of major septa	complex, lamellae and steep tabellae	anastomosing tabellae	4-6 rows irregular and herringbone	holotype 28:10 mm paratypes 25:9-26:11 mm
sp. 1	3/4 corallite radius	1/4 to 1/3 major septa	meets median lamella	absent	only axial septum	loose, narrow, irregular	tabellae loose, spaced regularly	single row	16:4.3 mm
sp. 2	2/3 to 3/4 corallite radius	1/2 to 2/3 major septa	equal to major septa	?	?	lamellae numerous, irregular, scattered	?	4-6 rows irregular	29:9.3 mm
sp. 3	1/3 to 1/2 corallite radius	2/3 to 3/4 major septa	long	absent	narrow, simple with few septal lamellae	complex, lamellae and steep tabellae	anostomosing tabellae	1-3 rows lonsdaleoid, absent	18:4.7 mm

Table 1. Distinguishing mature morphological characters of *Dirimia* species described in this paper

GEOLOGICAL SETTING

Suite C_2^1 (Limestone F) in the Donets Basin was established at the end of the 19th century by the Russian Geological Committee and is included in the modern stratigraphic scheme as the Mandrykinka Suite (Poletaev *et al.* 2011; Gozhyk 2013). Its original extent and composition is still accepted today. The polyfacial cyclic sedimentation of that suite comprises sandstones, siltstones, mudstones, coal seams and limestones; all of these interbedded deposits vary in thickness, content, and sequence (Poletaev *et al.* 2011, figs 12, 13). The suite belongs to the 265–400 m thick Mandrykinian macrocycle and corresponds to the Blahodatnian Regional Horizon of the Mandrykinian Regional Stage, middle Bashkirian in age. The Mandrykinian Regional Stage comprises two horizons: the lower Manuilivian Horizon, which is composed of Limestones E_8 and E_9, and the upper Blahodatnian Horizon, which comprises all limestones of group F (Poletaev *et al.* 2011; Gozhyk 2013).

The Blahodatnian Regional Horizon and the limestones of group F are exposed in both the southern (Donetsk Region) and northern (Luhansk Region) parts of the Donets Basin (Text-fig. 1). In the Donetsk Region, the Limestone F group is exposed in the Kalmius River, Krynka River, and Solona River areas (Text-fig. 2), with the stratotype section near Blahodatne Village. The extension of the Blahodatnian Horizon in the Luhansk region is limited to the area between the Olkhivka and the Luhanchyk Rivers (Text fig. 3A–C).

The junior author examined most of the outcrops bearing the Mandrykinian Regional Stage deposits, including the stratotype, and determined Limestone F_1 to be the thickest (2.0–12 m) and most stable limestone of the group (Ogar 2012). It is composed of blue-grey algal massive limestones with rare macrofauna. The other limestones of group F are thinner (0.1–2.5 m) and less stable. They are composed of dark-grey to light-brown argillites, in some cases with uncommon brachiopods, solitary rugose corals and very rare tabulate corals.

An unusual section of the lower Blahodatnian Horizon is exposed in a quarry on the left bank of the Luhanchyk River, 1.5 km west of Volnukhyne Village (Luhansk Region) (Text-fig. 3A–C). It features the thickest, and one of the most fossiliferous, Limestone F_1 sections discovered so far. The lower part of the section is composed of a blue-grey bafflestone, up to 15 m thick, that contains numerous phylloid algae but otherwise is almost barren of macrofossils. It is overlain by a 1.5–2 m thick layer of dark-grey to black wackestone containing rhodoliths (red algal nodules), crinoid fragments, brachiopods, bivalves, and small solitary rugose corals. The complex composition of the Limestone F_1 in this outcrop allowed the junior author to distinguish its lower part as an algal bioherm (Ogar 2012), 200×600 m in size with a maximum thickness of 15 m.

The macrofossil-barren algal limestones that formed the bioherm probably accumulated in shallow, clear water permitting a sufficient sunlight penetration. Such intensive illumination was necessary for the active growth of phylloid algae and the formation of an algal framework for the bioherm. However, the surface of the growing algal build-up was unfavourable for the attachment of other macroorganisms. The absence of sessile attaching organisms such as corals, crinoids, and brachiopods from the bioherm may have resulted from a surface composed of actively growing algal tissue and with unconsolidated mud between algal patches, together leading to a lack of rigid surfaces on which larvae could attach and metamorphose.

As a result of regional tectonic subsidence, the biohermal area deepened to below wave base and clay slurry flowed into the basin, changing the environment considerably. Reduced sunlight penetration and increased nutrient supply from the surrounding wetlands replaced the oligotrophic, clear-water environmental conditions that allowed the bioherm to develop. Algal frame growth in the bed of limestone that overlies the bioherm, and the accumulation of mud filling the framework, were drastically reduced. Most of the algae died, and their skeletons consolidated into a rigid mound-like structure that rose slightly above the seafloor. The combination of uncompensated sedimentation, a hard substrate, and a sufficient amount of nutrients created conditions acceptable for macrofauna, especially for solitary rugose corals, to develop. Sixty-eight specimens of the latter were collected, the majority of which belong to the new subfamily described in this paper. Several specimens of non-dissepimented corals, assigned to the genera *Rotiphyllum* Hudson, 1942 and *Falsiamplexus* Fedorowski, 2009, and a single colony of *Michelinia*-like tabulate coral were collected.

The thickness of the coral-bearing bed reached up to 2 m. Algal skeletal constructions and coral skeletons are present throughout, suggesting the patchy and diminished, yet permanent, growth of algal frame constructors and uncompensated mud sedimentation between those patches. This, in turn, suggests a long-lasting accumulation of the bed, which is important in the context of differentiating the taxa

described here. The exclusively solitary growth form of the rugose corals, the exceptionally small dimensions for dissepimented taxa, their well-preserved external surfaces, and the development of talons all record a mixture of characters that renders difficult to univocally interpret the living conditions of the corals documented here. The positions of corals in the rock vary. Those with strong talons were perhaps buried in their life positions as indicated by comparison to algal skeletons. Some were removed from their life positions, but remained *in situ* as suggested by the asymmetric overgrowth of algae on one side. A lack of long distance transport is confirmed by the coral surfaces being either well preserved or slightly corroded, but not eroded. Together, these characters may suggest a rather low-energy environment with generally reduced sedimentation and nutrient supply. However, higher energy episodes may have occurred. That increased energy resulted in the fragmentation of some coral skeletons, while an increased sediment supply and mudflow into polyps resulted in their rejuvenation if/when the volume of mud was impossible for the polyps to remove. Some polyps were wounded, but overgrew the destroyed fragments (e.g., Text-fig. 9I, J, L, M).

The conditions suggested above were episodically violated during shallowing events, leading to the partial mixing of sediments. The appropriate habitat for the coral fauna was destroyed during such episodes; local seafloor elevations became inhabited by crinoids and red algae, as indicated by the presence of local clusters of crinoid debris and rhodoliths within the bed. Solitary corals recolonised the area as soon as conditions available for their development returned. Fluctuations in coral occurrences within the bed allow for a differentiated approach to that fauna. They may well belong to two categories: autochthons and immigrants (see Considerations).

The described ecosystem disappeared due to the commencement of compensation for the tectonic subsidence of the basin floor. In lieu of carbonate accumulation, clastic sedimentation constituted the bulk of these deposits: i.e., environmental conditions unacceptable for the rugose corals. Pennsylvanian algal bioconstructions, similar in morphology and composition to those from the Donets Basin, have been described from Spain (Samankassou 2001) and the USA (Samankassou and West 2003).

Fomichev (1953) did not collect corals from the Volnukhyne Village area when completing a collection for his fundamental paper devoted to the upper Bashkirian and younger Carboniferous rugose corals from the Donets Basin. Also, only a single specimen was collected by him from Limestone E_1 and identified as *Lophophyllum* sp. That lone finding in Limestone E_1 and several specimens collected from Limestone F_1 led him to the conclusion (Fomichev 1953, pp. 527, 558) that the first corals of the 'mid-Carboniferous' type appeared in the Donets Basin during the deposition of the Mandrykinian limestone. '*Stereophrentis*' *postuma* forma *mandrykinensis* Fomichev, 1953, *Axolithophyllum*? sp. and *Lophophyllum* cf. *grabaui* (Chi) [=*Dibunophylloides finalis* (Vassilyuk, 1960) of Fedorowski 2017b, p. 483] were described by Fomichev (1953) from Limestone F_1. *Bothroclisia crassiseptatum* Fomichev, 1953 was collected by him from a layer below Limestone F_3, which does not have an assigned term in the modern indexation of limestones but supplements the total number of species identified and described by Fomichev (1953) from the Limestone F Group. That list has been supplemented by subsequent authors. Vassilyuk (1974) described four species of Tabulata from the Limestone F_1 Group and named some lower Bashkirian taxa (Vassilyuk in Aisenverg *et al.* 1983). Further work by Fedorowski (2009a, b, 2017b, 2019b) and Fedorowski and Vassilyuk (2011) provided descriptions of several new taxa of dissepimented and non-dissepimented rugose corals from the Limestone F Group. Finally, new data on lower and middle Bashkirian rugose corals from the Donets Basin were developed in new collections assembled by the junior author (Fedorowski and Ogar 2013 and this report). A detailed analysis of that fauna will be conducted in the future, in a concluding paper on the Bashkirian Rugosa from the Donets Basin. The existing data allow us to contest Fomichev's (1953) suggestion and lower the time of appearance of the 'mid-Carboniferous' type of rugose corals in the Donets Basin. In contrast, Fomichev (1953) was correct in considering Limestone F_1 to be a stratigraphic level rich in Pennsylvanian corals.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder incertae sedis
Family Kumpanophyllidae Fomichev, 1953
Subfamily Dirimiinae subfam. nov.

DIAGNOSIS: Kumpanophyllidae with septal lamellae attached to median lamella, but separated from each other to form an axial structure in transverse section that may disappear in advanced maturity; ax-

ial column absent; columnotheca incomplete, evolving towards disappearance; biform character of tabularium varies from weak to strong.

CONTENT OF GENERA: Monotypic.

REMARKS: The Family Kumpanophyllidae Fomichev, 1953 has been recently widely discussed and emended as a valid, independent taxon (Fedorowski in press). The taxonomic status proposed contrasts with the position of Hill (1981), who synonymised Kumpanophyllidae with Aulophyllidae Dybowski, 1873. The extreme poverty of the original collection (six fragments of specimens) studied and illustrated by Fomichev (1953, pl. 15, figs 5–9a, b) and a number of shared characteristics between the families were perhaps the reasons for that synonymy. Indeed, the scarcity of a collection may lead to mistakes in the identification, as illustrated by ?*Zakovia* sp. and ?*Spirophyllum* sp. 2 of Fedorowski (2017a): both of those species were incorrectly assigned to the Family Aulophyllidae. Only the comparatively large collection and differentiated morphology of the specimens studied herein allows for correction of that false assignment. A permanent columnotheca has been suggested in the diagnosis (Fedorowski in press) as one of the main diagnostic characters of the Family Kumpanophyllidae. The new collection studied here restricts that criterion to the nominative subfamily and documents the evolution of that character towards a complete reduction of the columnotheca. Specimens lacking a columnotheca can easily be assigned to the Family Aulophyllidae, as has been done in the taxa listed above. The collection studied here strongly suggests that in the case of some taxa, a wide faunal context, an adequate number of specimens available for study, and a careful consideration of compatible morphological details are required for correct taxonomic assessment. Therefore, only completely studied taxa that bear characters similar to *Dirimia* gen. nov. should be considered when searching for potential synonyms and relatives. Such taxa are unknown to us in the existing literature. Thus, we have decided to avoid any suggestions of the relationships of *Dirimia* gen. nov. other than to *Kumpanophyllum* Fomichev, 1953, or to establish a list of its synonyms.

Creation of the new Subfamily Dirimiinae can be contested for three reasons. Firstly, on the basis of the occurrence in Limestone F_1 of some species of *Kumpanophyllum* together with all species of *Dirimia* gen. nov. identified so far. Secondly, due to a close similarity of *D. similis* sp. nov. to *Kumpanophyllum*. The columnotheca in that species is almost complete

(e.g., Text-figs 6J, K, 7M, N, P, Q), whereas free septal lamellae occur in some species of *Kumpanophyllum* (e.g., Fedorowski in press, text-fig. 9A–F, I–K). In addition, the early ontogeny in both genera is closely comparable up to the late neanic/early mature growth stage. Thirdly, due to the morphological similarity of the longitudinal section in *D. extrema* sp. nov. to some Aulophyllidae (see below), rather than to Kumpanophyllidae. *Dirimia recessia* sp. nov., with an axial structure disappearing at the late mature growth stage as it does in *Kumpanophyllum decessum* Fedorowski, 2019, provides an additional argument against the introduction of a new subfamily. The reasons for disregarding the arguments above are discussed in Considerations.

Genus *Dirimia* gen. nov.

TYPE SPECIES: *Dirimia multiplexa* sp. nov.

ETYMOLOGY: *Lat. dirimio, emi, emptum* – to divide, to disconnect, after septal lamellae isolated from each other to form the axial structure.

DIAGNOSIS and REMARKS: As for the subfamily until monotypic.

SPECIES ASSIGNED: *Dirimia multiplexa* sp. nov., *D. composita* sp. nov., *D. extrema* sp. nov., *D. nana* sp. nov., *D. recessia* sp. nov., *D. similis* sp. nov., *Dirimia* sp. 1, *Dirimia* sp. 2, *Dirimia* sp. 3, and ?*Zakovia* sp. of Fedorowski (2017b).

Dirimia multiplexa sp. nov.
(Text-figs 4, 5)

HOLOTYPE: Specimen UAM-Tc.Don.1/306.

TYPE LOCALITY: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village, Ukraine.

TYPE STRATUM: Limestone F_1. Blahodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. multiplex, icis* – multiple, after complex morphology of axial structure in transverse section and incomplete columnotheca in longitudinal section.
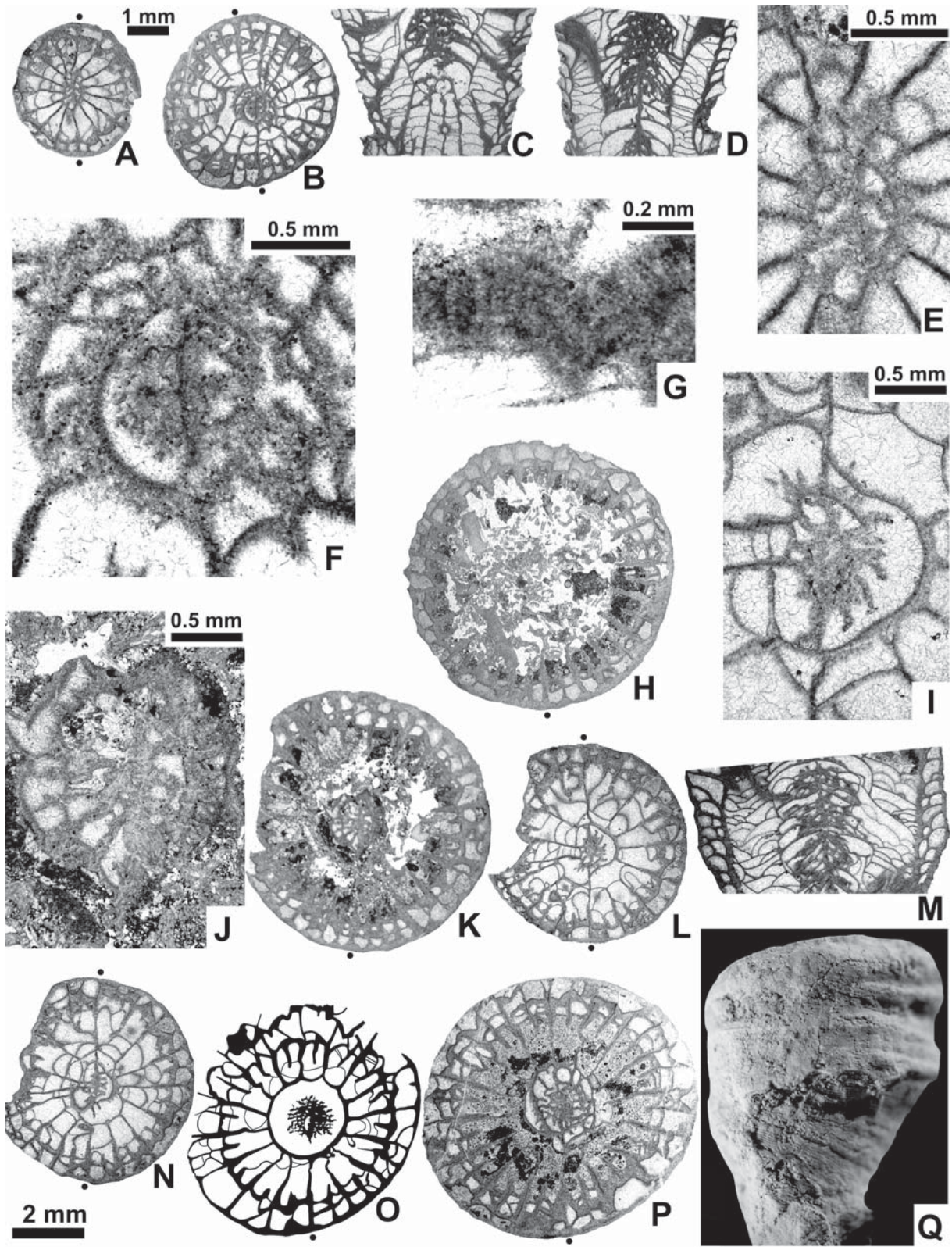
DIAGNOSIS: A species of *Dirimia* gen. nov. with n:d value 20:7.5 mm (holotype) and 17:6.0 mm to 21:8.5 mm (paratypes); major septa strongly amplexoid, 1/2 to 2/3 corallite radius long; minor septa 1/2 to 2/3 major septa; connection of median lamella to protosepta long lasting; axial structure strong, continuous, composed of thin median lamella, numerous septal lamellae in both transverse and longitudinal sections; columnotheca ranging from almost complete in some specimens to very incomplete in others; axial tabellae elevated steeply; peripheral tabellae densely packed; their biform character varying; lonsdaleoid dissepiments common.

MATERIAL: Holotype UAM-Tc.Don.1/306 and fifteen incomplete paratypes UAM-Tc.Don.1/307–312; TSNUK 3P267/F-01, 06, 67, 74, 75, 81, 89, 92, 94. Earliest growth stages lacking from all. Incomplete calice present in one corallite. Skeletons of all specimens altered diagenetically, but main characters distinguishable in all. Probable remnants of septal microstructure recognised in one corallite only. Twenty-three thin sections and twenty-two peels available for study.

DESCRIPTION: Corallite external surface almost smooth with delicate growth striae arranged in bands and very shallow septal grooves (Text-fig. 4Q). Calice shallow (Text-fig. 5J) with margin almost flat, and walls gently sloping down. Major and minor septa in calice margin similar in their elevation and thickness. In inner part of calice, major septa slightly dominate over minor septa in length (Text-figs 4H, 5J). Axial structure elevated up to 2/3 of calice depth. Immediately above calice floor (Text-fig. 4K, P), major septa reach 2/3 to 3/4 corallite radius, whereas length of minor septa remains constant.

Premature growth stages missing from all corallites studied. Earliest growth stage studied represents perhaps late neanic/early mature growth stage (Text-fig. 4A, E). Almost all major septa in that growth stage approach or meet thin median lamella. Free septal lamellae rare. Minor septa differentiated in length; most short, some interrupted by lonsdaleoid dissepiments. Interseptal dissepiments rectangular,

mostly in one row, two rows in restricted fragments of transverse sections. In slightly more advanced growth stage, as preserved in holotype (Text-fig. 4L, N), major septa long, differentiated in length due to amplexoid morphology; some meet median lamella. Protosepta either united with median lamella or temporarily disconnected from it. Almost all septal lamellae free from major septa, either united with irregular median lamella or resting on sections of axial tabellae (Text-fig. 4I).

In early to advanced mature growth stage with selected n:d values 17:6.0 mm, 17:7.2 mm, 19:7.5 mm, 20:7.5 mm, 21:8.3 mm, major septa amplexoid in character, strongly differentiated in length and thickness; most continuous, a small number interrupted by lonsdaleoid dissepiments. Major septa reach at least 2/3 corallite radius in sectors terminated at tabellae of columnotheca (Text-figs 4B, L, N–P; 5A, L, T). Slightly oblique transverse section (Text-fig. 5G) illustrates differentiation in length of major septa according to their positions against tabulae. In rare corallites (Text-fig. 5N–Q), length of major septa decreases in course of corallite growth to approximately one-half corallite radius. Cardinal and counter septa indistinguishable from remaining major septa by length and thickness when disconnected from median lamella, but that connection may last long in some specimens (Text-figs 4A, B, L, 5D, F, G). In lower part of calice, i.e., almost to upper limit of elevation of axial structure, major septa remain long (Text-fig. 4P). Their slightly reduced length in the holotype (Text-fig. 4K) is perhaps secondary caused by dolomitisation. Cardinal fossula absent. Minor septa in all corallites mostly continuous, rarely interrupted by small lonsdaleoid dissepiments, penetrate only peripheral part of tabularium. Comparative length of these septa to major septa varies greatly depending on length of the latter. Comparatively longest minor septa reach 2/3 length of shortest major septa. Axial structure well developed. In early mature growth stage axial structure rather simple (Text-fig. 4I). In more advanced mature growth stage, axial structure differentiated in morphology from simple and narrow (Text-fig. 5E, F, M, P), through moderately complex (Text-fig. 4J, K, P) to complex, either

Text-fig. 4. *Dirimia multiplexa* sp. nov. Transverse thin sections except when stated otherwise. A-G – UAM-Tc.Don.1/309. Paratype. A – late neanic/early mature growth stage, B – mature growth stage, C – oblique longitudinal thin section, D – centric longitudinal thin section, E – axial structure (enlarged from A), F – axial structure (enlarged from B), G – remnants of trabeculae in longitudinal thin section. H–N – UAM-Tc. Don.1/306. Holotype. H – upper part of calice, I – axial structure (enlarged from L), J – axial structure (enlarged from K), K – mature growth stage immediately above calice floor, L, N – early mature growth stage, M – centric longitudinal thin section. O-Q – UAM-Tc.Don.1/307. Paratype. O – mature growth stage (drawing on image taken from peel), P – mature growth stage immediately above calice floor, Q – side view. For stratigraphic positions see text. Cardinal counter and alar septa marked by black dots when recognisable. Scale bar beneath N corresponds to all images except for those marked separately
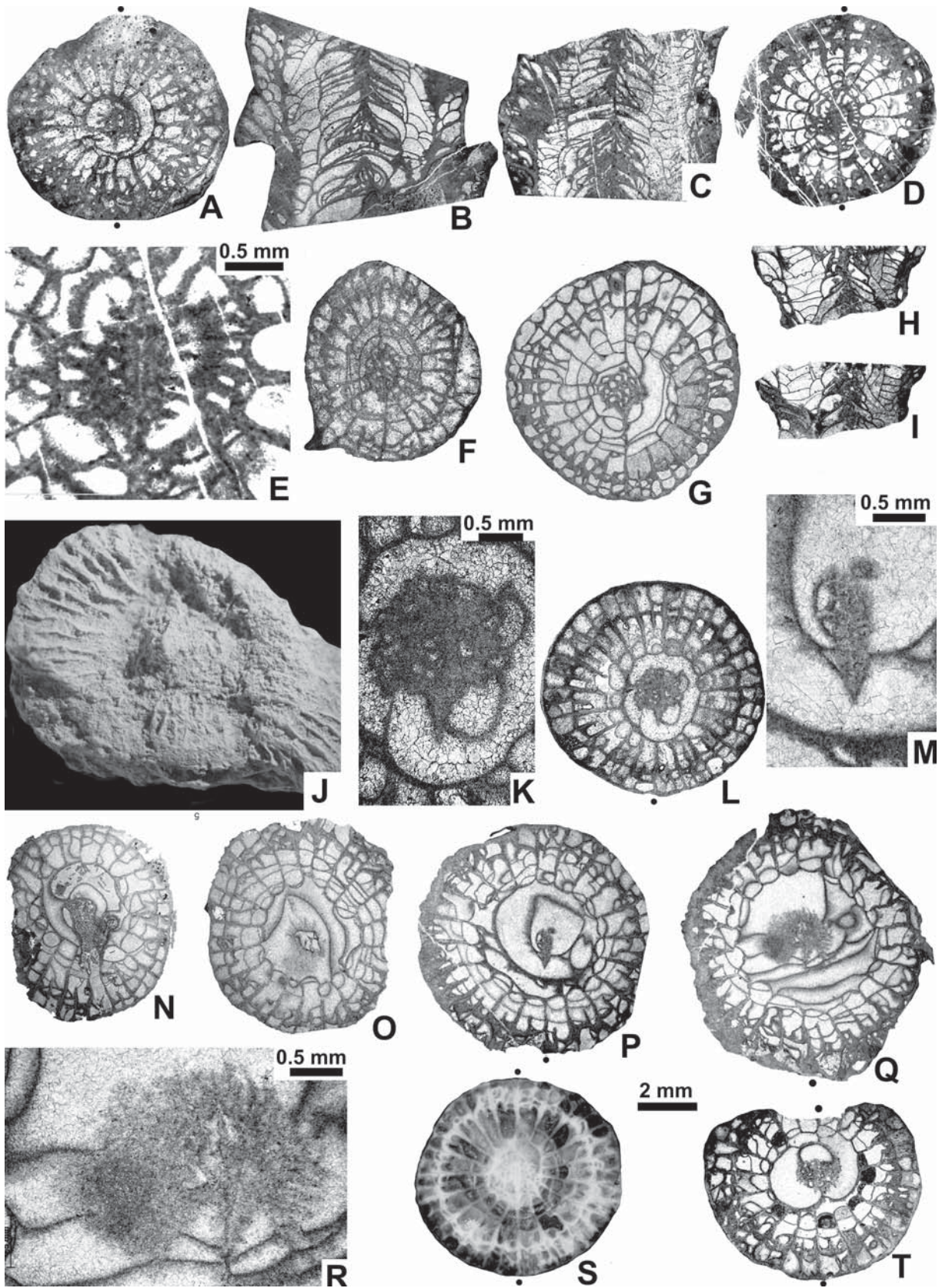
loose (Text-figs 4F, 5E) or compact (Text-fig. 5K) and similar to that in *Kumpanophyllum columellatum* Fedorowski, 2019 (see Fedorowski in press). Median lamella (Text-figs 4E, F, I, J, 5E, K, R) varies in length and thickness; slightly thickened in most specimens, commonly free, but elongated towards cardinal septum. Most septal lamellae united with median lamella. However, firm recognition of mutual relationship of these two skeletal elements precluded by diagenetic alteration. Text-fig. 5M suggests incorporation of septal lamellae into median lamella and formation of composite pseudocolumella, whereas it seems to be monoseptal in some other specimens (Text-figs 4F, J, 5S). Number of septal lamellae varies both during corallite growth and between individual corallites as demonstrated both in transverse sections described above and in longitudinal sections (Text-figs 4D, M, 5B, C, H, I). Columnotheca well developed in some parts of corallites (Text-figs 4D, lower, 5B); almost disappears during corallite growth (Text-fig. 4D, upper). In several specimens, holotype included, thin sections show axial tabellae resting on each other on one side, but attached to various underlying tabellae on the opposite side of the section (Text-figs 4M, 5C, H, I). Microstructure of septa completely destroyed by diagenesis in most corallites studied. Darker bodies arranged in fans following dissepiment surfaces in one paratype (Text-fig. 4G) are interpreted here as remnants of trabeculae.

REMARKS: *Dirimia multiplexa* sp. nov. features the fundamental diagnostic characters of the genus developed to a moderate level. Additionally, specimens assigned to this species, while similar to each other in diagnostic characters, display wide intraspecific variability, making it a morphologically convenient comparison target for other species of *Dirimia* gen. nov. Thus, it is selected as the type species and the remaining species of *Dirimia* gen. nov. are compared relative to it.

One corallite assigned to this species is significantly smaller than the rest in diameter, perhaps as a result of its immature growth stage as suggested by its cone-like shape. The smaller diameter, along with the shape of a short fragment of the axial structure in the longitudinal section (Text-fig. 4D, lower), strikingly resembles *D. similis* sp. nov. However, the remaining parts of the longitudinal section and the complex axial structure in the ontogenetically most advanced growth stage of that specimen (Text-fig. 4F) are typical for *D. multiplexa* sp. nov.

OCCURRENCE: As for the holotype.

Dirimia similis sp. nov.
(Text-figs 6, 7)

HOLOTYPE: UAM-Tc.Don.1/313.

TYPE LOCALITY: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village, Ukraine.

TYPE STRATUM: Limestone F_1. Blahodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. similis* – comparable, after morphology comparable to *D. multiplexa* sp. nov.

DIAGNOSIS: A species of *Dirimia* gen. nov. with n:d value 18:5.0 mm (holotype) and 16:6.0 mm to 19:5.8 mm (paratypes); major septa amplexoid, radially arranged, 1/3 to 1/2 corallite radius long; minor septa penetrate peripheral tabularium; small number of major and larger number of minor septa interrupted by minor lonsdaleoid dissepiments; cardinal septum commonly meets median lamella; axial structure narrow, consists of thin median lamella and scattered septal lamellae; in longitudinal sections, portions of columnotheca common, septal lamellae sporadic; peripheral tabellae moderately to widely spaced; peripheral tabularium distinctly biform.

← Text-fig. 5. *Dirimia multiplexa* sp. nov. Transverse thin sections except when stated otherwise. A-B – TSNUK 3P267/F-01. Paratype. A – mature growth stage, B – longitudinal thin section. C-E – UAM-Tc.Don.1/306. Paratype. C – longitudinal thin section, D – mature growth stage, E – axial structure (enlarged from D). F–J – UAM-Tc.Don.1/308. Paratype. F – early mature growth stage (peel), G – mature growth stage, H, I – longitudinal centric thin sections made at distance of 0.5 mm apart (peels), J – partly preserved calice. K, L – UAM-Tc.Don.1/310. Paratype. K – septal lamellae in axial structure so thickened as to make it almost compact (enlarged from L), L – mature growth stage (peel). M-R – UAM-Tc.Don.1/311. Paratype. Mature growth stage. M – solid pseudocolumella with rare short septal lamellae (enlarged from P), N – specimen wounded in axial part, O – beginning of recovery, P, Q – growth up to full recovery, R – wide, complex axial structure (enlarged from Q). S, T – UAM-Tc.Don.1/312. Paratype. Mature growth stage. S – polished surface with most major septa approaching pseudocolumella, T – most major septa reduced in length, axial structure compact. For stratigraphic positions see text. Cardinal and counter septa marked by black dots when recognisable. Scale bar between S and T corresponds to all images except for those marked separately
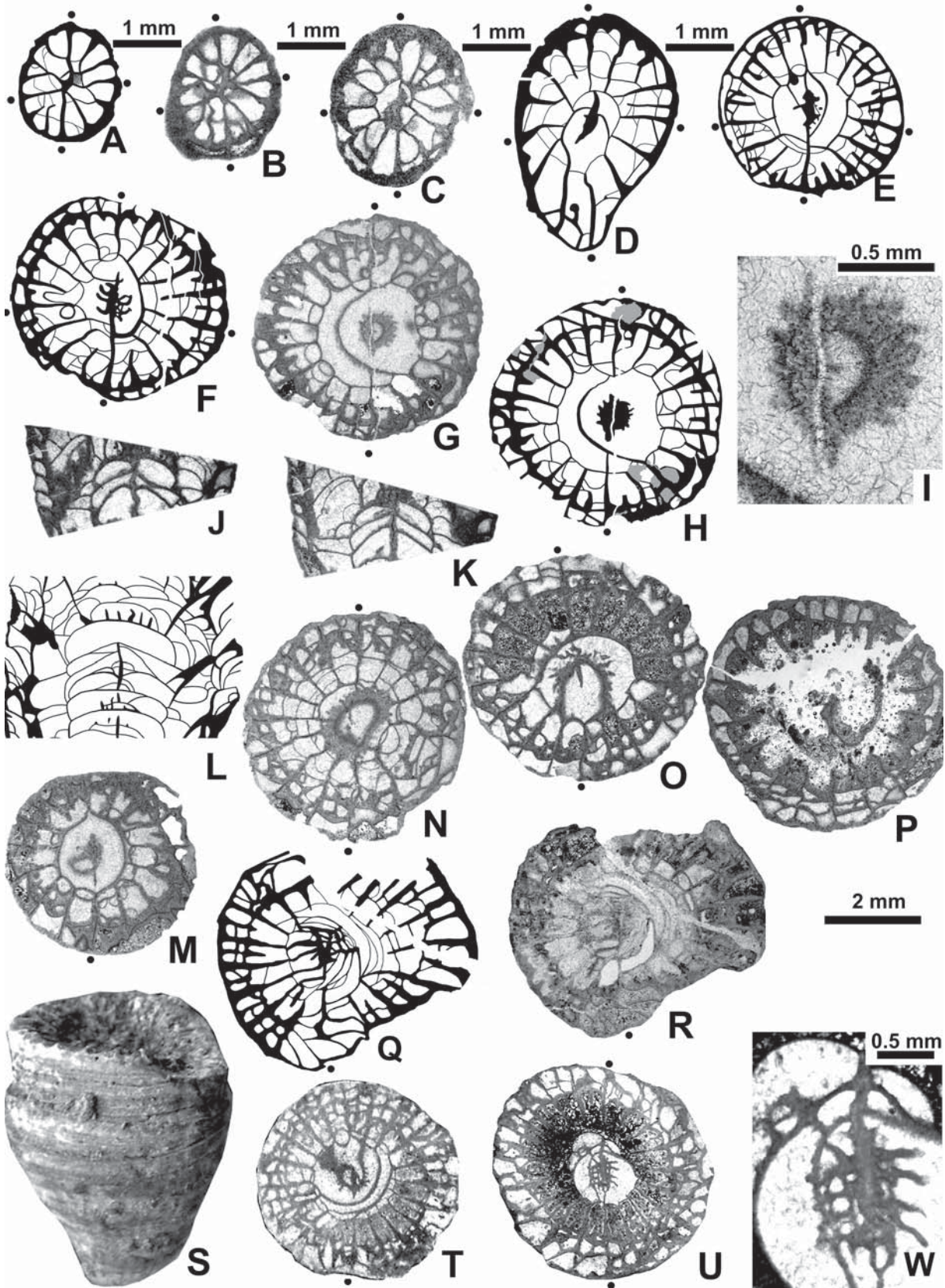
MATERIAL: Holotype UAM-Tc.Don.1/313 and twelve paratypes UAM-Tc.Don.1/314–320; TSNUK 3P267/F-02, 72, 77, 88, 91, 97. One specimen assigned tentatively. All specimens incomplete with calices lacking and skeletons recrystallised. Early growth stages preserved in three corallites, in one paratype almost completely (Text-fig. 7A–O). Only brephic growth stage from that corallite missing. Unfortunately, calcitic fissures have destroyed fragments of its premature skeleton. Also, a part of an early mature skeleton was destroyed during the specimen's life, as suggested by tabula covering the damaged skeleton, a continuous border between the damaged part and the coral skeleton beside it, and a complete skeleton present above the destroyed portion (Text-fig. 7M, N, L respectively). All those skeletal structures must have been secreted by living polyp tissue. Twenty-six thin sections and thirty-five peels available for study.

DESCRIPTION: Surfaces of thin external walls preserved in parts of most corallites (Text-figs 6S, 7A). Delicate growth striae form bands of increments. Septal furrows extremely shallow or absent. Attachments to substrate strong (Text-fig. 7A). Rotiphylloid arrangement of major septa in the earliest neanic growth stage of the almost complete paratype (Text-fig. 7B–D). N:d values: 11:0.7 mm, 11:0.9 mm. Major septa thickened. Minor septa absent from corallite lumen and from external wall. Above that earliest growth stage, very strong talon (Text-fig. 7A, F, lower) visibly separated from remaining skeleton due to curvature. N:d value of that growth stage, measured without talon: 11:1.2 mm. Major septa reduced in thickness, begin to re-arrange into bilateral symmetry. Earliest preserved growth stage of holotype comparable to described above in paratype (Text-fig. 6A), n:d value 12:1.6×2.1 mm. Major septa thin, arranged bilaterally. Axial part of wavy axial septum slightly thickened. Minor septa not traced either in this or in further, late neanic growth stage with n:d values 13:1.6×2.0 mm and 14:2×2.4 where first dissepiments appear (Text-fig. 6B, C). Growth stage of best preserved paratype, with mean n:d values 15:2.5 mm and

15:3.2 mm (Text-fig. 7G–I) interpreted as late neanic growth stage. Major septa remain bilaterally arranged and axial septum continues to occur, but middle part of that septum thickened strongly with inner margins of some major septa incorporated. Latest neanic growth stage of holotype, with n:d value 16:2.5×3.5 mm (Text-fig. 6D), deformed by attachment to substrate. Its major septa, including protosepta, separated from free, slightly thickened pseudocolumella. Crests of minor septa and small interseptal dissepiments present in some loculi. In contrast to early growth stage of two corallites described above, major septa in one paratype arranged radially. First dissepiments appear in that specimen already at n:d value 13:2.7×3.0 mm (Text-fig. 7R). That difference is treated here as intraspecific variant, but may be more significant (see Remarks).

Early mature growth stage similar in most specimens studied (Text-figs 6E, F [holotype], M, T; 7J, S). Major septa arranged radially, continuous, weakly wedge-shaped. Connection of slightly thickened median lamella to protosepta varies from both protosepta connected, through only cardinal septum connected, to free. Minor septa penetrate tabularium; several of them interrupted by small lonsdaleoid dissepiments. Axial structure narrow with varying number of free ended septal lamellae united with median lamella. Dissepimentarium in one row of rectangular dissepiments doubled in some septal loculi. Oblique and/or small lonsdaleoid dissepiments present in some septal loculi. Inner wall thickened.

Advanced mature growth stage (Text-figs 6G, H [holotype], N–P, U; 7L, T, U) similar to early mature growth stage in several characters. Major septa arranged radially, differentiated in length due to their amplexoid character. Their shortest sectors approximately 1/2 corallite radius long. Minor septa penetrate only peripheral tabularium. Dissepimentarium occupies approximately 1/4 corallite radius with most dissepiments interseptal and rare lonsdaleoid. Morphology of axial structure differentiated stronger than skeletal structures listed above, thus requiring more detailed description. In holotype (Text-fig. 6G, I), median lamella thin, monoseptal, surrounded

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← Text-fig. 6. *Dirimia similis* sp. nov. Transverse thin sections except when stated otherwise. A-K – UAM-Tc.Don.1/313. Holotype. A-D – subsequent sections of neanic growth stage (D deformed by attachment to substrate), E-H – early to late mature growth stage, I – scattered lamellae in axial structure (enlarged from G) (A, D-F, H computer drawings on peel images), J, K – longitudinal sections made at distance of 0.5 mm apart (J – peel). L-P – UAM-Tc.Don.1/314. Paratype. L – Longitudinal section (computer drawing on peel image), M – early mature growth stage, N-P – mature growth stage including calice (P). Q, R – UAM-Tc.Don.1/320. Paratype. Mature growth stage (Q – computer drawing on R). S-W – TSNUK 3P267/F-02. Paratype. S – corallite side view with calice preserved in part, T – mature growth stage, U – lower part of calice, W – axial structure (enlarged from U). For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between P and W corresponds to remaining images except for I and W marked separately
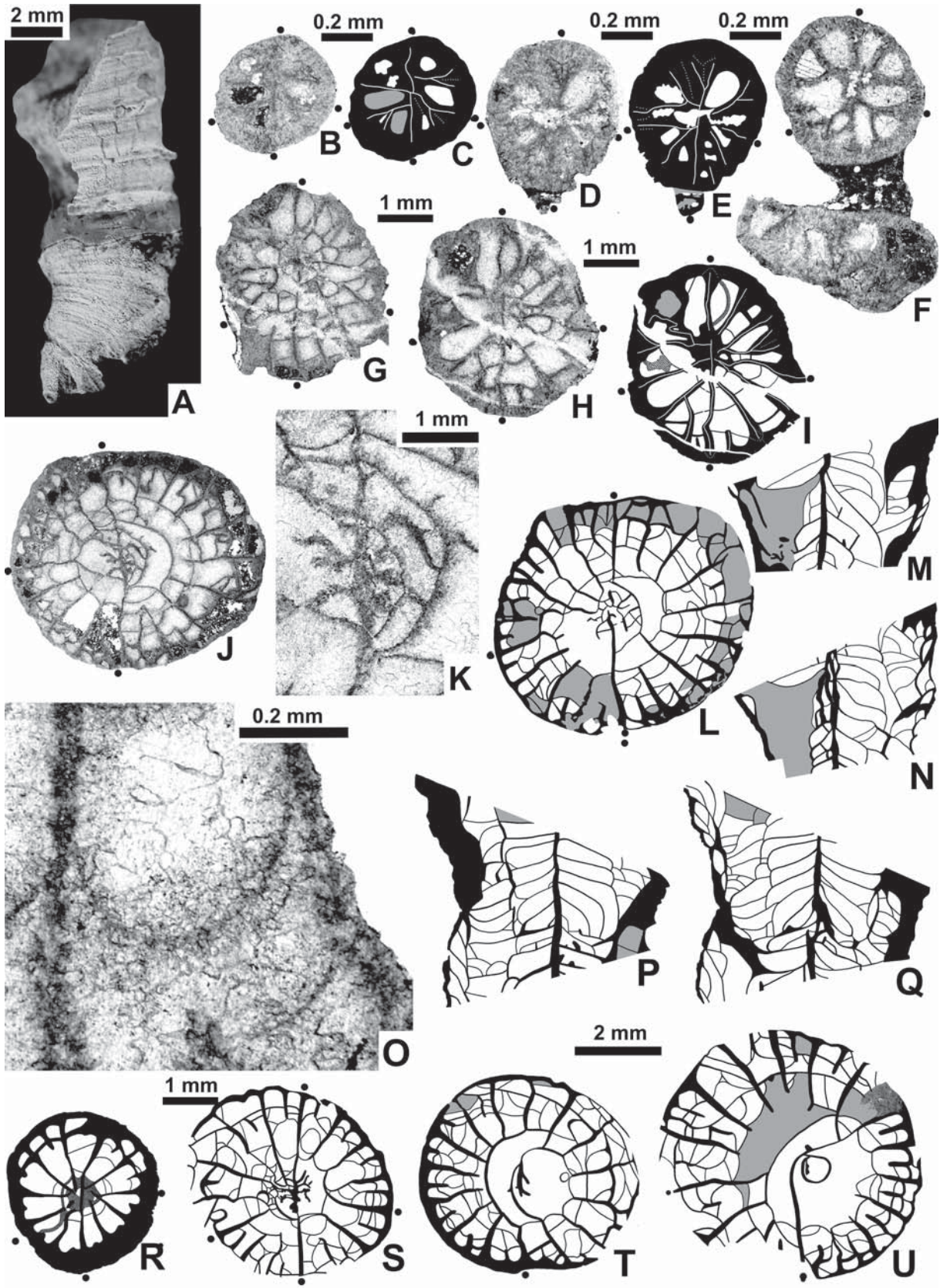
by many short septal lamellae attached to section of axial tabellae surrounding median lamella. That image changes when sectioned along the surface of tabula. Septal lamellae remain numerous, but the empty area surrounding median lamella disappears (Text-fig. 6H). One paratype (Text-fig. 6N, O) repeats morphology of holotype except for wider free area and more scattered arrangement of septal lamellae. Similar morphology of axial structure, occurring in early mature growth stage of another specimen, replaced by more regular and compact axial structure in lower part of its calice (Text-fig. 6T and U respectively). Scattered septal lamellae with or without median lamella present in most remaining paratypes (e.g., Text-fig. 7L).

Longitudinal sections with columnotheca well developed during long periods of corallite growth (Text-figs 6J–L, 7M, N, P, Q). Axial tabellae elevated gently towards sections of median lamella. Arrangement of peripheral tabellae biform, depending on their position against minor septa: i.e., either horizontal or elevated towards columnotheca. Sections of septal lamellae sporadic. Dissepiments small, arranged almost vertically, in one or two rows.

Microstructure of septa strongly diagenetically altered. Bunches of crystalline fibrils recognised in fragments of one corallite (Text-fig. 7O), weakly suggest occurrence of fine trabecular structure.

REMARKS: One specimen has enough individual characters different from the holotype and the remaining corallites of *D. similis* sp. nov. to make its identification with that species somewhat doubtful. Its longitudinal section and the early mature growth stage are typical for *D. similis* sp. nov. (Text-fig. 7P, Q, S), but its early growth stage differs from the one seen in the other two corallites investigated in detail and its advanced mature growth stage tends towards *D. reducta* sp. nov. by having the axial structure reduced to a thin and short median lamella (Text-fig. 7R and T, U respectively). It may be distinguished as new species if more specimens of a similar morphology are collected.

As indicated by its name, *D. similis* sp. nov. resembles *D. multiplexa* sp. nov. in several characters exposed in transverse sections; in addition, the n:d value in several specimens of both species is similar. However, a substantial difference in the morphology of the longitudinal sections, internally constant in both groups of corallites, is the main reason for their distinction at a species level. *Dirimia multiplexa* sp. nov. is characterised by many sections of axial lamellae and densely packed peripheral tabellae, whereas a simple axial structure, commonly reduced to the median lamella and rare septal lamellae, if any, occurs in *D. similis* sp. nov.

OCCURRENCE: As for the holotype.

Dirimia recessia sp. nov.
(Text-figs 8, 9)

HOLOTYPE: UAM-Tc.Don.1/321.

TYPE LOCALITY: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village, Ukraine.

TYPE STRATUM: Limestone F_1. Blahodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. recessio* – disappearance, atrophy, after disappearance of axial structure in mature growth stage.

DIAGNOSIS: A species of *Dirimia* gen. nov. with n:d value 18:7.8 mm (holotype) and 19:6.0 mm to 21:8.0 mm (paratypes); major septa 1/3–1/2 corallite radius long; protosepta indistinguishable; minor septa 1/2–3/4 length of major septa; axial structure present to early mature growth stage, in advanced maturity disappearing completely or remaining as short fragments of septal lamellae**;** incomplete columnotheca up to 1/2 corallite diameter wide; axial tabellae hemispherical when axial structure absent; biform arrangement of short peripheral tabellae well accentuated.

← Text-fig. 7. *Dirimia similis* sp. nov. Transverse thin sections except when stated otherwise. A-O – UAM-Tc.Don.1/315. Paratype. A – side view of corallite, B-I – early to late neanic growth stage; F – fragment of corallite with strong talon (C, E, I drawings on B, D, H), J – early mature growth stage, K – axial structure (enlarged from J), L – advanced mature growth stage (drawing on peel image), M, N – longitudinal sections approximately 0.5 mm apart (drawings on peel images), O – microstructure of two septa with remnants of trabeculae. P-U – UAM-Tc. Don.1/316. Paratype. Drawings on peel images. P, Q – longitudinal sections approximately 0.5 mm apart, R – late neanic growth stage, S-U – subsequent transverse sections of mature growth stage; U – partly above calice floor (shadowed). For stratigraphic positions see text. Cardinal counter and alar septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between P, T, and U corresponds to remaining images except for those marked separately
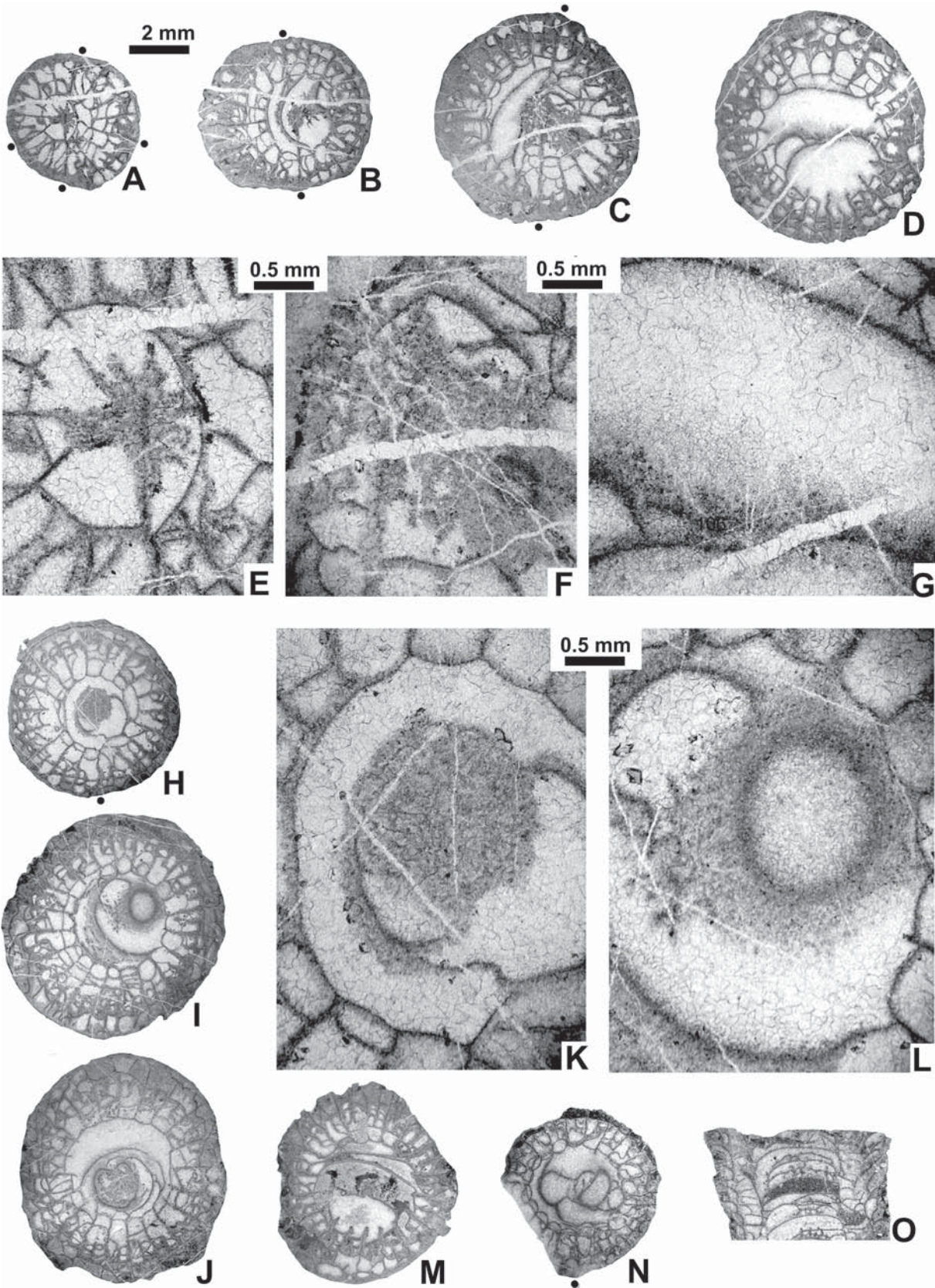
MATERIAL: Holotype UAM-Tc.Don.1/321 and ten paratypes UAM-Tc.Don.1/277, UAM-Tc.Don.1/322–329; TSNUK 3P267/F-82. All specimens incomplete. Calices and earliest growth stages lacking. Microstructure of septa and pseudocolumella altered by diagenesis. Thus, composition of pseudocolumella uncertain. One specimen rejuvenated axially. Most corallites, including holotype, used for transverse sections. Remaining fragments too short for longitudinal sections. Thus, only two longitudinal thin sections prepared. However, specimens lacking longitudinal sections possess their middle parts wide, empty, or almost empty from septal lamellae, and intersected by widely spaced tabulae. That close resemblance to transverse sections of specimens where longitudinal sectioning was possible allows for species assignment. Seventeen thin sections and twenty peels available for study.

DESCRIPTION OF HOLOTYPE: Earliest growth stage preserved (Text-fig. 8A, E), with n:d value 16:4.5 mm and dissepimentarium incomplete, corresponds to late neanic/early mature growth stage. Major septa amplexoid, continuous, most terminate at different sections of tabulae; three united with their thickened lamellae that either attach to or penetrate thickened middle part of axial septum. Most septal lamellae in axial structure free-ended. Minor septa present in all septal loculi; developed as septal crests where dissepimentarium absent or fully developed and penetrating tabularium where dissepimentarium present. Dissepiments irregular, in one incomplete row. In further holotype growth (Text-fig. 8B, C), major septa thickened and shortened except for some that continue to meet axial structure. Minor septa thick, almost as long as major septa where latter short. Axial structure most complex immediately prior to its almost total reduction (Text-fig. 8F). In most advanced growth stage (Text-fig. 8D), major septa thinner than in slightly younger growth stage, less than 1/2 corallite radius long, uniform in length, including protosepta. Minor septa vary from slightly shorter than major septa to almost totally reduced at a number of septal loculi. Some major and minor septa broken by small lonsdaleoid dissepiments. Axial structure either totally reduced, or restricted to very short crests of septal lamellae (?) attached to upper

surface of axial tabellae (Text-fig. 8G). Diagenetic alterations prevent indisputable recognition of these short structures. Rare axial tabellae span free axial area of corallite, more than 1/2 of its diameter in width (Text-fig. 8D). Dissepimentarium occupies 1/4 corallite radius or less. Dissepiments in 1–3 rows, most interseptal, small lonsdaleoid rare.

INTRASPECIFIC VARIABILITY: Major septa in paratypes complete, amplexoid, equal in length when sectioned beneath tabulae, do not reach axial structure above tabulae surfaces. Protosepta indistinguishable. Cardinal fossula absent. Most minor septa in all paratypes complete, rarely interrupted by minor lonsdaleoid dissepiments (Text-figs 8M, 9B, H, J). In early mature growth stage (Text-fig. 9B–D), axial structure well developed. In one specimen (Text-fig. 8H, K), axial structure almost compact, resembling that in *Kumpanophyllum columellatum* Fedorowski, 2019 (see Fedorowski in press), whereas only short septal lamellae attached to section of axial tabellae present in more advanced growth stage of that corallite (Text-fig. 8I, L). Reduction of axial structure occurs early in ontogeny in some specimens (n:d value 19:5.3 mm; Text-fig. 8N, O), but up to n:d value 21:8 mm in other corallites (Text-fig. 9J, K). Dissepimentarium approximately 1/4 corallite radius wide in all specimens. Dissepiments mostly interseptal, arranged in 2–4 rows, with peripheral dissepiments largest. Lonsdaleoid dissepiments rare, small, interrupting only minor septa. Tabularium two-partite. Columnotheca almost complete (Text-figs 8O, 9I). Axial tabellae long, convex, either spanning entire axial area of corallite, or incomplete. Bubble-like tabellae may reach dissepimentarium in some parts of corallite (Text-fig. 9I, right). Most peripheral tabellae short and flat, arranged in accordance to positions I or II of Sutherland (1965).

REMARKS: Changes in the morphology of the rejuvenated corallite (Text-fig. 9A–G) are worth special attention as exposing a sequence of structural developments apparently opposite to that in the holotype and the remaining paratypes. Its earliest rejuvenated growth stage (Text-fig. 9A) with several major septa shared in both the old and the rejuvenated part of the skeleton, lacks an axial structure. That structure ap-

← Text-fig. 8. *Dirimia recessia* sp. nov. Transverse thin sections except for O. A-G – UAM-Tc.Don.1/321. Holotype. A – late neanic/early mature growth stage, B-D – successive sections of mature growth stage, E-G – axial structures (enlarged from A, C, D respectively). H-L – UAM-Tc.Don.1/323. Paratype. H-J – successive sections of mature growth stage, K, L – axial structure (enlarged from H and I respectively). M – UAM-Tc.Don.1/327. Paratype. Mature growth stage. N, O – UAM-Tc.Don.1/322. Paratype. N – mature growth stage, O – longitudinal thin section. For stratigraphic positions see text. Cardinal and counter septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between A and B corresponds to remaining images
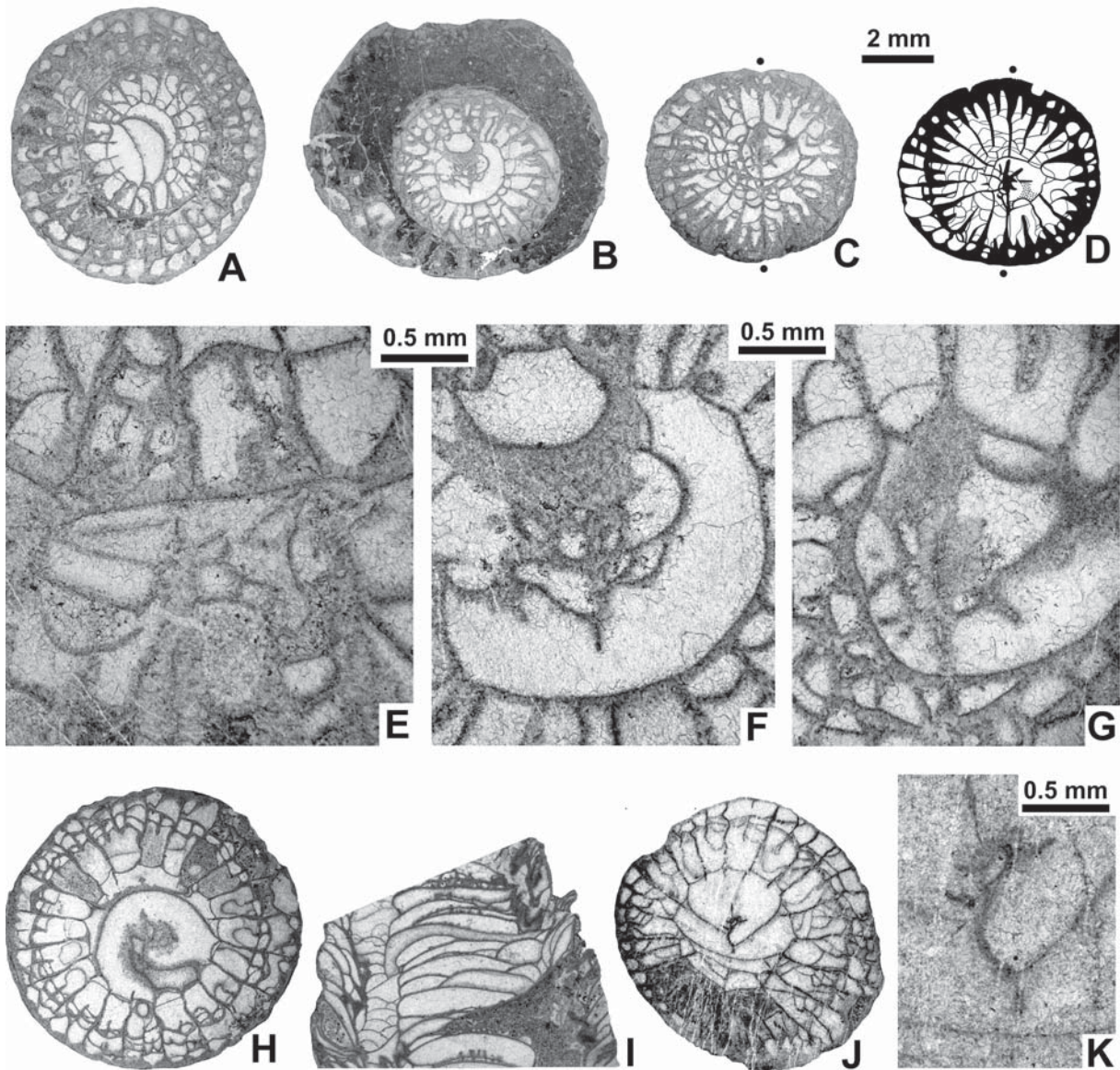
Text-fig. 9. *Dirimia recessia* sp. nov. Transverse thin sections except for I. A-G – UAM-Tc.Don.1/325. Paratype. A-D – successive section of rejuvenating corallite, E – Major septa divided by neotheca (enlarged from A), F, G – axial structures (enlarged from B and C respectively). H, I – UAM-Tc.Don.1/326. Paratype. H – mature growth stage, I – longitudinal thin section. J, K – UAM-Tc.Don.1/324. Paratype. J – mature growth stage, K – strongly simplified axial structure (enlarged from J). For stratigraphic positions see text. Cardinal and counter septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between C and D corresponds to remaining images except for K

pears soon after the total separation of the rejuvenated corallite from the earlier secreted skeleton left by the polyp (Text-fig. 9B). The reappeared axial structure, irregular at its re-introduction, eventually achieves a regularity typical of the early mature growth stage of *Dirimia* gen. nov. (Text-fig. 9B–D, F, G). Both the axial structure and remaining skeleton of the rejuve-

nated part of the corallite closely resemble the immature growth stage of the holotype.

The size of the rejuvenated corallite (n:d value 18:8.0×7.4 mm), the width and morphology of its dissepimentarium, the major septa, including a protosepta equal in length, document a fully mature growth stage of that specimen when it started the re-

juvenation. The starting phase of that process is not documented. However, a neotheca secreted in the middle length of the major septa (Text-fig. 9E) suggests a dramatic reduction in the size of the polyp, which apparently restricted itself to the middle, acolumellate part, and left behind the entire remaining skeleton. Thus, the part of the skeleton preserved in the diminished polyp has a dual provenience: its axial area and the major septa cut from peripheral parts of the same septa are remnants of the older skeleton and should be considered a mature growth stage, whereas the neotheca, crests of minor septa, and a few newly secreted dissepiments are new skeletal elements. Therefore, only the peripheral part of the skeleton should be treated as being rejuvenated. The complete rejuvenation began when the diminished polyp secreted completely new skeletal structures (Text-fig. 9B). Remnants of the old calice remain recognisable up to this stage of rejuvenation. Thus, the process as reconstructed here does not contradict the regular sequence of changes in the morphology.

Disappearance of the axial structure is the most important character distinguishing the species discussed from all remaining species of *Dirimia* gen. nov. That character makes *D. recessia* sp. nov. similar to *Kumpanophyllum perirum* Fedorowski, 2019 (see Fedorowski in press). Different morphologies of the axial structure in the juvenile and early mature growth stages and the incomplete columnotheca in *D. recessia* sp. nov. are characters adequate for distinguishing these two species on a genus level. The same characters, and the morphology of axial structure in particular, make early growth stages of *D. recessia* sp. nov. closely comparable to *D. multiplexa* sp. nov. and *D. similis* sp. nov., allowing for its placement within *Dirimia* gen. nov.

OCCURRENCE: As for the holotype.

Dirimia composita sp. nov.
(Text-fig. 10)

HOLOTYPE: UAM-Tc.Don.1/330.

TYPE LOCALITY: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village, Ukraine.

TYPE STRATUM: Limestone F_1. Blahodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. compositus*, *a*, *um* – complex, after complex morphology in the axial area of the corallite.

DIAGNOSIS: A species of *Dirimia* gen. nov. with holotype n:d value 17:9 mm; major septa, thick and wedge-shaped in tabularium, only slightly thinner in dissepimentarium; minor septa 1/2 to 2/3 length of major septa; axial structure very complex, consists of numerous, wavy septal lamellae and axial tabellae; median lamella in maturity probably absent; 1–2 rows of irregular dissepiments; small lonsdaleoid dissepiments sporadic; columnotheca absent; peripheral tabularium strongly biform.

MATERIAL: Holotype UAM-Tc.Don.1/330, with only fully mature growth stage preserved. Paratypes UAM-Tc.Don.1/331, 332 are juvenile forms found in a small piece of rock next to each other and the holotype. Specimen UAM-Tc.Don.1/333 reached only the brephic growth stage, but found next to the remaining ones, may belong to that species. All corallites diagenetically altered. Calcitic veins and dolomitisation made some characters hardly recognisable. Thirteen thin sections and sixteen peels available for study.

DESCRIPTION: In transverse section of fully mature growth stage, made partly along calice floor and partly immediately above it (Text-fig. 10B, C, F), major septa thickened, radially arranged, most free-ended, less than 1/2 corallite radius in length; several cut just above surface of tabula extend to axial structure and unite with their lamellae. Protosepta indistinguishable. Minor septa thick, enter tabularium for 0.4–0.8 mm, reach 1/3 length of major septa just above tabulae and 1/2 length of major septa below tabulae. Axial structure consists of numerous septal lamellae, arranged irregularly; sections of axial tabellae span those lamellae. Occurrence of median lamella uncertain: either thin lamella inside axial structure or lamella extending from that structure (Text-fig. 10B) plays that role. Dissepiments interseptal, mostly rectangular, in single row in most septal loculi. Their size reduced by strong sclerenchymal thickenings of major and minor septa. Morphology in early mature growth stage of holotype (Text-fig. 10A), with n:d value 17:7.5 mm, similar to that described above. Only axial structure differs, consisting of thick, compact pseudocolumella accompanied by some free septal
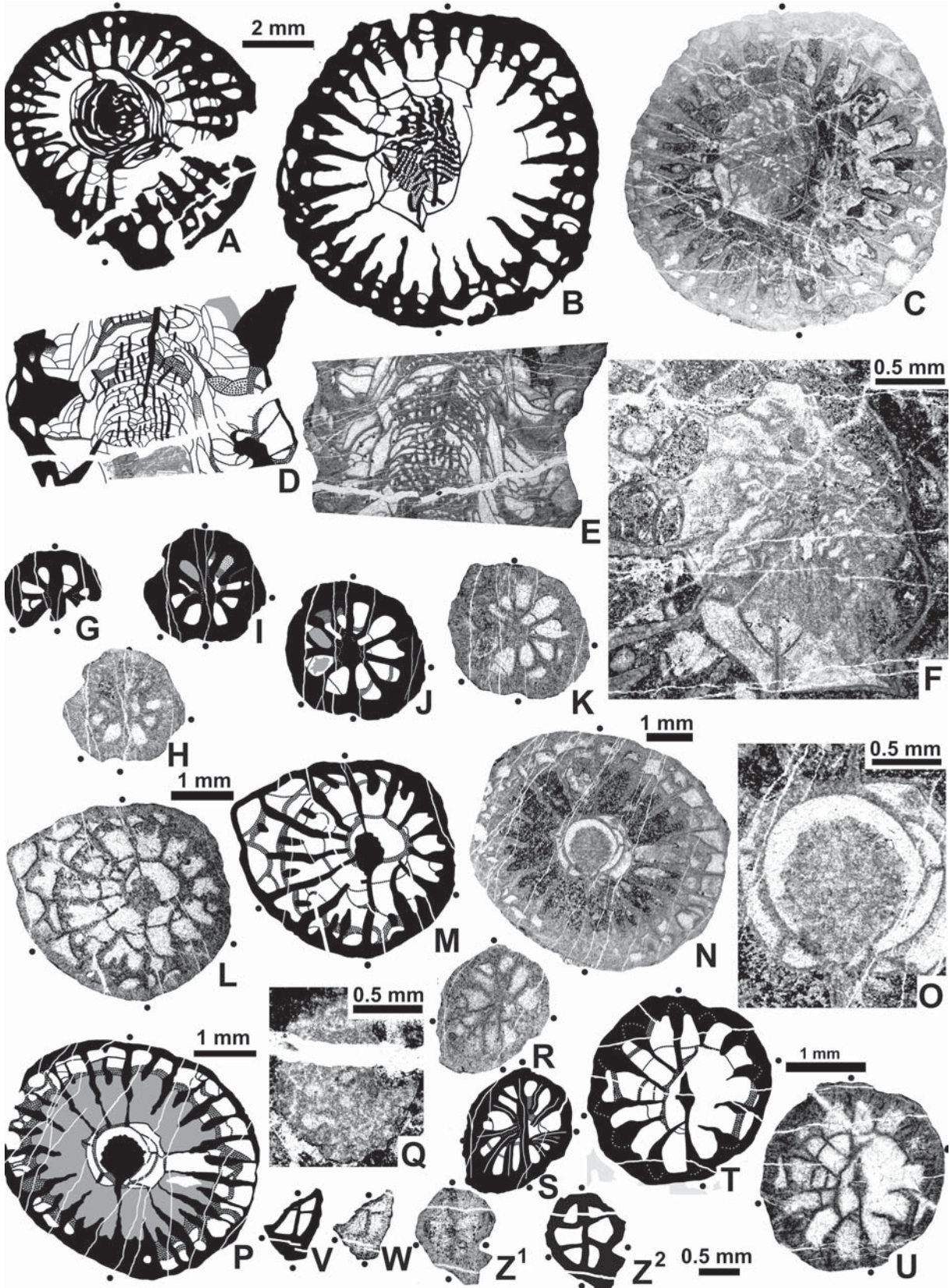
lamellae and surrounded by many sections of axial tabellae, densely packed and thick. Longitudinal section of holotype (Text-fig. 10D, E) spans distance between transverse sections illustrated in Text-fig. 10A and 10B. Axial structure occupies almost 1/2 corallite diameter and consists of densely packed axial tabellae arranged in hemispherical pattern with peripheral tabellae or their peripheral parts almost vertical. Some axial tabellae rest upon underlying ones to imitate columnotheca; other axial tabellae anastomose with peripheral tabellae arranged in accordance to their position in biform tabularium. Most peripheral tabellae short. Septal lamellae in axial structure numerous, differentiated in length and thickness. One long septal lamella, obliquely arranged, may correspond to median lamella.

Early ontogeny investigated in three specimens. Two of them developed to growth stage advanced enough to be included in *D. composita* sp. nov. as paratypes (Text-fig.10G–U). One specimen (Text-fig. 10V–Z) preserved in brephic growth stage only. Its dominating axial protoseptum and one pair of metasepta, perhaps counter-lateral, occur in the earliest growth stage observed, 0.9×0.5 mm in size. Second pair of metasepta, perhaps alar septa, inserted at 1.2×0.9 mm corallite size, within 1 mm of its growth. That specimen disappeared from record within approximately 1 mm thick section of rock cut for the next thin section.

In two more complete specimens, arrangement of major septa rotiphylloid (Text-fig. 10G–K and R, S). In course of neanic growth of more complete corallite (n:d values 9:1.5 mm and 11:1.7 mm) middle part of axial septum thickens distinctly (Text fig. 10G–K). In comparable growth stage of less complete specimen (n:d value 12:1.6×1.2 mm), middle part of axial septum not thickened (Text-fig. 10R, S). In late neanic growth stage of the latter specimen, with n:d value 14:2.0 mm, middle part of axial septum only slightly thickened, major septa amplexoid, strongly thickened near corallite wall and differentiated in length according to their location beneath or just above surfaces of tabulae (Text-fig. 10T, U). Crests of minor septa and first dissepiments appear at that growth stage. Specimen in question terminated its existence

approximately 2 mm above, remaining in late neanic growth stage with n:d value 14:2.5 mm.

Most of the growth stage described above from corallite UAM-Tc.Don.1/332 is missing from the more complete corallite UAM-Tc.Don.1/331 as result of slightly oblique cutting and grinding. However, right side of its thin section (Text-fig. 10L, M) with n:d value 14:4.0×3.4 mm shows late neanic morphology, closely resembling that found in paratype UAM-Tc.Don.1/332, while central and left parts of that thin section illustrate the earliest mature growth stage. Most major septa in that part of corallite continuous, one interrupted by lonsdaleoid dissepiment. Major septa terminate at section of tabula close to thick, complex pseudocolumella. Cardinal septum thick, prolonged into median lamella of pseudocolumella. Counter septum reaches pseudocolumella with its thin inner part. Minor septa well developed, thick, some interrupted by lonsdaleoid dissepiments. In more advanced early mature growth stage of this corallite, with n:d value 16:5×6 mm, cut mostly above calice floor (Text-fig. 10N–P), major septa remain long, some reach sections of axial tabellae surrounding compact axial structure. Septal lamellae in that structure strongly thickened, wavy and irregularly arranged with gaps between them barely distinguishable, imitating arrangement in compact pseudocolumella (Text-fig. 10O). Cardinal septum reaches axial structure. Minor septa enter calice for approximately 0.2–0.4 mm. Dissepimentarium in one or two rows of rectangular, interseptal dissepiments. Lonsdaleoid dissepiments absent. In transverse section made approximately 1.5 mm higher, i.e., through middle part of calice with n:d value 16:8.5×7.0 mm, axial structure continues to occur (Text-fig. 10Q). Inner morphology of that structure looser here than deeper in calice. Gaps between irregular septal lamellae more easily distinguishable, but further details destroyed by wide calcitic vein.

REMARKS: *Dirimia composita* sp. nov. is poorly represented in the collection. However, the morphology of the corallites studied distinctly differs from almost all remaining specimens of the collection, with the exception of *Dirimia* sp. 2 described

← Text-fig. 10. *Dirimia composita* sp. nov. Transverse thin sections except when stated otherwise. A-F – UAM-Tc.Don.1/330. Holotype. A – early mature growth stage, B, C – mature growth stage, D, E – longitudinal section, F – axial structure (enlarged from C) (A, B, D – computer drawings on peel images). G-Q – UAM-Tc.Don.1/331. Paratype. G-K – neanic growth stage, L, M – late neanic/early mature growth stage, N, P – early mature growth stage, O, Q – compact axial structure (O enlarged from N). R-U – UAM-Tc.Don.1/332. Paratype. R, S – neanic growth stage, T, U – late neanic growth stage. V-Z² – UAM-Tc.Don.1/333. ?Paratype. V, W – brephic growth stage, Z¹, Z² – early neanic growth stage. (All computer drawings conducted on corresponding thin section images). For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between A and B corresponds to A-E. Scale bar between Z² and U corresponds to G-K, R, S, and V-Z². Remaining images marked separately

separately below. Also, specimens with a comparable morphology are unknown to us from the literature. Difference in the morphology of the axial structure between the holotype and the most completely preserved paratype may eventually appear adequate for a distinction of those two at species level. However, the similarity in the other characters of those specimens, the probably early mature growth stage represented by the paratype, and the poverty of the collection made their location in one species more rational.

OCCURRENCE: As for the holotype.

Dirimia extrema sp. nov.
(Text-fig. 11)

2017b. ?*Spirophyllum* sp. 2; Fedorowski, p. 467, text-fig. 7.

HOLOTYPE: Specimen TSNUK 3P267/F-05.

TYPE LOCALITY: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village, Ukraine.

TYPE STRATUM: Limestone F_1. Blahodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. extremus* – extreme, ultimate, after the morphology in the longitudinal section showing extreme differences from typical members of the Kumpanophyllidae.

DIAGNOSIS: A species of *Dirimia* gen. nov. with n:d value 28:10 mm (holotype) and 25:9 mm to 26:11 mm (paratypes); major septa closely approach, some reach median lamella in strong, dense axial structure; protosepta almost permanently united with median lamella; minor septa restricted to dissepimentarium; columnotheca absent.

MATERIAL: Holotype TSNUK 3P267/F-05, four paratypes UAM-Tc.Don.1/334–337 and two specimens identified previously as ?*Spirophyllum* sp. 2 in Fedorowski (2017b, p. 467), i.e., UAM-Tc.Don.1/169 and UAM-Tc.Don.1/239. All specimens incomplete, lacking brephic and neanic growth stages, and calices. Skeletons of all specimens recrystallised. Nineteen thin sections and 21 peels available for study.

DESCRIPTION: Early growth stages preserved only in specimens identified earlier as ?*Spirophyllum* sp. 2 (Fedorowski 2017b, text-fig. 7A, B, G, H). Traces of zaphrentoid arrangement of major septa in neanic growth stage, established in that paper, remain recognisable in late neanic/early mature growth stage of one paratype with n:d value 24:6.5 mm described here (Text-fig. 11I). Youngest major septa in particular quadrants underdeveloped. Inner margins of these septa connected to lateral surfaces of precedent major septa, indicate alar pseudofossulae and shallow cardinal fossula present up to this growth stage. Arrangement of major septa bilateral with axial septum as axis of symmetry; most major septa either meeting thickened middle part of that septum or closely approaching it and forming axial structure (Text-fig. 11I, J). Counter-lateral septa shorter than those of pairs inserted later. Minor septa barely recognisable as short septal crests. Dissepimentarium incomplete.

Arrangement and nature of major septa in mature growth stage of individual specimens differ somewhat. Major septa radially arranged in holotype (Text-fig. 11A–C), in paratypes tend towards bilateral symmetry with amplexoid character very weak or absent (Text-fig. 11G, N; Fedorowski 2017b, text-fig. 7C–E). They either meet median lamella directly (Text-fig. 11M, N; Fedorowski 2017b, text-fig. 7C–E) or closely approach their thickened lamellae where later separated (Text-fig. 11G, H). All major septa in all specimens wedge-shaped in tabularia, thickest at the tabularium/dissepimentarium border, distinctly thin towards corallite axis, but only slightly thinning in dissepimentarium. Cardinal septum almost directly and permanently united with median lamella; breaks in that continuity short-lasting (e.g., Text-fig. 11B), if present. Connection of counter septum with median lamella less accentuated, but almost permanent as well. Axial structure in transverse section clearly distinguishable, but not recognisable in longitudinal section (Text-fig. 11D). Pseudocolumella probably complex – i.e., incorporating median lamella and septal lamellae (Text-fig. 11F; Fedorowski 2017b, text-fig. 7J). However, diagenetic alterations prevent firm recognition of mutual relationships between listed skeletal elements. Minor septa mostly as septal crests, rarely extending more than half width of dissepimentarium, and absent from some septal loculi. In longitudinal section tabulae incomplete (Text-fig. 8D). Peripheral tabellae mostly short, either anastomosing with middle tabellae or flat and almost horizontal. Inner tabellae either complete,
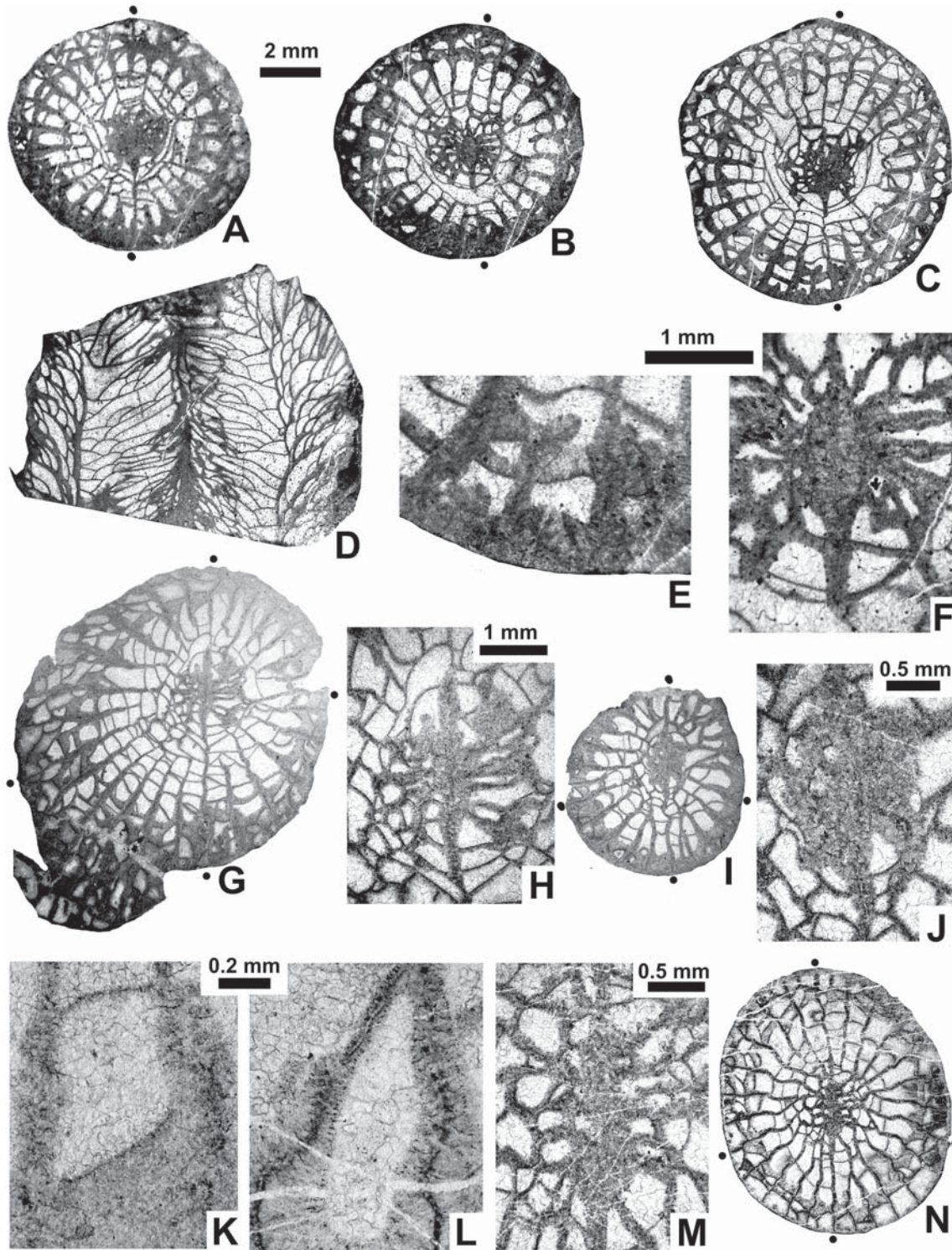
Text-fig. 11. *Dirimia extrema* sp. nov. Transverse thin sections except when stated otherwise. A-F – TSNUK 3P267/F-05. Holotype. A-C – successive sections of mature growth stage, D – longitudinal thin section, E – major septum last inserted in left cardinal quadrant and crests of minor septa (enlarged from C), F – axial structure (enlarged from B). G-K – UAM-Tc.Don.1/336. Paratype. G – mature growth stage, I – early mature growth stage, H, J – axial structure (enlarged from G and I respectively), K – microstructure of septa damaged by recrystallisation. L-N – UAM-Tc. Don.1/337. Paratype. L – microstructure of septa; bunches of crystalline fibrils left by recrystallisation of fine trabeculae, M – axial structure, N – early mature growth stage. For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bars between two images correspond to both. Scale bar between A and B corresponds to remaining images except for those marked separately

meet sections of median lamella directly, or 1–3 tabellae occur between peripheral tabellae and median lamella. Innermost margins of tabulae elevated more steeply towards median lamella than their middle sections irrespective of composition. Some sclerenchymal deposits attached to tabulae and probably derived from septal lamellae make innermost part of tabularium dense, but axial structure in form of axial column and portions of columnotheca absent. Dissepimentarium 1/4–1/3 corallite radius wide. In transverse section dissepiments mostly herringbone, some regular. Lonsdaleoid dissepiments absent. In longitudinal section dissepiments differentiated in size, mostly small, bulbous, sloping down at approximately 45º, inner row vertical and slightly thickened. Microstructure of septa either altered so as to make any recognition impossible, or bunches of crystalline fibrils remain in some septa and suggest occurrence of fine trabeculae (Text-fig. 11K, L respectively).

REMARKS: The morphology of *D. extrema* sp. nov., especially its longitudinal section, resembles some taxa of the Subfamily Dibunophyllinae Wang, 1950 (Family Aulophyllidae Dybowski, 1873), and the mature growth stage of *Dibunophylloides* Fomichev, 1953 in particular. Moreover, the stratigraphic range of the latter genus includes Limestone F_1 (Fedorowski 2017b, text-fig. 27). The previous family identification of ?*Zakovia* sp. and ?*Spirophyllum* sp. 2 (Fedorowski 2017b, pp. 461 and 467) illustrates both that similarity and the dangers of attempting taxonomic identification on the basis of limited, low quality material, particularly without access to suitable, better represented, and more fully studied taxa as points of comparison. The lack of columnotheca rudiments in the longitudinal section of *D. extrema* sp. nov. weakens the taxonomic assessment proposed herein. However, the step by step reduction of the columnotheca in *Dirimia* gen. nov., as demonstrated in *D. multiplexa* sp. nov., *D. composita* sp. nov. and *D. similis* sp. nov., and a morphology in transverse section that is strikingly similar to *D. multiplexa* sp. nov. and *D. similis* sp. nov. is a strong argument in favour of this assessment. While some doubts remain, in our view the characters listed above are sufficient to include *D. extrema* sp. nov. in *Dirimia* gen. nov. and to distinguish it from the remaining species of that genus.

OCCURRENCE: Paratypes as for the holotype. ?*Spirophyllum* sp. 2, Kalmius River Area, Solona River bank, Novotroitske Village. Remaining data as for the holotype.

Dirimia nana sp. nov.
(Text-fig. 12)

HOLOTYPE: Specimen UAM-Tc.Don.1/338.

TYPE LOCALITY: Solona River Area. Novotroitske Village, Limestone F_1, Ukraine.

TYPE STRATUM: Blagodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancellocera* ammonite Biozone, *Pseudostaffella praegorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

ETYMOLOGY: *Lat. nanus* – dwarf, after very small size of mature corallites.

DIAGNOSIS: A species of *Dirimia* gen. nov. with n:d values 14:3.0 mm (holotype) and 15:4.0 mm, 16:3.0 mm (paratypes); major septa 2/3–3/4 corallite radius; axial septum long lasting in corallite growth; minor septa mostly as short crests, absent from some septal loculi; axial structure weak, only median lamella in some specimens; dissepimentarium incomplete, only one row where present; lonsdaleoid dissepiments common; columnotheca absent or in short fragments; tabulae complete, hemispherical where axial structure absent.

MATERIAL: Holotype UAM-Tc.Don.1/338 and four paratypes UAM-Tc.Don.1/339–342. All specimens incomplete. Holotype preserved in neanic and mature growth stage, but its advanced mature growth stage broken in half and calice not preserved. Two paratypes (UAM-Tc.Don.1/339, 340) preserved in neanic and mature growth stage. Two other paratypes (UAM-Tc.Don.1/341, 342) preserved only in mature growth stage. Fragment of only one specimen long enough for longitudinal sectioning. Morphology of longitudinally broken part of holotype supplements data achieved from that longitudinal section. Nine thin sections and ten peels available for study.

DESCRIPTION OF HOLOTYPE: Corallite cone-shaped in early growth stage, with strong talon developed during late neanic/early mature growth stage (Text-fig. 12A). Distinctly curved above talon with further growth of similar size, if growth bands not considered. Growth striae and growth bands distinct, but septal furrows lacking. In neanic growth stage, with n:d value 7:0.9 mm and 10:1.7×1.1 mm (Text-fig. 12C, D), major septa arranged in manner typical
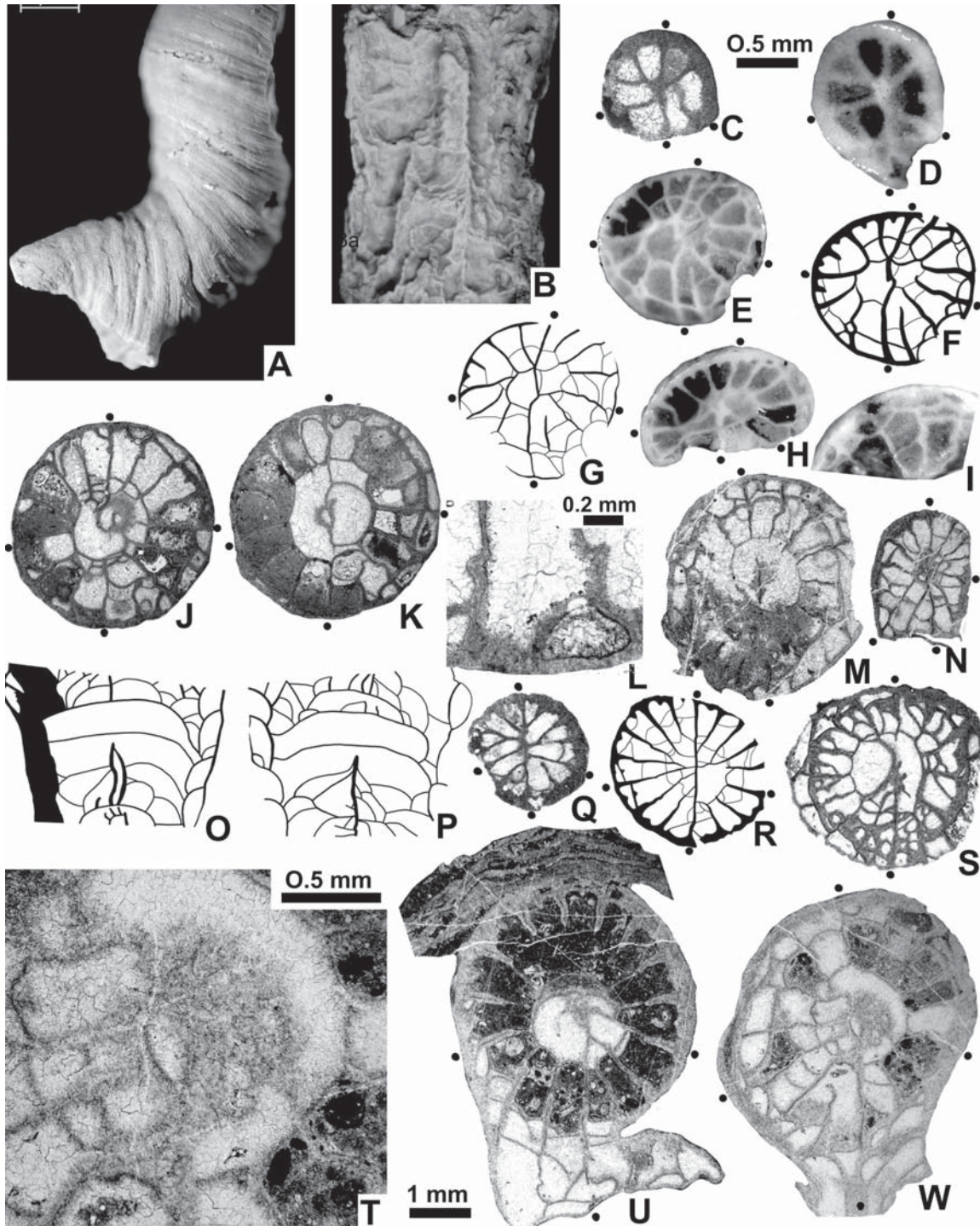
Text-fig. 12. *Dirimia nana* sp. nov. Transverse thin sections except when stated otherwise. A-I – UAM-Tc.Don.1/338. Holotype. A – side view of corallite, B – mature part of corallite broken longitudinally and slightly weathered; continuous axial septum and positions of some tabulae, C, D – neanic growth stage, E-G – early mature growth stage, H – mature growth stage immediately below broken part, I – mature growth stage, uppermost part of corallite (D, E, H, I – polished surfaces, F, G – computer drawings on images). J-L – UAM-Tc.Don.1/341. Paratype. J, K – mature growth stage, L – deformation in growth of major septa. M, N – UAM-Tc.Don.1/340. Paratype. M – mature growth stage, N – late neanic growth stage. O-S – UAM-Tc.Don.1/339. Paratype. O, P – longitudinal sections, Q – neanic growth stage, R – Late neanic/early mature growth stage, S – mature growth stage (O, P, R – computer drawings on peel images). T-W – UAM-Tc.Don.1/342. Paratype. T – axial structure (enlarged from W), U, W – mature growth stage. For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bar between two images corresponds to both. Scale bar between T and U corresponds to remaining images except for those marked separately

for most Rugosa with axial septum as corallite axis. Symmetry failed due to curvature of axial septum. In early mature growth stage, with n:d value 14:3.0 mm, major septa amplexoid, continuous, slightly differentiated in length, do not meet axial septum when sectioned beneath tabula (Text-fig. 12E–G), but some may meet it above tabula (Text-fig. 12H). Axial septum remains curved and almost equally thin all along. Minor septa in early maturity incomplete, form septal crests when present in some septal loculi. In slightly more advanced growth stage (Text-fig. 12H), minor septa present in all septal loculi in fragment of corallite preserved. At least one crosses dissepimentarium. Dissepiments interseptal, regular. Lonsdaleoid dissepiments breaking major septa, present in ontogenetically most advanced fragment of corallite preserved (Text-fig. 12I) Minor septa absent from that part of corallite. Advanced mature growth stage of holotype broken longitudinally along 6.4 mm corallite growth (Text-fig. 12B). Corallite diameter widens for only 0.3 mm during that distance of growth. Axial septum continuous. One row of dissepiments recognised at corallite periphery. Weathered tabulae incomplete, elevated towards axial septum at various angles, some almost horizontal. Most best preserved tabulae extend to dissepimentarium, but tabellae of some incomplete tabulae may rest on underlying ones. The question of whether they form portions of columnotheca remains open.

INTRASPECIFIC VARIABILITY: Paratype UAM-Tc.Don.1/341 (Text-fig. 12J–L), preserved only in mature growth stage, resembles holotype closer than remaining paratypes with a solitary median lamella, underdeveloped minor septa, and incomplete dissepimentarium. It differs in a more amplexoid character of major septa and separation of median lamella from protosepta. Strong curvature of several of its major septa (Text-fig. 12L) suggests initial stage of rejuvenation. Early growth stage of two paratypes more advanced in ontogeny than that investigated in holotype. Their n:d values 13:3.0×2.4 mm (Text-fig. 12N), 12:2.0 mm, and 16:3.0 mm (Text-fig. 12Q, R). Arrangement of major septa in first paratype rotiphylloid, but with median lamella already thickened. Arrangement of major septa in second paratype clearly bilateral, with axial septum thin, straight, continuous up to appearance of first dissepiments. N:d values of mature growth stage of all paratypes similar to one another (15:3.5 mm, 16:3.5 mm, 15:4.0 mm; in the last instance elongation resulting from attachment not considered). Morphology of axial structure in mature growth stage of three para-

types (Text-fig. 12M, S, U, W) more complex than in holotype and paratype described above. Median lamella in those paratypes thickened and united directly with cardinal septum. 2–3 short septal lamellae join median lamella to form simple axial structure. Septal lamellae scattered in one section of paratype UAM-Tc.Don.1/342 (Text-fig. 12T) resemble some sections of *D. similis* sp. nov. Minor septa in two paratypes (Text-fig. 12M, S) differentiated in length: rare few atrophied completely, some divided by lonsdaleoid dissepiments with peripheral segments short or reduced and inner segments penetrating tabularium, and some continuous, either penetrating tabularium or restricted to dissepimentarium. In one paratype (Text-fig. 12U, W), minor septa either in form of crests or reduced from some septal loculi. Dissepimentarium in all specimens incomplete, ranging from almost absent in two paratypes (Text-fig. 12J, K, U), to almost complete, with lonsdaleoid dissepiments well developed in two others (Text-fig. 12M, S). Morphology of longitudinally sectioned corallite, approximately 0.7 mm apart (Text-fig. 12O, P), documents disconnection of axial structure. Tabulae in disconnected part complete, hemispherical. One of them rests on underlying tabula on right side of corallite. In part of this corallite with axial septum or axial structure present, tabulae incomplete, bulbous, elevated towards axial septum; some axial tabellae may rest on underlying tabellae to form fragments of columnotheca (Text-fig. 12P, upper). Dissepiments in a single vertical row.

REMARKS: A large degree of intraspecific variability, demonstrated particularly in the morphology and complexity of the axial structure, forms a sequence starting from the simplest forms present in the holotype and paratype UAM-Tc.Don.1/341, and ending with the most complex developed in paratype UAM-Tc.Don1/342. Two specimens with an axial structure complexity intermediate between the extremes mentioned allow for a temporary assignment of all of them to the same species. However, the number of specimens available for this study is too restricted to establish trends and ultimately group the specimens into subsets (potentially subspecies or species).

Some differences in the length, number, and shape of the minor septa established in particular corallites, and the clearly bilateral symmetry of major septa in the early growth stage of the specimen UAM-Tc.Don.1/339, are worthy of attention as potential signals of an artificial grouping of the specimens discussed. However, the morphology

of almost of the all characters changing in various configurations speaks in favour of a large intraspecific variability, rather than a need of subdivision into separate species. The large variability of the axial structure in *D. nana* sp. nov. resembles that described by Webb (1984) and Webb and Sutherland (1993) in *Lophophyllidium imoense*. In both species, which are quite taxonomically distant, the reason for such a multidirectional variability of one character and a rather low variability of the remaining skeletal characters remains unknown.

The tiny diameters and small number of septa in *D. nana* sp. nov. distinguish it from all species of *Dirimia* gen. nov. described so far, except for *Dirimia* sp. 1, from which it differs mainly in the morphology exposed in the longitudinal section, the scattered septal lamellae in the axial structure, the mostly continuous minor septa developed in full number, and the complete row of regular dissepiments.

OCCURRENCE: Holotype see above. Paratypes Luhansk Region, Left bank of the Luhanchyk River. Quarry near Volnukhyne Village. Remaining data as for the holotype.

Dirimia sp. 1
(Text-fig. 13)

MATERIAL: Single, almost complete specimen UAM-Tc.Don.1/343. Macromorphology well preserved. Microstructure of septa diagenetically altered. Five transverse thin sections, one longitudinal thin section, and six peels available for study.

DESCRIPTION: In early growth stage corallite curved in cardinal/counter septa plan with cardinal septum located on convex corallite side. Only growth lines preserved on corallite surface. Its diameter fluctuated during mature growth (Text-fig. 13I, upper). In brephic and neanic growth stages, with n:d values 6:0.8×0.6 mm, 10:1.5×1.3 mm, and 11:1.8×1.5 mm (Text-fig. 13A–D), axial septum permanent, with the alar and counter-lateral major septa attached to it in a way classic for the Rugosa. Development and length of further metasepta irregular. Their thickness slightly reduced. In late neanic/earliest mature growth stage, with n:d value 11:2.2×1.8 mm (Text-fig. 13E), three major septa disconnected from axial septum, terminated on sections of tabulae, with first dissepiments appearing in some septal loculi. Minor septa not recognised. In mature growth stage, observed only on polished surface (Text-fig. 13F) with n:d value 16:4.5×4.0 mm, axial septum con-

tinues to occur, with its middle part slightly thickened. Most major septa terminated on section of tabula surrounding corallite axial area, suggesting occurrence of columnotheca in that growth stage. Presence of septal lamellae uncertain. Minor septa penetrate tabularium. Complete ring of regular interseptal dissepiments. Thin section with n:d value 16:5.0×4.8 mm, made approximately 1 mm above aforementioned one, exposes lowermost part of calice except for axial structure elevated above calice floor (Text-fig. 13G). Major septa remain long and continuous. Cardinal septum meets median lamella while counter septum and some major septa terminate on section of elevated axial tabula. Cardinal fossula absent. Minor septa penetrate calice; three of them interrupted by flat lonsdaleoid dissepiments. Remaining dissepiments interseptal, regular, form single ring. Axial structure narrow, irregular, composed of three or four short, thin, irregular septal lamellae. It disappears approximately 1.2 mm higher (Text-fig. 13H). Morphology of peripheral part of calice as described above.

Three subsequent images of corallite fragment located between Text-fig. 13E and 13F (Text-fig. 13J–L) illustrate corallite morphology from periphery of tabularium to corallite axis. In late neanic/early mature growth stage dissepiments absent from fragment sectioned. Peripheral tabularium much wider than in more advanced corallite growth, but consists of straight or slightly convex tabellae arranged in accordance to their positions in biform tabularium. Some of them approach sections of median lamella, some others attach to axial tabellae that form irregular fragments of columnotheca. Some axial tabellae in mature part of longitudinal section almost hemispherical, some others less convex, either resting on underlying axial tabellae or anastomose with peripheral tabellae. Sections of bodies septal in microstructure reduced in number from periphery toward axis. Thus, major septa rather than septal lamellae sectioned. Restricted number of latter confirmed by transverse section described above.

REMARKS: The specimen described resembles, in n:d value, the smallest corallites assigned to *D. similis* sp. nov.; its axial structure with scattered septal lamellae also bears some similarity to that species. However, the axial structure in the specimen discussed is much simpler, its dissepimentarium is more regular, and its morphology in the longitudinal section differs not only from *D. similis* sp. nov., but also from all other species described in this paper. Despite the completeness of the specimen discussed and our
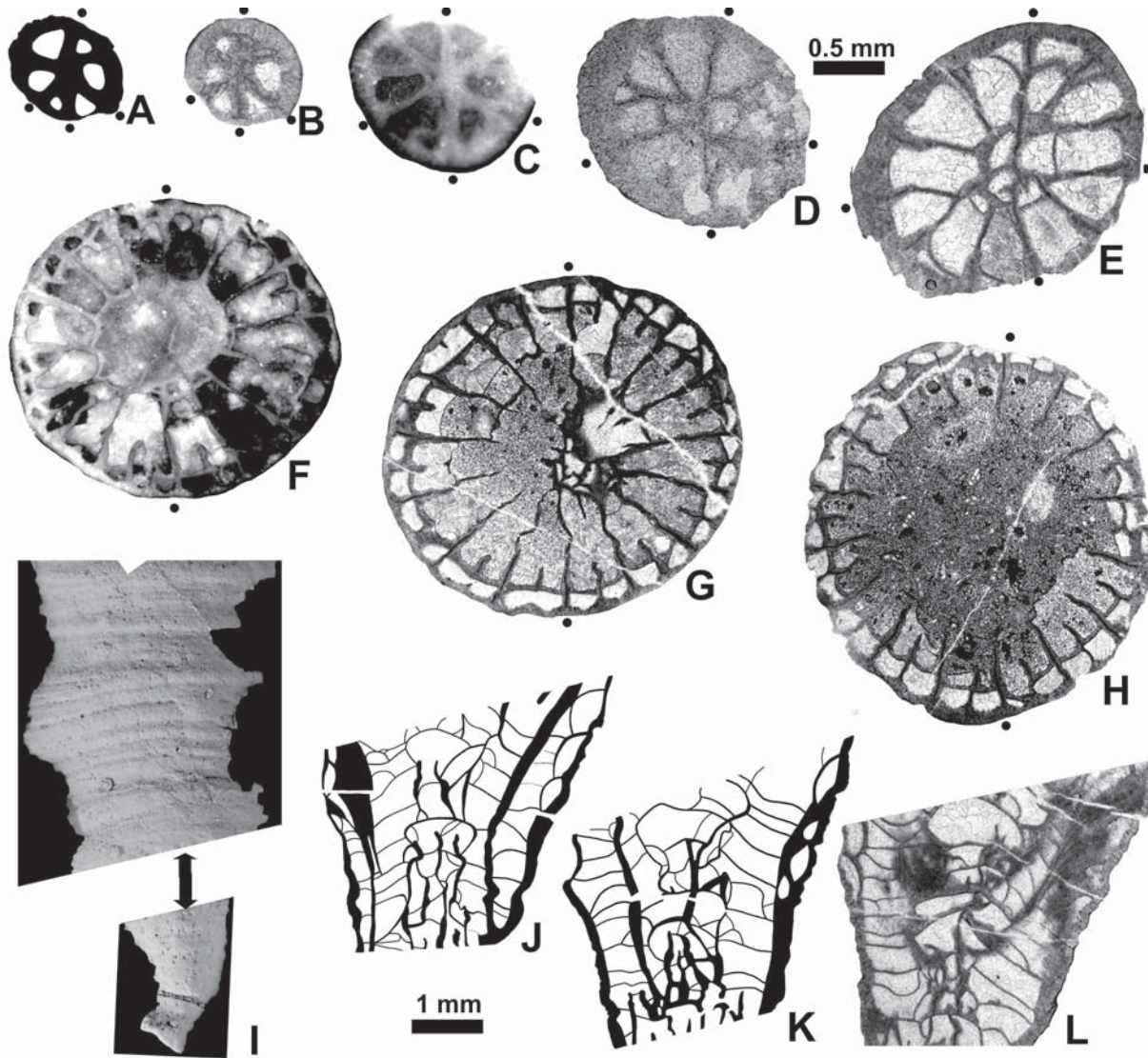
Text-fig. 13. *Dirimia* sp. 1. UAM-Tc.Don.1/343. Transverse thin sections except when stated otherwise. A, B – early neanic growth stage, C, D – neanic growth stage, E – late neanic/early mature growth stage, F – mature growth stage (polished surface), G – mature growth stage, lowermost part of calice, H – middle part of calice, I – side view (gap corresponds to D, E), J-L – longitudinal sections from periphery of tabularium (J) to axis (L) (J, K – computer drawings on peel images). For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bar between D and E corresponds to A-E. Scale bar beneath J corresponds to remaining images

detailed investigation on it, we have decided to postpone the introduction of a formal species name until a richer collection is studied.

OCCURRENCE: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village. Limestone F_1. Blagodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella praegorskyi– Staffelleformes staffelleformis* foraminiferal Biozone,

Idiognathodus sinuosus conodont Biozone. Upper middle Bashkirian.

Dirimia sp. 2
(Text-fig. 14)

MATERIAL: One corallite, UAM-Tc.Don.1/344, preserved in 3.5 mm long mature growth stage. Four transverse thin sections prepared from entire fragment. Part of tabularium and inner fragments of ma-
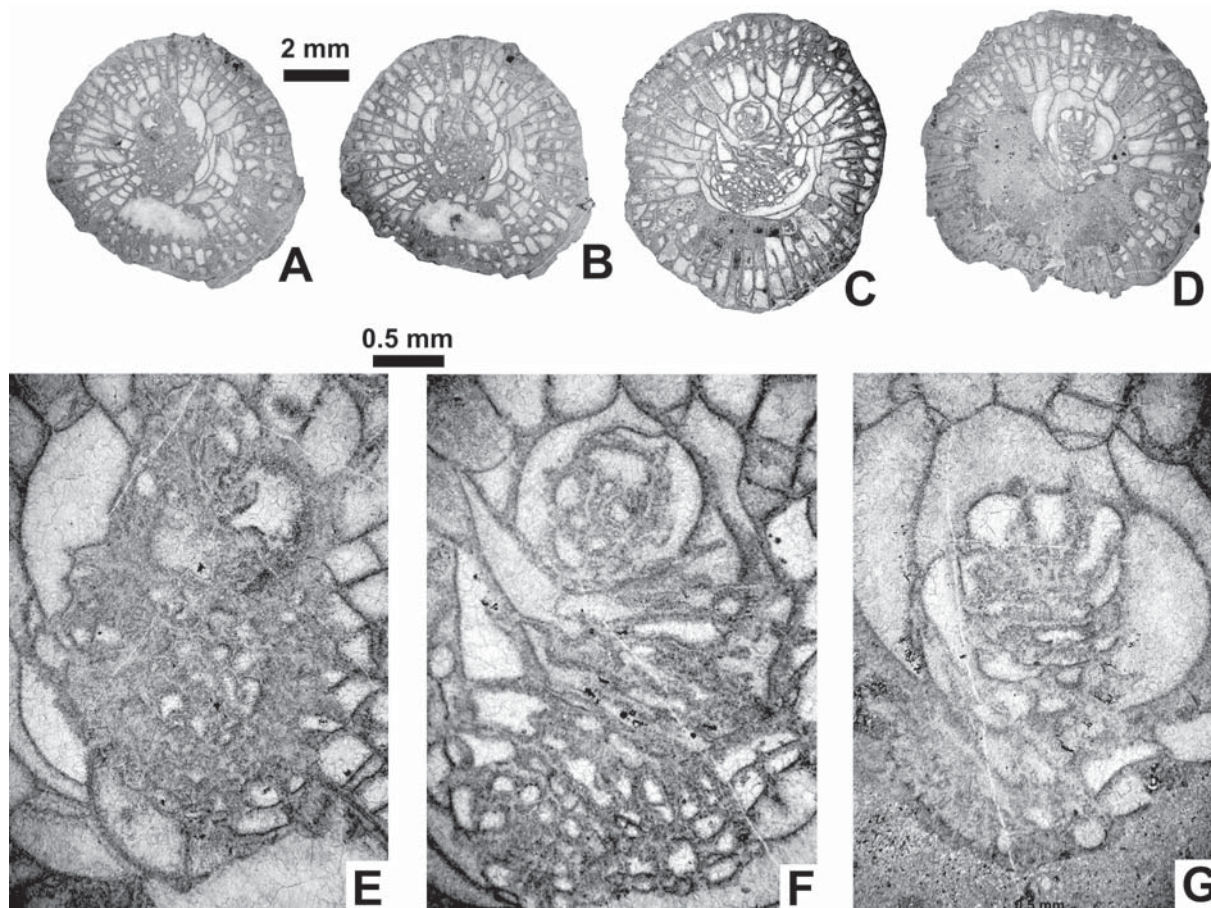
Text-fig. 14. *Dirimia* sp. 2. UAM-Tc.Don.1/344. A–D – successive transverse thin sections, mature growth stage, E-G – axial structure (enlarged from A, C, D respectively). For stratigraphic positions see text. Scale bar between A and B corresponds to A-D. Scale bar between E and F corresponds to E-G

jor septa damaged. Damage increases from A to D in Text-fig. 14.

DESCRIPTION: Corallite diameter increases slightly (n:d value 29:7.5 mm to 29:9.2 mm). Major septa thin, continuous, amplexoid as demonstrated by change in their length in successive transverse thin sections (Text-fig. 14A–D). Shortest sections of major septa reduced to 1/2 corallite diameter. Protosepta equal to remaining major septa in length and thickness. Cardinal fossula absent. Minor septa thin, continuous, approximately 1/4–1/3 corallite radius long, penetrate tabularium deeply. Axial structure (Text-fig. 14E–G) complex, varied in content and width. Median lamella unrecognisable or absent at growth stage studied. Septal lamellae numerous, differentiated in shape, length, and arrangement, united with their septa when latter elongated. Inner tabellae numerous; innermost small, peripheral large; some surround parts of axial structure when major septa shorten. Sections of tabulae more numerous in circumaxial part of corallite, whereas peripheral parts of tabularium bear very few sections. Arrangement described suggests elevation of tabulae towards axial structure and their more horizontal arrangement in middle part of tabularium. Sections of peripheral tabulae more numerous on one side of minor septa than on their opposite side, documenting biformity of tabularium. Dissepimentarium approximately 1/5 corallite radius wide with 4–6 rows of dissepiments differentiated in size and shape from comparatively large and regular to small, irregular, or oblique. Inner wall absent.

REMARKS: The axial structure of the corallite discussed closely resembles that of *D. composita* sp. nov., but its remaining characters differ to an extent

precluding the assignment of both taxa to a single species. That axial structure differs from axial structures in other species of *Dirimia* gen. nov. strongly enough to accept a separate species position of *Dirimia* sp. 2 and to make a detailed comparison unnecessary. However, a single fragmentary specimen cannot form a basis for a formally named species.

OCCURRENCE: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village. Limestone F_1. Blagodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella praegorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

Dirimia sp. 3
(Text-fig. 15)

MATERIAL: One corallite, UAM-Tc.Don.1/345, with neanic and mature growth stages preserved. One side of corallite corroded, but its opposite side preserved completely enough to expose details (Text-fig. 15E). Microstructure of septa destroyed by diagenesis. Three thin sections and four peels available for study.

DESCRIPTION: Shallow rejuvenations or sharp reductions in diameter repeated for several times during corallite growth available for study. Distances between reduced diameter and its extension differentiated. Corallite surface bears delicate growth striae arranged in bands and hardly recognisable septal furrows. In neanic growth stage with n:d value 12:2.5×1.9 mm (Text-fig. 15A), major septa arranged in manner typical for most Rugosa with axial septum as corallite axis. Peripheral parts of major septa and external wall thickened. Minor septa not traced. Dissepimentarium not yet developed. In early mature growth stage with n:d value 16:4.7×4.3 mm (Text-fig. 15B), major septa radially arranged, 1/3–1/2 corallite radius long, wedge-shaped in tabularium, thin in dissepimentarium. Protosepta united with slightly thickened median lamella to form axial septum. Minor septa penetrate tabularium with their thickened inner margins, thin in dissepimentarium. Axial structure narrow with 3–4 very short septal lamellae attached to median lamella each side. Single row of rectangular dissepiments, doubled in rare septal loculi. Morphology in fully mature growth stage, with n:d value 18:4.7 mm (Text-fig. 15C), similar in most details to that described above. More complex and
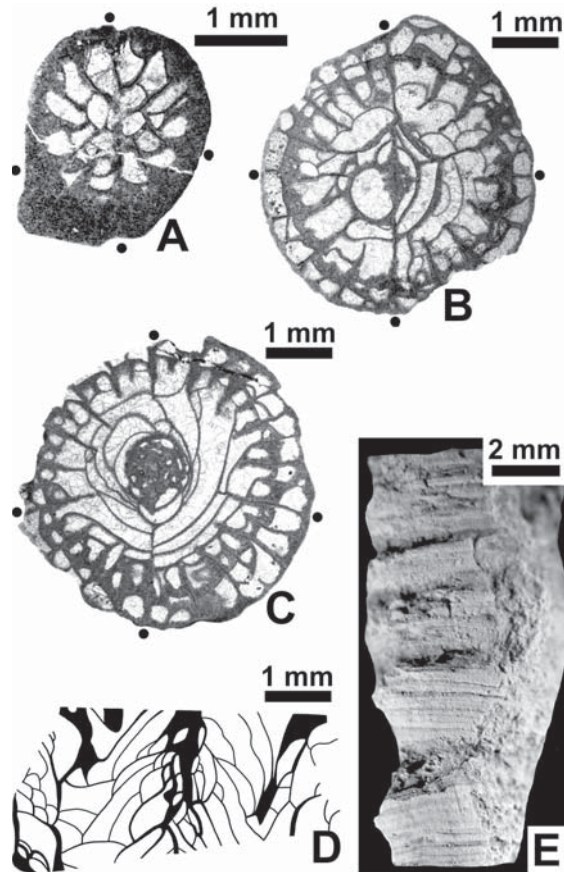
Text-fig. 15. *Dirimia* sp. 3. UAM-Tc.Don.1/345. A-C – transverse thin sections. A – neanic growth stage, B, C – early and late mature growth stage, D – longitudinal section (computer drawing on peel image), E – side view of corallite with four shallow rejuvenations. For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots

wider axial structure, free from protosepta, cardinal septum elongated, counter septum equal to adjacent major septa and dissepimentarium comprising more dissepiments in some septal loculi form main differences compared to the ontogenetically earlier growth stage. In longitudinal section (Text-fig. 15D), dissepiments strongly differentiated in size. Some small bubble-like, some others big, occupying entire dissepimentarium width. Tabularium biform. Tabulae incomplete. Their peripheral tabellae either down sloping or almost horizontal, depending on their positions (Text-fig. 15D, right and left respectively). Middle and inner tabellae convex, steeply elevated toward section of median lamella. Innermost tabellae very steep, most rest on underlying tabellae. Median lamella differentiated in thickness, accompanied by two or three sections of septal lamellae.

REMARKS: The specimen described resembles *D. similis* sp. nov. in most characters exposed by transverse section, except for the axial structure in the mature growth stage that remains compact in *Dirimia* sp. 3 with septal lamellae not scattered. However, the longitudinal section of the latter species resembles that of *D. extrema* sp. nov. in the absence of the columnotheca and in a tabulae consisting of a few convex tabellae, elevated steeply towards the median lamella. Strongly biform tabularium in *Dirimia* sp. 3, but weakly accentuated in *D. extrema* sp. nov., the axial structure in the latter species connected to several major septa but free in *Dirimia* sp. 3, and different n:d values are characters distinguishing the latter two species.

OCCURRENCE: Luhansk Region. Left bank of the Luhanchyk River. Quarry near Volnukhyne Village. Limestone F_1. Blagodatnian Regional Horizon (Yeadonian Substage), upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella praegorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

CONSIDERATIONS

The case of taxonomic assignment of morphologically variable taxa, such as *Dirimia* gen. nov. and those case studies selected below as examples, allows for the evaluation of different styles of taxonomy, specifically 'lumping' *vs.* 'splitting'. A discussion on this important topic is only started here in order to legitimise the content of this paper. Comprehensive considerations and discussions are postponed to the concluding paper of this series of papers dealing with all the Bashkirian rugose coral taxa from the Donets Basin known so far. Many taxa of both the dissepimented and non-dissepimented corals will make documentation more satisfactory than a discussion based on a single genus.

The introduction in this paper of six new species and three species left in open nomenclature could be evaluated as being overly split. Most specimens were derived from the same locality, and all from the same Limestone F_1. Also, some features of the two morphologically ultimate species point to two different families allowing us to contest the taxonomic value of those features. The taxonomic splitting introduced here is in sharp contrast to the approach of some other authors dealing with extremely variable taxa (Fedorowski 1978; Webb 1987; Oliver and Sorauf 2002). Fedorowski (1978) assigned to the same species some of the solitary, protocolonial, fasciculate colonial, and cerioid colonial specimens derived from one locality of the Bone Spring Formation in south-western Texas, USA. However, the inner morphology of those specimens, although variable, was similar to each other in particular variants irrespective of the growth form, and was thus described by Fedorowski (1978) as the unnamed *Heritschioides* sp. Fedorowski *et al.* (2007, p. 62) accepted that approach when questionably assigning those corals to their new genus *Sandolasma* as the new species ?*S. cooperi*. The simplified morphology of that species in comparison to the type species of *Sandolasma*, *S. elegans* Fedorowski, Bamber, and Stevens, 2007, not their variety of growth forms, was the reason for their doubts.

The approach by Webb (1987) to the corals he redescribed as *Caninostrotion variabilis* Easton, 1943 was even wider than the approach of Fedorowski (1978) to his specimens. He not only assigned to that species solitary specimens, incipient colonies, and colonial specimens, but also accepted an enormous variability in their morphology (Webb 1987, p. 479, figs 6.1–6.6, 7.1–7.7). The collection studied by Webb (1987, p. 483) consists of "hundreds of individual corals and colonies… from the Pitkin Formation localities (late Mississippian) in Independence County, Arkansas, to Cherokee County, Oklahoma". Thus, he dealt with a group of enormously variable specimens occurring in a comparatively large area. Webb (1987) illustrates many morphological variants documenting the author's conclusion. However, it would have been more convincing if transverse and longitudinal sections of entire colonies, derived from various areas instead of the selected corallites were illustrated. Documentation of variants within colonies on the top of the ontogeny of protocorallites and blastogeny of morphologically different mature daughter specimens would offer incontestable proof of the conspecific position of all specimens included by Webb (1987) in *C. variabilis*.

Oliver and Sorauf (2002) redefined the genus *Heliophyllum* Hall in Dana, 1846, which is common in the Givetian strata of the eastern United States. The approach of those authors is opposite to that of Webb (1987). According to their redefinition, the very variable type species of that genus, *H. halli* Milne Edwards and Haime, 1850, traditionally treated as combining both solitary and colonial species, should be subdivided into four subspecies with only the nominative subspecies having a solitary form; three new subspecies introduced by those authors are colonial. Their distinction is based on the type of colonies, differences in some morphological details, and their geographical and stratigraphic distribution. The approach

of Oliver and Sorauf (2002), i.e., the distinction of subspecies rather than species, may be contested since we lack the ability to check the level of that relationship on a genetic basis. However, a species-level relationship of those corals can easily be accepted.

The three examples discussed above are introduced in order to express possibilities and traps waiting for a scientist dealing with a group of corals that are similar in several aspects on the one hand, but differ considerably from each other on the other. Also, they illustrate three different situations: 1) A single bed hosting all variants of ?*S. cooperi* Fedorowski, Bamber and Stevens, 2007 was accumulated during a stabilised phase of rugose coral evolution (Cisuralian), whereas the palaeobiogeography of that time allowed widespread distribution of rugose corals as documented by seven species of *Sandolasma* (Fedorowski *et al.* 2007, p. 61). 2) *Heliophyllum* subspecies (?) or species, although geographically widespread, were most probably restricted in their occurrence to the endemic Appalachian Coral Province. Also, their stratigraphic positions, characterised as differentiated, were all included in one stage (Givetian), representing a stabilised phase in rugose coral evolution. 3) *Caninostrotion* Easton, 1943 is a genus moderately widespread within the large Western Interior Province of North America. All of the representatives studied were collected from approximately the same stratigraphic level (Webb 1987). However, the time of their occurrence corresponds to dramatic changes in rugose coral evolution.

The occurrence of *Dirimia* gen. nov. (upper middle Bashkirian) was slightly higher than that of the fauna described by Webb (1987) and Webb and Sutherland (1993), i.e., the upper Serpukhovian. However, the occurrence of both of those faunas aligns with a period of great rugose coral turnover. Both genera were short-lived, restricted to single basins, and consist of taxa with strongly variable morphology. Thus, they seem to be ideal for a discussion on the splitting *vs.* lumping approach to taxonomy.

Irrespective of the approach: lumping or splitting, three obvious facts must be taken in mind when any collection of fossils is studied: 1) Genetic barriers dividing particular species precede their easily recognisable morphological characters. This recognition is especially important for fossils for which all data are provided by purely mineralogical exoskeletons and extant representatives do not occur, as in the case of rugose corals. The hypothetical speed of speciation within such fossil taxa and the taxonomic value of their newly appearing characters are invariably subordinated to a personal approach of the scientist, since there is nothing else to compare to; i.e., deci-

sions are necessarily subjective, at least in part. A repetition of particular skeletal structures, common among organisms as primitive as corals, forms an additional factor necessary to apply in their taxonomy (e.g., Fedorowski 1984; Webb 1996). 2) Fossilised specimens preserved in rocks are dramatically restricted in number and variability in comparison to members of the living populations to which they belonged. 3) Even the largest collections of macrofossils are very restricted in comparison to the total number of fossils present in a given bed of rock. Combined, these well known facts mean that the fossil data available for a study will never be complete. That incompleteness can be interpreted in favour of the lumping approach by pointing to the possibility of the intermediate specimens remaining hidden in the rocks. However, the same argument speaks in favour of the splitting approach. To accept the intra-, but not the inter-specific position of those theoretical hidden intermediates is enough to allow the splitting approach. Moreover, the impossibility of confirming or negating the suspected relationships by analysing genetic content of analysed taxa and the delay in the appearance of morphological changes relative to genetic differentiation made a splitting approach more appropriate. This is especially true for taxa living in intervals of faunal turnover, which are always characterised by increased radiation.

The statement above does not imply a total negation of the lumping approach. It may be correct when many hundreds of specimens etched out, or by other methods removed, from a single and morphologically uniform bed are available for study, as was in the case in Fedorowski (1978). It is correct in the case of *Lophophyllidium imoense* investigated by Webb (1984) and Webb and Sutherland (1993) on the basis of a huge collection of specimens, of which only a single character, pseudocolumella, contained substantial variation. It may well be true for *Caninostrotion variabilis* if/when confirmed by additional studies. However, we do not consider that approach to be proper for the specimens identified here as members of *Dirimia* gen. nov. We in this paper, and the senior author in all his papers dealing with the Bashkirian rugose corals from the Donets Basin (Fedorowski 2009a, b, 2017a, b, 2019, in press), followed a splitting approach for the following reasons:

1) Not only one character, as in ?*Sandolasma cooperi* (Fedorowski 1978; Fedorowski *et al.* 2007) or *Lophophyllidium imoense* (Webb 1984; Webb and Sutherland 1993), but several characters of *Dirimia* gen. nov. underwent diversification in various combinations (Table 1). These include the columnotheca,

which varies from almost complete to non-existing; the axial structure, which varies from a single median lamella to a complex axial structure composed of several lamellae and axial tabellae; the axial structure, which can be either permanent or disappear in the mature stage; the dissepimentarium, which ranges from consisting of one incomplete row of interseptal dissepiments to being wide and composed of both interseptal and lonsdaleoid dissepiments; the biformity of tabularium, which ranges from hardly recognisable to well developed. The set of differences listed, which appear in various combinations constant within individual groups of specimens, cannot be purely somatic, and a supposition of their different genetic background must end with the conclusion of their taxonomical differentiation.

2) Two trends in skeletal characters are observed in *Dirimia* gen. nov.: specimens sharing some characters with *Kumpanophyllum* form its one extreme, whereas specimens repeating the characters of the Subfamily Dibunophyllinae form the opposite extreme. The first of these extremes suggests a close relationship to *Kumpanophyllum* and forms the reason for placing *Dirimia* gen. nov. in the Family Kumpanophyllidae. The second is interpreted here as homeomorphic, since there are no rigid data that allow a suggestion of a relationship between *Dirimia* gen. nov. and any genus of the Subfamily Dibunophyllinae.

The occurrence of most species of *Dirimia* gen. nov. within a single bed has already been identified as an argument for contesting the splitting approach to this group of fossils. However, the history of the accumulation of that coral-bearing bed was long lasting and variable (see Geological Setting). Additionally, there are species of that genus that occur outside of that fauna-rich bed. Both those facts allow for the consideration of faunal exchange within the Donets Basin. Thus, diversification at the species level may well occur both within that bed during its extended accumulation and outside of it. This, in turn, allows for the possibility that this bed hosts both autochthons and immigrants. We consider that possibility and the morphological variability pointed out above as adequate for establishing the taxonomical variability accepted here.

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