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Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 4. *Cordibia*, a new protocolonial genus

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ABSTRACT:

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Cordibia pumila gen. et sp. nov. (Aulophyllidae, Dibunophyllinae) from the Lower Bashkirian E_1 Limestone of the Donets Basin, Ukraine is described. The term "protocolony" is formally defined as a growth form intermediate between the solitary and colonial. Protocolonies consist of protocorallites and verticils of non-reproductive offsets [i.e., the lost structures]. The early ontogeny of a protocorallite is compared to the blastogeny in the same species in order to establish characters in common during both processes and to document the usefulness of blastogeny for phylogenetic reconstructions. The short duration and abundance of the occurrence (Limestones E_1^{up} acme, E_1^1) of that species also makes it a good marker for the lowest Feninian (= Krasnopolyanian) strata in the Donets Basin.

Key words: Rugosa (Anthozoa); *Cordibia*; Protocoloniality; Bashkirian; Donets Basin; Ukraine.

INTRODUCTION

The present paper belongs to a series of papers devoted to Early Bashkirian rugose corals from the Donets Basin, Ukraine, written by the senior author either alone or with co-authors. Thus, information concerning the history of the investigation and methods applied are to be found in the first paper of the series (Fedorowski 2009a) and are not repeated here. Text-figures 1–3, showing the location of the study area and particular sets of limestones, are repeated from that paper. The senior author wrote the systematic part of this paper, the nomenclatorial note, and the considerations. He also prepared the illustrations except for the photographs included in the Text-fig. 9, which were taken by the junior author. The junior author is responsible for descriptions of the geological setting, the map of the type locality (Text-fig. 4) and the stratigraphic column (Text-fig. 5A, B). Both authors are co-authors of the new genus and species introduced in this paper.

Rugose corals of protocolonial growth form are rare, but not unique. *Craterophyllum verticillatum* Barbour, 1911 was the first taxon of that kind introduced into the literature and can serve as an example. Also, rare genera comprising various growth forms (solitary, protocolonial and colonial) are known among the Rugosa (e.g. Fedorowski 1978; Oliver and Sorauf 2002). Those subjects are more thoroughly treated in the Considerations section.

Terminology applied in description of the blastogeny follows Fedorowski and Jull (1976, p. 39) and the papers mentioned by those authors. Symbols characterizing n:d value means: n – number of major septa, d – corallite diameter.

MATERIAL AND METHODS

The collection studied comprises 144 specimens, 37 thin sections and 98 peels. Unfortunately, the great majority of the specimens are flattened and all are incomplete. Forty-eight fragmented corallites are housed in the Institute of Geology, Adam Mickiewicz University in Poznań, Poland (Acronym UAM-Tc/Don.1). Some of those specimens were collected by Dr. N.P. Vassilyuk and offered to the senior author for this study. They are labelled: Berestovaya River (right bank) near Fenino Village, Limestone E_1. Some were collected by the senior author during his field study on the Carboniferous deposits of the Donets Basin, led by Dr. N.P. Vassilyuk. The latter specimens were derived from the same poorly exposed, natural outcrops of the lower Limestone E_1 group as the former. Of those specimens 22 produced the lost structures. Several specimens were given by the junior author to be included in the Poznań University collection. Calices are preserved in seven specimens out of 48 studied in Poland. Twenty-four thin sections and 45 peels were prepared from that part of the collection.

The majority of the specimens were collected by the junior author from mudsone and marly limestone underlying the E_1^{up} Limestone, and some from the E_1^1 group of Limestones exposed along the circumferential channel of the Berestovaya River (see Geological Setting chapter for details). That collection, now housed in the Geological Museum of Taras Shevchenko National University of Kyiv, Ukraine (Acronym TSNUK 3P267/E), consists of 96 incomplete corallites including the 22 which illustrate the lost structures, and eight which possess incomplete calices. Thirteen thin sections and 53 peels were made from corals from this part of the collection. All reasonably well preserved specimens were sectioned, peeled, polished, or thin sectioned. Drawings were made of several specimens using a computer method which allowed a very high enlargement of details. One complete series of peels and drawings taken from the offsetting corallite (Text-fig. 7), and one complete series of polished surfaces and photographs (Text-fig. 9), taken from the other offsetting corallite, were prepared in order to illustrate the process of the blastogeny. The process of the early ontogeny (Text-fig. 10) is investigated from the closely spaced thin sections prepared with help of a cutting machine with 0.05 mm thick wire.

NOMENCLATORIAL NOTE

The terms *protocolony*, *protocoloniality,* and *protocolonial growth form* in the sense used in the present paper are defined as follows:

Protocolony: an unit consisting of a protocorallite and the *lost structures* of Fedorowski (1978). This term corresponds in part to the *verticillate colony* of Hill, 1981 but is introduced as pointing unambiguously to the growth form intermediate between solitary and colonial, i.e., between the growth form characterized above and others consisting of a protopolyp (protocorallite) and a few generations of daughter clones (corallites) capable of reproducing sexually and asexually.

Protocoloniality: a genetically controlled ability of a protopolyp to produce offsets that cannot reproduce asexually (lost structures).

Protocolonial growth form: result of the protocoloniality.

GEOLOGICAL SETTING

The geography of the study area has undergone major changes between the time when early collections were made and the present. Formerly, the poorly exposed Lower Bashkirian (Voznesenskian and Feninian = Krasnopolyanian) deposits, known as the 'Chorna Skelya' section, were located near the former Fenino Village (Starobeshevo Village area, the Donetsk City region) at the right bank of the Starobeshevo Water

Text-fig. 1. General map of Ukraine showing the approximate position of the study area (After Fedorowski 2009a)
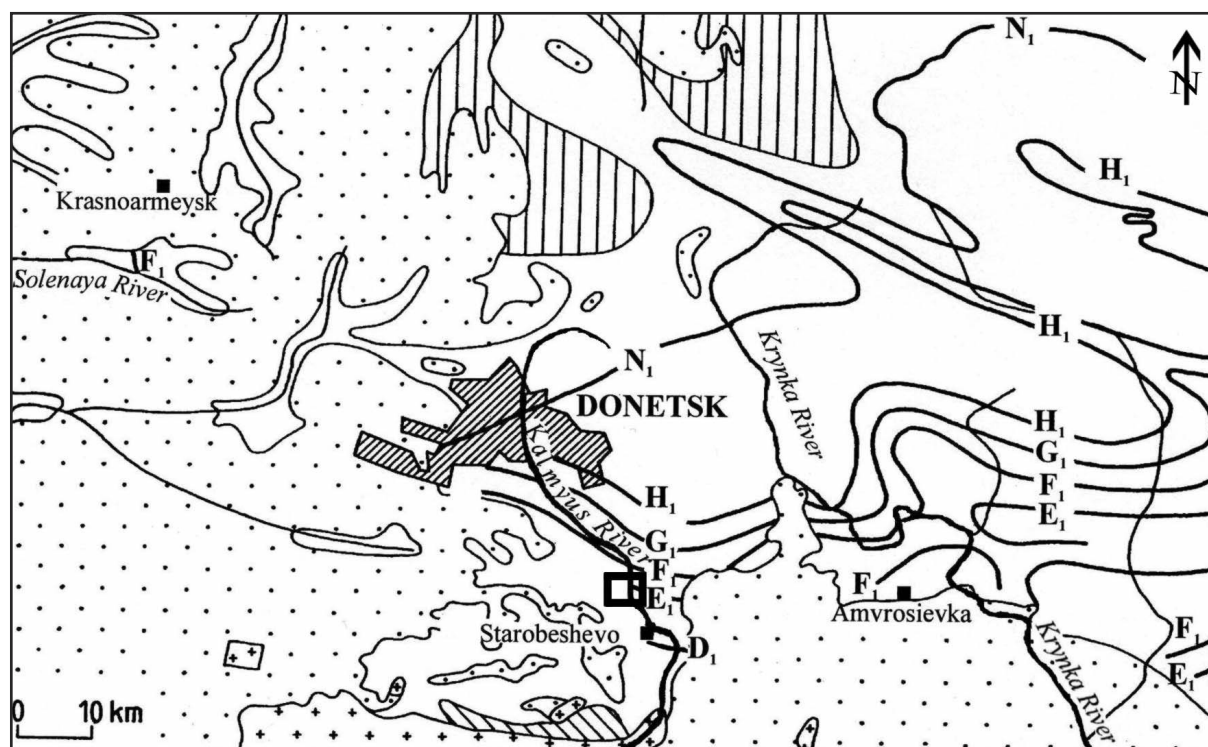
Text-fig. 2. Location of individual limestones D_1 to N_1 in the vicinity of the town of Donetsk. Carboniferous deposits left in white. Study area outlined (after Fedorowski, 2009a)

Reservoir of the Kalmyus River and the left bank of the Berestovaya River, a right tributary to the former (Text-figs 1–3). Limestones present in that part of the Carboniferous strata were designated by Aizenverg (1958) as E_1^I E_1^{II} E_1^{III}, E_1^{IV}, E_1^V and further described by Poletaev *et al*. (1988). Both the village that gave name to the Feninian Horizon, and the natural outcrops mentioned above, do not exist today.

The Fenino Village was in the meantime evacuated and the area was converted into a water reservoir for the Starobeshevo power plant. The Berestovaya River was directed to the Kalmyus River through the artificial riverbed, i.e., the circumferential channel north of the reservoir (pond of the plant) (Text-fig. 4). Limestones E_1–E_3 formerly exposed in the natural outcrops now crop out along the channel. These changes made recognition of the type localities in the 'Chorna Skelya' baseless. Thus, we re-designate the type locality for *Cordibia pumila* as follows: 'Banks of the Berestovaya River along the circumferential channel near the Starobeshevo power plant.'

The 5-m-thick Fenino Sandstone with flora remnants, located close to the artificial riverbed mouth of the Berestovaya River marks the base of the 176-m-thick, continuous type locality section. The Lower Voznesenskian deposits underlying that sandstone are actually covered with water and not measured. This is
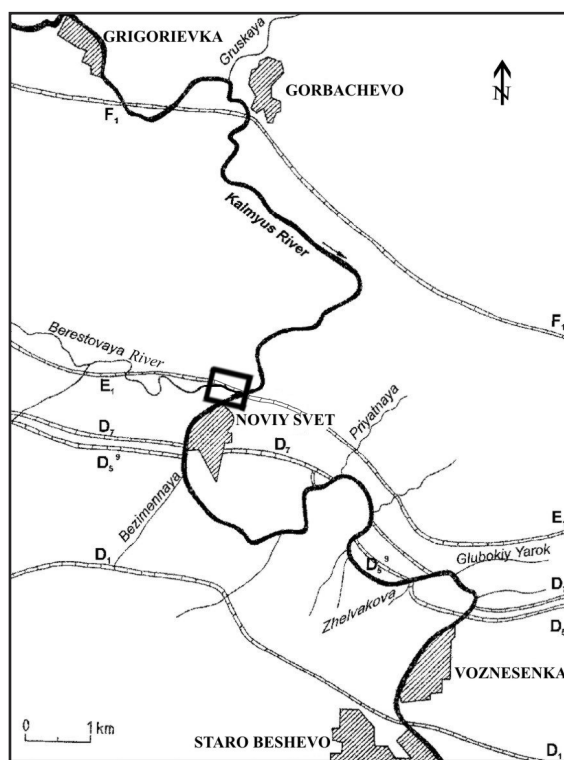
Text-fig. 3. Outcrops of Limestones D to F in the Starobeshevo Village area. Study area outlined (After Fedorowski 2009a)
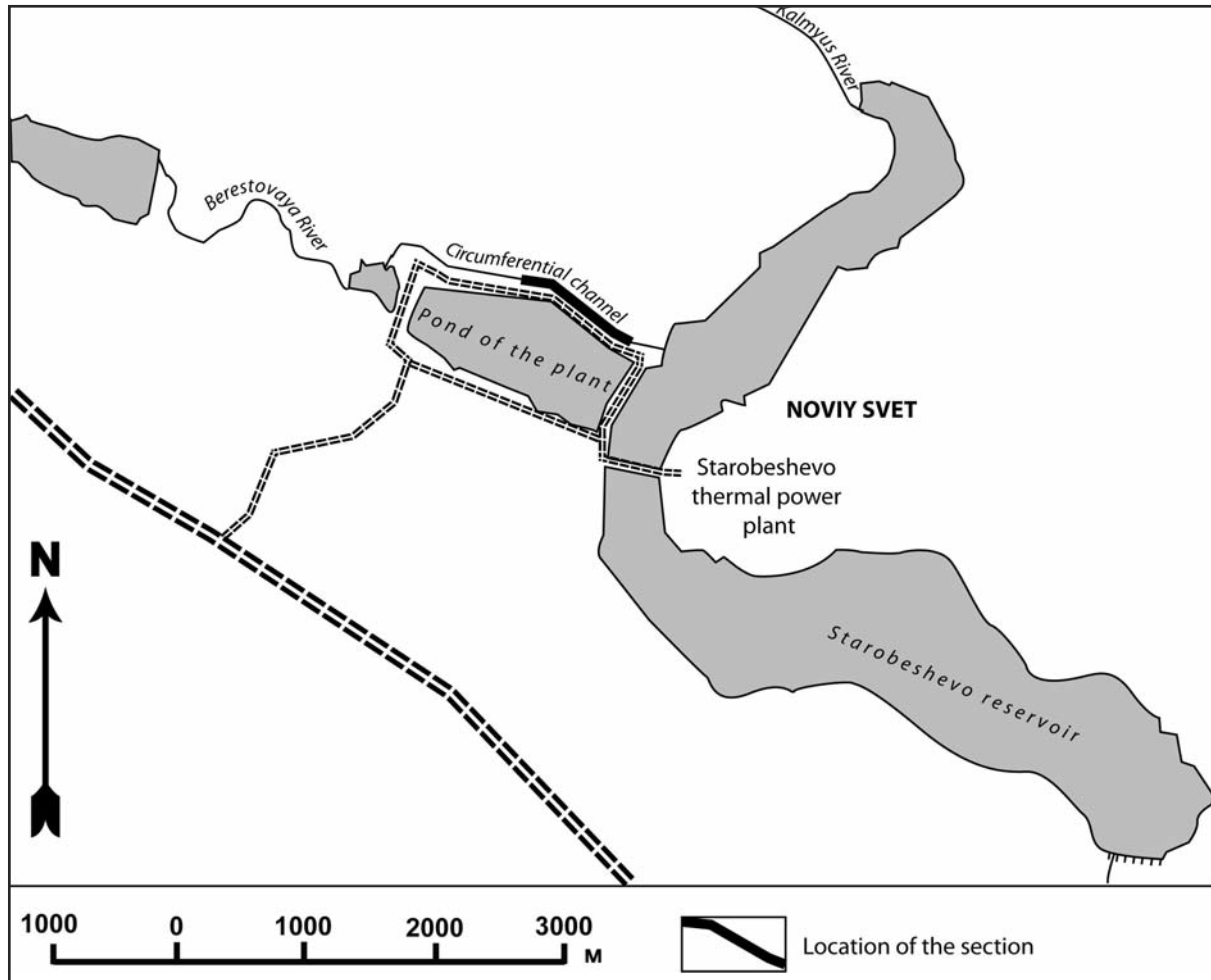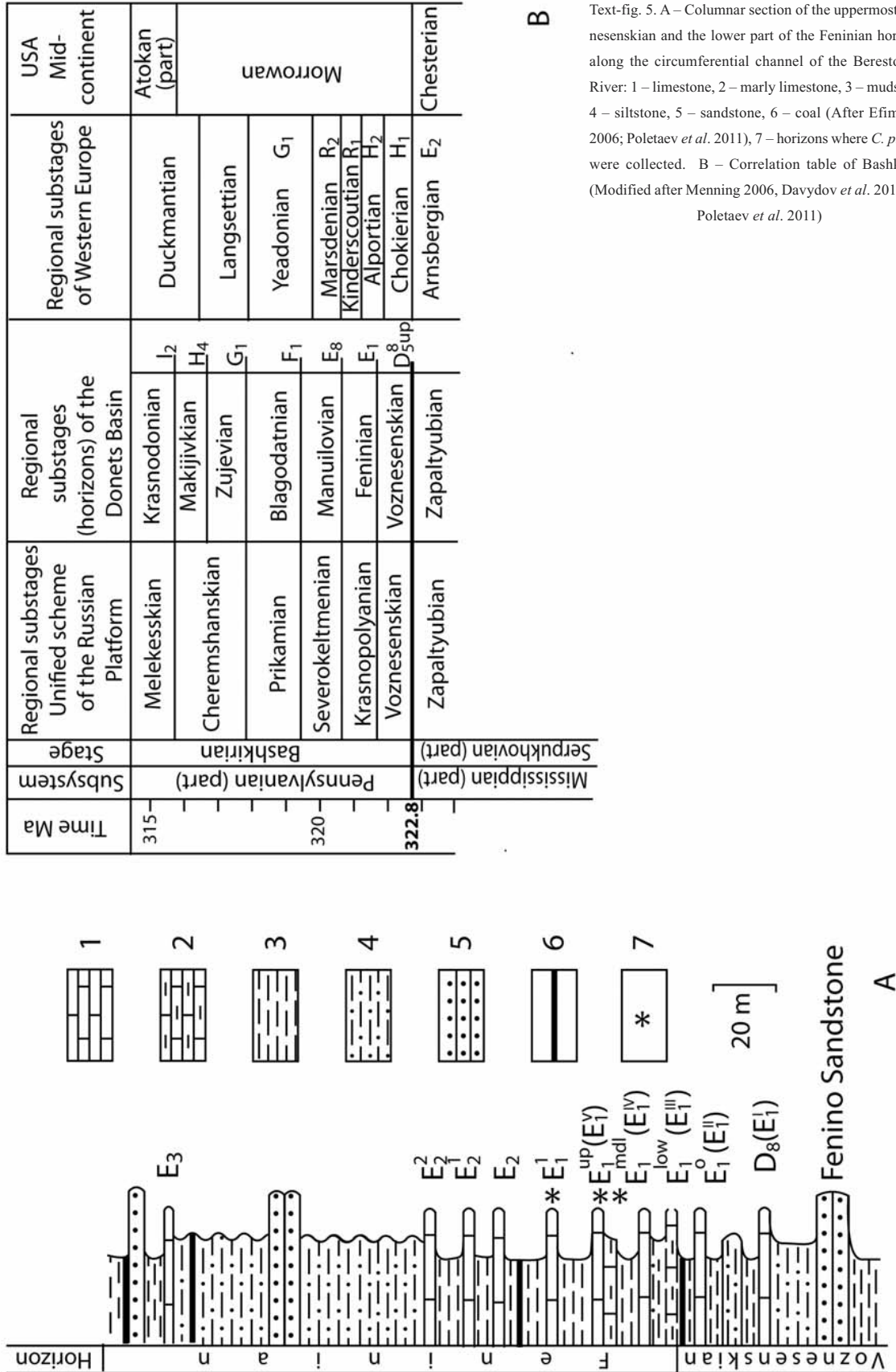
Text-fig. 4. Detailed map of the type locality vicinity

reflected by an open bottom of the stratigraphic column (Text-fig. 5A). The Fenino Sandstone is followed by 40 m of dark grey mudstones followed by higher mudstones and siltstones with a single intercalation of limestone (limestone D_8, see below) and a thin coaly silt near the top of this lower part of the section (Text-fig. 5A). All of those units and the subsequent deposits dip NE at an angle of 4°–5°. As a result of the nearly horizontal orientation, these deposits crop out widely on both banks of the circumferential channel, allowing investigation over a wide area.

As a result of the investigation of several groups of animal and plant fossils, and in order to correlate Aizenverg's (1958) Limestone group E_1 with other E Limestones, a new nomenclatural system was introduced (see Poletaev et al. 2011 for details). According to that new system and the investigation of conodonts by Nemyrovska (1999), the limestone included in the set of beds described above, i.e., the Limestone E_1^1 of Aizenverg (1958) and Poletaev et al. (1988) was designated

as Limestone D_8 and its position was established as Upper Voznesenskian. Fedorowski (2009a, Table 1) accepted the Upper Voznesenskian position of the Limestone D_8, but he made an error by following Efimenko (2006) in accepting her Limestone E_1^0 as the beginning of the Feninian Horizon. According to Poletaev et al. (2011), the Limestone E_1^0 of Efimenko should in fact have been E_1^{II} of Aizenverg (1958) or E_1^{low} according to the new designation which is followed in the present paper. Other new designations corresponding to those introduced by Aizenverg (1958) are as follows: $E_1^{IV} = E_1^{mdl}$, and $E_1^V = E_1^{up}$. Limestone E_1^{III} of Aizenverg (1958) is missing from the set of newly designated limestones and is considered part of Limestone E_1^{low} (Poletaev et al. 2011). The limestones above E_1^1, not described here in detail, are referred to as E_2, E_2^1, E_2^2, E_3 (Text-fig. 5A) up to E_7 where the limestones of the Feninian Horizon, corresponding to the *Reticuloceras-Bashkortoceras* ammonoid Zone or to most of the *Idiognathoides sinuatus/I. sulcatus sulcatus* conodont

Text-fig. 5. A – Columnar section of the uppermost Voznesenskian and the lower part of the Feninian horizons along the circumferential channel of the Berestovaya River: 1 – limestone, 2 – marly limestone, 3 – mudstone, 4 – siltstone, 5 – sandstone, 6 – coal (After Efimenko 2006; Poletaev *et al*. 2011), 7 – horizons where *C. pumila* were collected. B – Correlation table of Bashkirian (Modified after Menning 2006, Davydov *et al*. 2010 and Poletaev *et al*. 2011)

B

Time Ma	Subsystem	Stage	Regional substages Unified scheme of the Russian Platform	Regional substages (horizons) of the Donets Basin	Regional substages of Western Europe	USA Mid-continent
315	Pennsylvanian (part)	Bashkirian	Melekesskian	Krasnodonian (I_2)	Duckmantian	Atokan (part)
			Cheremshanskian	Makijivkian (H_4)	Langsettian	Morrowan
			Prikamian	Zujevian (G_1)	Yeadonian (G_1)	
320				Blagodatnian (F_1)	Marsdenian (R_2)	
			Severokeltmenian	Manuilovian (E_8)	Kinderscoutian (R_1) / Alportian (H_2)	
			Krasnopolyanian	Feninian (E_1)	Chokierian (H_1)	
322.8			Voznesenskian	Voznesenskian (D_5^{8up})	Arnsbergian (E_2)	Chesterian
	Mississippian (part)	Serpukhovian (part)	Zapaltyubian	Zapaltyubian		

A

Fenino Sandstone

E_3
E_2^2
E_2^1
E_2
E_1^1
$E_1^{up}(E_1^V)$
$E_1^{mdl}(E_1^{IV})$
$E_1^{low}(E_1^{III})$
$E_1^o(E_1^{II})$
$E_1(E_1^I)$
$D_8(E_1^I)$

Voznesenskian

Horizon: Feninian

20 m

Zone of Nemyrovska (1999) (Fedorowski 2009a) are terminated.

The Limestone E_1^{low} starts with 0.15 m of dark-grey packstone-grainstone, characterized by the occurrence of the goniatites *Stenoglaphyrites miseri* and *Homoceratoides tubidum* (Poletaev *et al*. 2011). Efimenko (2006) noted an occurrence of algae, Foraminifera and Brachiopoda. The conodont study by Nemyrovska (1999) confirms its Lower Feninian position.

That continuous limestone bed is followed by 4 m of grey, thin bedded mudstone with ferruginous-carbonate concretions in the lower part. Aizenverg (1958) designated those deposits as E_1^{III}. Poletaev *et al*. (2011) included thin, impersistent limestone layers present in that series in the upper part of Limestone E_1^{low}. Abundant brachiopods and diversified goniatites (*Reticuloceras tersum, R. feninse, R. berestovense, Phillipsoceras inconstatus, Ramosites corpulentus, Retites poletaevi* and *Isohomoceras inostrancevi*) occur within the ferruginous-carbonate concretions in those deposits.

The Limestone E_1^{mdl} consists of 1 m of dark grey, massive wackstone-packstone. Numerous species of algae, crinoids, foraminifers, conodonts and brachiopods derived from that wackstone-packstone are listed by Poletaev *et al*. (1988) and Efimenko (2006). Fedorowski (2009b) described *Axisvacuus verus* from that limestone in the vicinity of Razsypnaya Village.

Beds between Limestones E_1^{mdl} and E_1^{up} consist of 8 m of light grey, thin-bedded mudstones and marly limestones. Poorly preserved, mainly fragmented fossils, including variety of the rugose corals, are scattered throughout the entire thickness of those deposits, but are concentrated immediately below the Limestone E_1^{up}, i.e., below a 0.7-m-thick, dark-grey, medium-bedded wackstone-packstone. Vassilyuk (1960, 1964) described *Dibunophyllum finalis, Lytvophyllum dobroljubovae, Protokionophyllum facilis, Multithecopora sokolovi*, and *Chaetetiporella sokolovi* from this limestone.

The Limestone E_1^{up} is overlain by 10 m of dark-grey mudstones which underlies Limestone E_1^{1} which consists of brown-grey wackstone-packstone with fragmented brachiopods and gastropods and rare, deformed rugose corals, not yet identified.

Specimens of *Cordibia pumila*, collected by the junior author, were derived from Limestone E_1^{up} and mudstone and marly limestone immediately below it except for two specimens of *C. pumila* from Limestone E_1^{1}. In the former beds these corals are accompanied by dominant *Lytvophyllum dobroljubovae* Vassilyuk, 1960 and by several nondissepimented Rugosa, some of which may belong to *Rotiphyllum asymmetricum* Fedorowski 2009a and/or *Axisvacuus extendus* Fedorowski, 2009b described from the equivalent deposits

of the Donets Basin (Grigorievka Village, Kalmyus River basin and Svistuny Village, Krynka River basin, respectively).

SYSTEMATIC PALAEONTOLOGY

Order Stauriida Verrill, 1865
Family Aulophyllidae Dybowski, 1873
Subfamily Dibunophyllinae Wang, 1950

Genus *Cordibia* gen. nov.

TYPE SPECIES: *Cordibia pumila* sp. nov.

DERIVATION OF NAME: Combination of first two syllables of names *Corwenia* Smith and Ryder, 1926 and *Dibunophyllum* Thomson and Nicholson, 1876 pointing to the potential relationship to both those genera.

SPECIES ASSIGNED: *Cordibia pumila* sp. nov., *Dibunophyllum cylindricum* Dobrolyubova, 1937.

DIAGNOSIS: Dibunophyllinae with corals capable of forming protocolonies; offsetting lateral; offsets approach morphology but not size of parental skeletons; incomplete axial column in continuous dibunophyllid axial structure; microstructure of septa finely trabecular.

DISCUSSION: Corals included in this new genus are peculiar in being able to produce lateral offsets, commonly, but not always arranged in verticils. Some or many of those offsets may reach a morphology advanced enough to be identified at the genus level, but not enough to achieve mature characteristics of their parents. None of the well known solitary genera morphologically most similar to our corals, i.e., *Dibunophyllum* Thomson and Nicholson, 1876, *Arachnolasma* Grabau, 1922 and *Dibunophylloides* Fomichev, 1953 are capable of offsetting. Nevertheless, we consider them related to *Cordibia* at a subfamily level. The relationship to the solitary genus *Amandophyllum* Heritsch, 1941 is less certain. Fomichev (1953, p. 393) diagnosed *Dibunophylloides* as solitary and included it in his new Family Neokoninckophyllidae. Hill (1981, p. F395) accepted the solitary growth form of that genus, but synonymized it with *Amandophyllum* and included it in the Family Durhaminidae. Neither the synonymy proposed by Hill nor the position of the type species of *Amandophyllum*, i.e. *Clisiophyllum carnicum* Heritsch, 1936 within the Durhaminidae is accepted here. For more comprehensive remarks based on the re-examination by the senior

author of the holotype of *C. carnicum,* see Fedorowski *et al*. (2007, p. 53). This question is mentioned here because specimens described by Fomichev (1953) from the Donets Basin are morphologically similar to our corals and occur in the same area although higher in the stratigraphic column (Moscovian, Limestones M). We accept now a relationship between the Ukrainian *Dibunophylloides* and *Cordibia* at a subfamily level, and it will be considered even closer when/if *Dibunophylloides* is found to be protocolonial.

The taxonomic position of *Dibunophyllum cylindricum* Dobrolyubova, 1937 from the Myachkovian Horizon of the Moscovian Substage, is considered by us close enough to *Cordibia pumila* for those two taxa to be considered co-generic. Dobrolyubova (1937, p. 69) began the description of a growth form of her species with the sentence: "Some specimens expose lateral offsetting, not influencing further growth of a corallite." (translated herein from Russian). She then continued her description of details leaving no doubt as to the nature of those offsets as 'lost structures' of Fedorowski (1978). Her sketches (pl. 21, figs 14, 15; pl. 22, fig. 7) confirm that growth form as protocolonial. Thus, we here include *Dibunophyllum cylindricum* in *Cordibia*, but as a separate species (see remarks on *C. pumila* below).

Except for "*Dibunophyllum*" *cylindricum*, only *Dibunophyllum* and *Corwenia* are morphologically close to our specimens. Both are characterized by spiders web axial structure that forms continuous axial columns in *Dibunophyllum*, as seen in its longitudinal sections, whereas *Cordibia pumila* developed a continuous axial structure, but apparently not a continuous axial column (Text-fig. 8E, F, G, H, L). The morphology of the cardinal fossula and length of the cardinal septum are the next characters to be pointed out. Both of those characters in *C. pumila* are generally closer to Corwenia than to *Dibunophyllum*, i.e., the cardinal tabular fossula is either absent or is very shallow and hardly distinguishable in most specimens investigated whereas the cardinal septum either joins the median lamella or the latter is elongated towards it (Text-figs 8A–D, I–K, M, N; 6F–K; 9A–J). Other characters are common for both *Dibunophyllum* and *Corwenia* on the one hand and to *C. pumila* on the other, proving its position within the subfamily Dibunophyllinae. However, the protocoloniality is a growth form rare enough within the Rugosa to be treated as an important generic character, strongly supporting a separate generic status of the corals described. Morphological similarities listed above and the pseudocolonial growth form of *Cordibia* would have made that new genus intermediate between *Corwenia* and *Dibunophyllum* if appeared much earlier in the stratigraphic column. Its Bashkirian appearance vs

Viséan occurrences of the other two, forms only an indication of a possible evolutionary process leading from a primitive *Dibunophyllum* to *Corwenia*. This does not exclude derivation of *Cordibia* from *Dibunophyllum* as a separate offspring, postulated herein.

Protodurhamina Kozyreva, 1978, included by her in the Durhaminidae Minato and Kato, 1965 – a position accepted by Hill (1981) – is distant from that family, as redefined by Fedorowski et al. (2007). We follow the opinion of the later authors and omit a detailed analysis of characters of *Protodurhamina* from the present paper. Only the following characters should be mentioned: 1) The axial structure in the transverse section is simple with the median lamella elongated towards the cardinal septum; 2) The cardinal septum is equal in length to the remaining major septa; 3) 'Tabular floors broadly conical, drawn steeply upwards at axis' (Hill, 1981, p. F397). None of those characters occur in the Durhaminidae. A true relationship of *Protodurhamina* will remain unknown until its blastogeny and the microstructure of septa are described. Fedorowski *et al.* (2007) suggested its possible relationship to the Lithostrotionidae. We accept that as a possible variant, but the relationship of *Protodurhamina* to the Kleopatrinidae or Aulophyllidae cannot be excluded. A close relationship of *Protodurhamina* to *Cordibia* is unlikely irrespective of that final designation and of some morphological similarities of those two genera.

Copia admiranda Vassilyuk and Kozyreva, 1974 from the upper Viséan of the Voronezh Uplift, Russian Federation, is mentioned in this discussion only because of the colonial growth form and development of an axial structure. Vassilyuk and Kozyreva (1974) described their colonies as "ramoznye", i.e. furcated or ramified comprising corallites in both direct lateral contact and isolated. One of us (V.V.O.) confirmed that that genus and species is able to produce several generations of offsets, but its blastogeny remains unknown. In addition to a fully colonial growth form, *Copia* differs from *Cordibia* in possessing extra septal lamellae in its axial structure, a character not mentioned by its authors. Both of those characters are adequate to distinguish those genera at a subfamily or family level.

Cordibia pumila sp. nov.
Text-figs 6–10

HOLOTYPE: Specimen UAM-Tc.Don.1/98.

TYPE LOCALITY: Banks of the terminal part of the circumferential channel that surrounds the water reservoir of Starobeshevo power plant.

TYPE HORIZON: Limestone E_1^{up} and mudstone and marly limestone immediately beneath, Lower *Reticuloceras-Bashkortoceras* Zone.

ETYMOLOGY: Lat. *pumilus* – dwarf – after small dimensions.

DIAGNOSIS: *Codibia* with 22–26 × 2 septa at 7.0–12.0 mm mean corallite diameter; major septa do not approach dibunophyllid axial structure; minor septa of variable length, most penetrate outer tabularium'; cardinal septum almost equal to remaining major septa, commonly united with median lamella.

MATERIAL: See Material and Methods chapter for details.
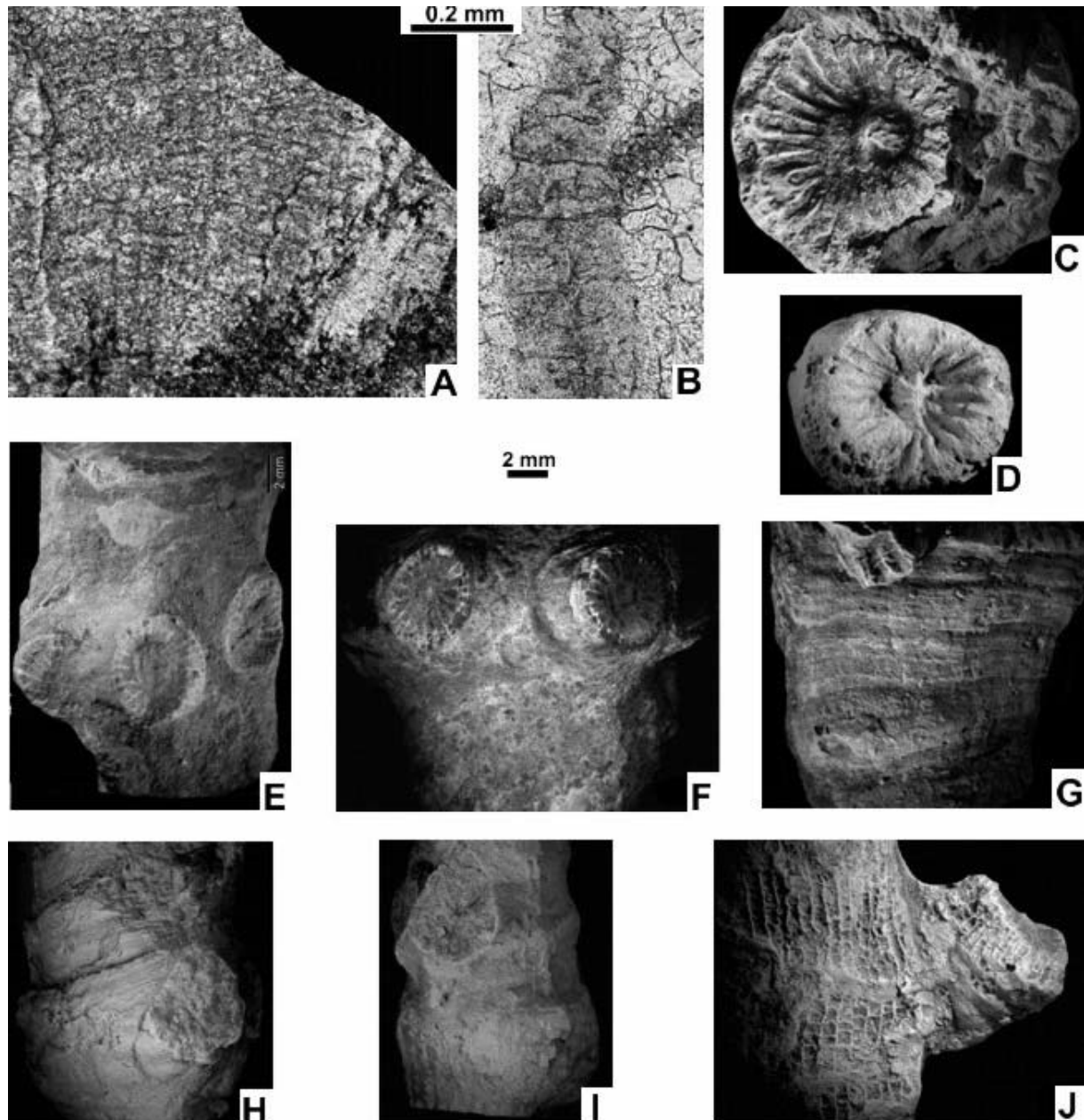
Text-fig. 6. *Cordibia pumila* sp. nov. Paratypes. A, B – UAM-Tc.Don.1_107. The microstructure of septa diagenetically altered in the longitudinal (A) and transverse (B) sections. C – UAM-Tc.Don.1_99. Calices of the protocorallite (large) and lost structures (periphery at right). D – UAM-Tc.Don.1_100. Calice of young protocorallite. E – UAM-Tc.Don.1_101. Verticil of three lost structures. F, G – UAM-Tc.Don.1_112. Verticil of several lost structures; three exposed, G – external surface with delicate growth striae. H, I – UAM-Tc.Don.1_113. Two subsequent verticils of the lost structures accompanying the protocorallite narrowing. J – UAM-Tc.Don.1_109. Single lost structure; rudiments of the external wall seen on it and the parent protocorallite; margins of dissepiments and septa exposed by corrosion in most surface. Scale bar in the middle corresponds to pictures C–J
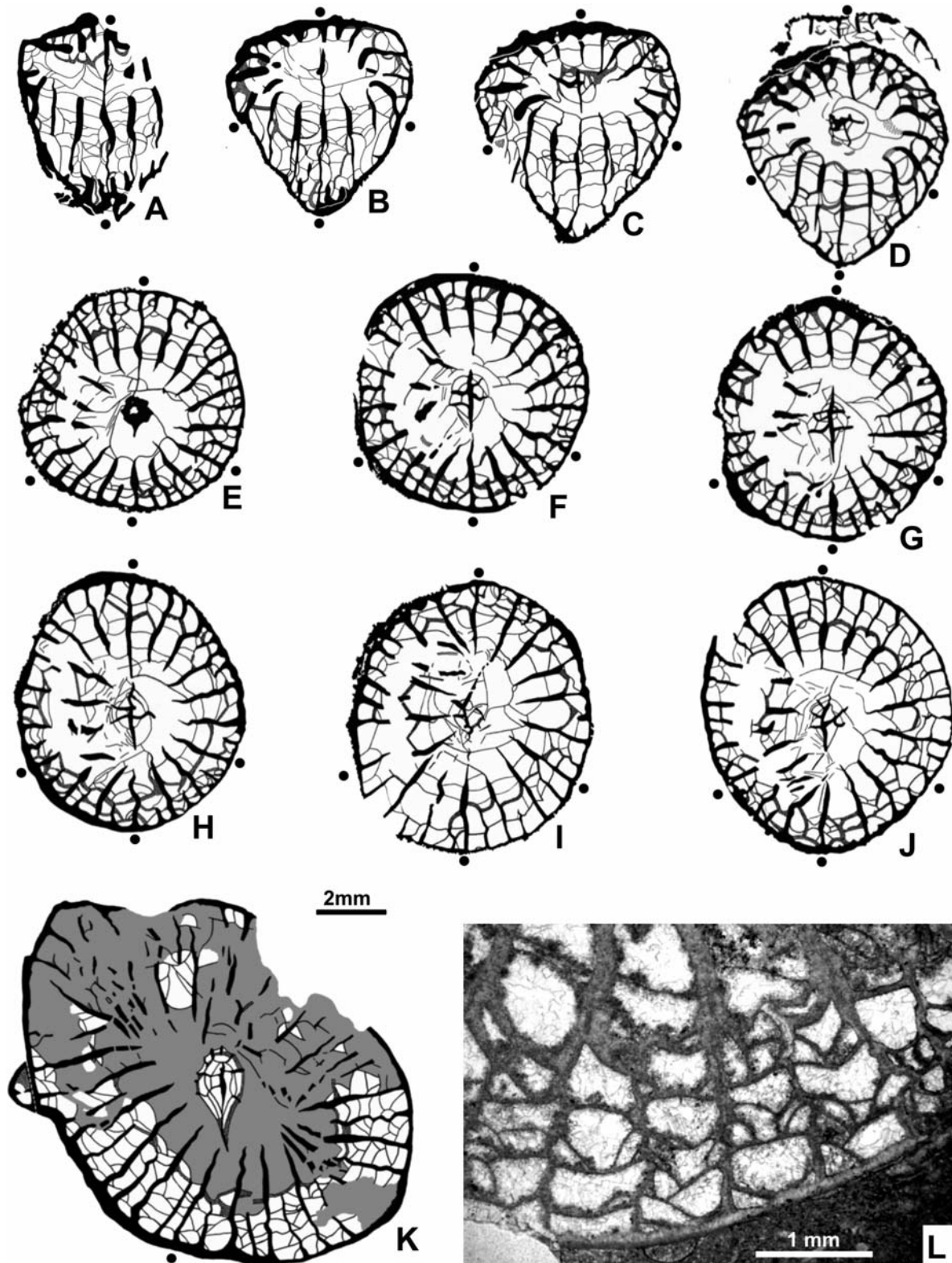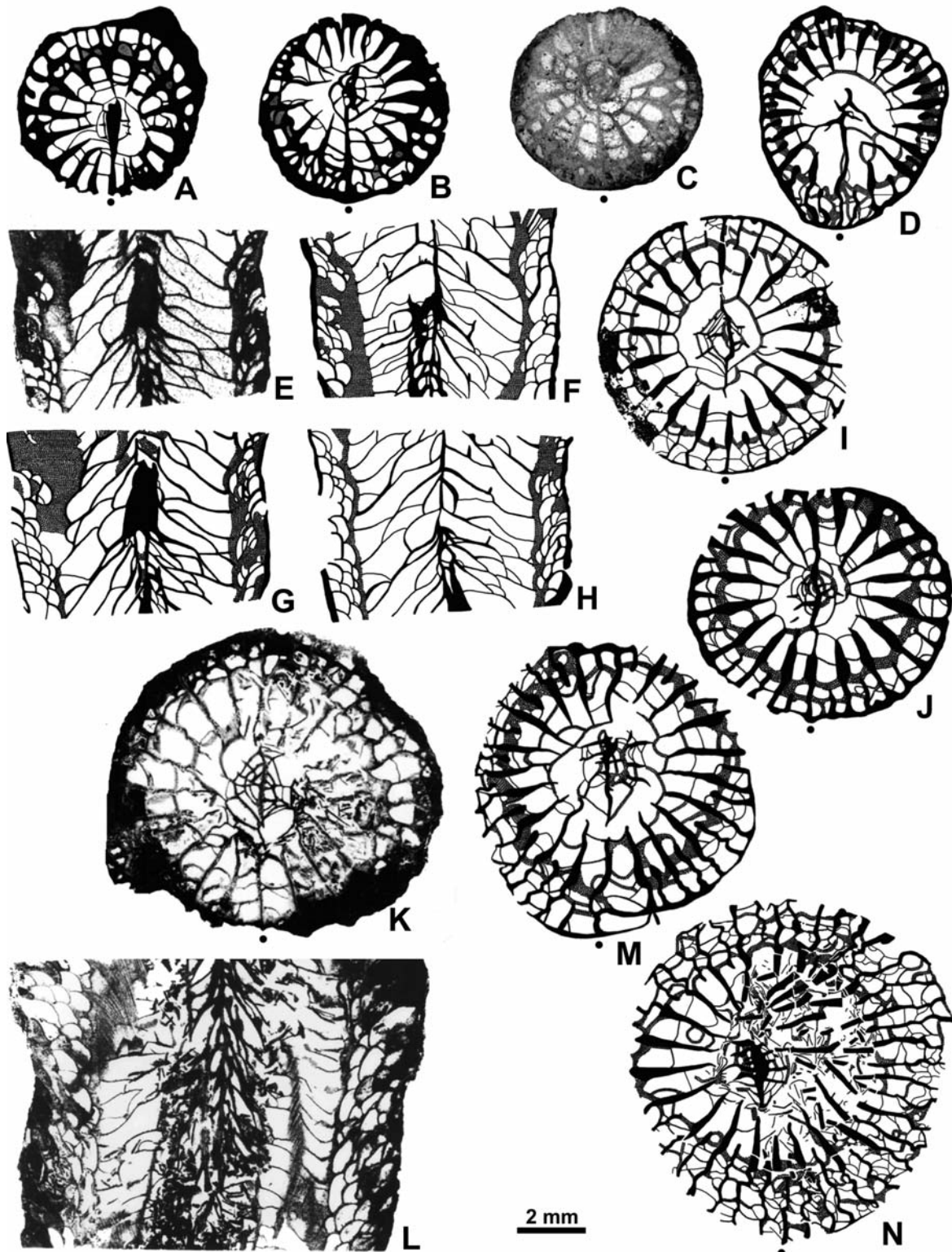
Text-fig. 7. *Cordibia pumila* sp .nov. A–L – UAM-Tc.Don.1_98. Holotype. Computer drawings, except when stated. A–J, series of grinding surfaces with peels of a lost structure. A–D – hystero-neanic growth stage, E – earliest separate growth stage, F–J – small morphological variability in the most advanced growth stage. K – transverse thin section of a mature protocorallite, L – image of enlarged portion of the transverse thin section illustrating the minor septa and the dissepimentarium. Scale bar above K corresponds to all pictures except L. Dots around the margin of specimens indicate position of cardinal (down) and.counter septum and two alar septa

Text-fig. 8. *Cordibia pumila* sp. nov. Paratypes. Transverse thin sections except when stated. A-C - UAM-Tc.Don.1/102. Immature growth stages of lost structures (A, B – drawings from peels). D – UAM-Tc.Don.1/103. Immature growth stage of lost structure (drawing from peel). E-J – UAM-Tc.Don.1/107. E-H – longitudinal sections of protocorallite. E, G – centric thin section; (E drawing from G), F, H – successive eccentric grinding with peels (drawings), I – mature growth stage of protocorallite just above longitudinal sections, J – early mature growth stage just below longitudinal sections. K, L – UAM-Tc.Don.1/105. K – early mature growth stage of protocorallite, L – longitudinal thin section. M – UAM-Tc.Don.1/106 – mature growth stage of protocorallite. N – UAM-Tc.Don.1/104. Late mature growth stage of protocorallite. Scale bar at the bottom corresponds to all pictures. Dots indicate position of cardinal septum.

DESCRIPTION: Individual characters demonstrated by the best preserved specimens rather than description of the holotype first and the intraspecific variability afterwards, is here introduced. External surface, preserved in small fragments of some corallites, is almost smooth with only delicate growth striae (Text-fig. 6G). The external wall is thin as is documented by its remnants. It is commonly corroded and the corallite surface exposes peripheral margins of septa and dissepiments (Text-fig. 6J).

Calices are shallow (Text-fig. 6C, D) with a moderately elevated axial structure consisting of a thin or slightly thickened median lamella, accompanied by 2–3 septal lamellae on each side. Upper margins of the major septa are elevated slightly above the dissepimentarium margin. Their inner parts may either be elongated along the calice floor to approach the axial structure, or stay short of it. The minor septa are restricted to the dissepimentarium in the preserved parts of calices. Upper margins of calices are missing.

Offsets appear commonly in verticils, rarely individually (Text-fig 6E, F and J, respectively) and at the very peripheral part of the parent's dissepimentarium (Text-fig. 6C, right). The process of offsetting is invariably lateral with offsets growing at a large angle, almost perpendicularly to the parent organism. They mostly appear without any obvious changes in the parents' skeletons. Offsetting must be a rare event during a corallite growth because two verticils of offsets were found in only one specimen. They correspond in this case to narrowing of the parent's skeleton (Text-fig. 6H, I), suggesting inconvenient extrinsic conditions as a factor pushing the polyp to reproduce. That explanation cannot be extended to the remaining corallites that produced offsets without any recognizable factor favouring that process.

Both the morphology and the n:d values of the mature corallites are variable, but the differences do not extend the boundaries acceptable for a species. The holotype's maximum n:d value (approximately 25:9–12.6 mm; Text-fig. 7K) is one of the largest and the paratype UAM-Tc.Don.1_107 (n:d value 18:7.1 mm; Text-fig. 8I, J) is the smallest. Also, the latter corallite possesses a narrow and simple dissepimentarium, characteristic mostly of immature corallites and lost structures. However, such a simple dissepimentarium is also present in some offsetting specimens (Text-fig. 9A–J – the parent corallite). The most complex dissepimentarium with both interseptal and pseudoherringbone dissepiments occurs only in the largest protocorallites (Text-figs 7K, L, 8N, 10M).

There is little variability in the shape of the major septa. They never reach the axial structure in the mature specimens and are very seldom connected to their axial lamellae in the early growth stage. Major septa are thicker in the tabularium than in the dissepimentarium where they are wavy. Sclerenchymal thickening may be stronger in young corallites (Text-fig. 8J), but that is not the rule. In mature corallites major septa in the tabularium are either clearly or slightly thickened (Text-figs 8M, N, 10M) or thin (Text-fig. 8K). The holotype possesses those parts of the major septa very slightly thickened (Text-fig. 7K). The same is true for its offsets, i.e., the lost structures (Text-fig. 7F–J), whereas offsets of other corallites may possess thickened major septa (Text-fig. 8A–D).

The cardinal septum is hardly distinguishable in most mature corallites and in the lost structures, but is slightly shortened in rare corallites (e.g., Text-fig. 8I). The cardinal fossula is either missing or is very shallow in most corallites, including the holotype. The counter septum rarely extends to the median lamella (Text-fig. 8I, J). It is mostly equal in length to the remaining major septa in the counter quadrants.

The minor septa are more variable than the major septa. In the holotype (Text-fig. 7K, L) and some paratypes (Text-figs 8K, 10M) they are mostly restricted to the dissepimentarium, but in several paratypes they enter the tabularium with thickened inner margins (Text-fig. 8I, M, N; 9A–J, parent corallite). That difference is reflected in the length of the minor septa in the lost structures (Text-fig. 8A–C *vs* 8D).

The axial structure as seen in the transverse section is typically dibunophyllid and shows little variability. It is always narrow and simple with the median lamella thin in most, rarely thickened in some (Text-fig. 8N), commonly elongated towards the cardinal septum. Two to four septal lamellae are attached to it each side, but are not incorporated into it (Text-fig. 7K, 8I–K, M, N).

The axial structure in the longitudinal section (Text-fig. 8E–H, L) is incompletely studied because most specimens are flattened. Only two corallites were longitudinally sectioned. The longitudinal section of the largest corallite in the collection (Text-fig. 8L) shows the axial column composed of steeply arranged axial tabellae, contrasting with much less steeply arranged tabulae and tabellae of the tabularium. The centric section (Text-fig. 8E, G) of the smaller corallite illustrates a substantial difference in the axial structure compared to the one described above. A continuous axial column separated from the tabularium is not developed, but the axial structure consists of some axial tabellae in addition to tabulae which extend to the pseudocolumella. That image changes toward the periphery (Text-fig. 8F, H, respectively), ending with the *Koninckophyllum*-like longitudinal morphology. That series of sections documents the probability of errors resulting from an
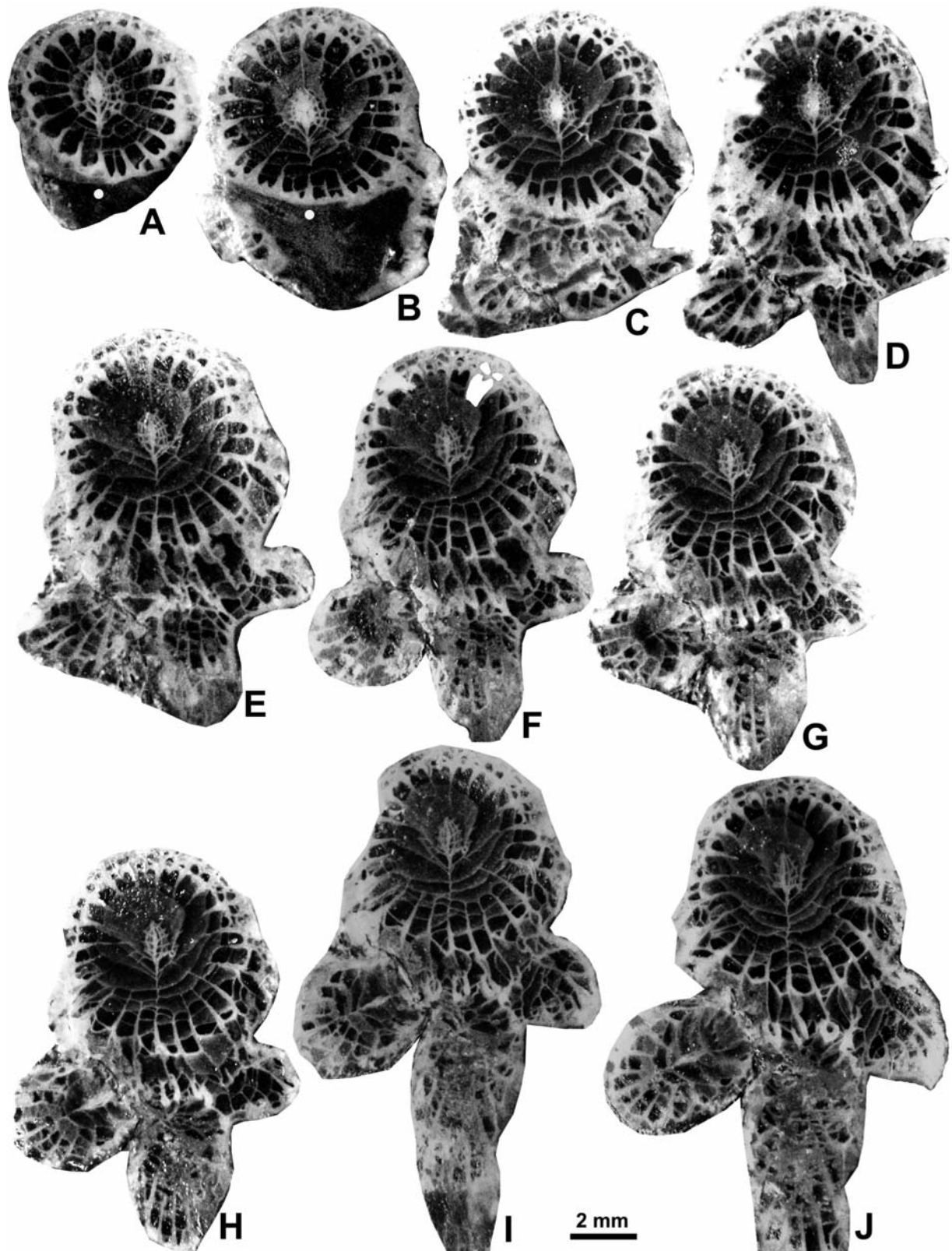
Text-fig. 9. *Cordibia pumila* sp. nov. TSNUK 3P267/E_10. Series of the polished surfaces. Development of a parent and a verticil of three lost structures. Scale bar at the bottom corresponds to all pictures. Dots in A and B indicate position of cardinal septum identical in all images
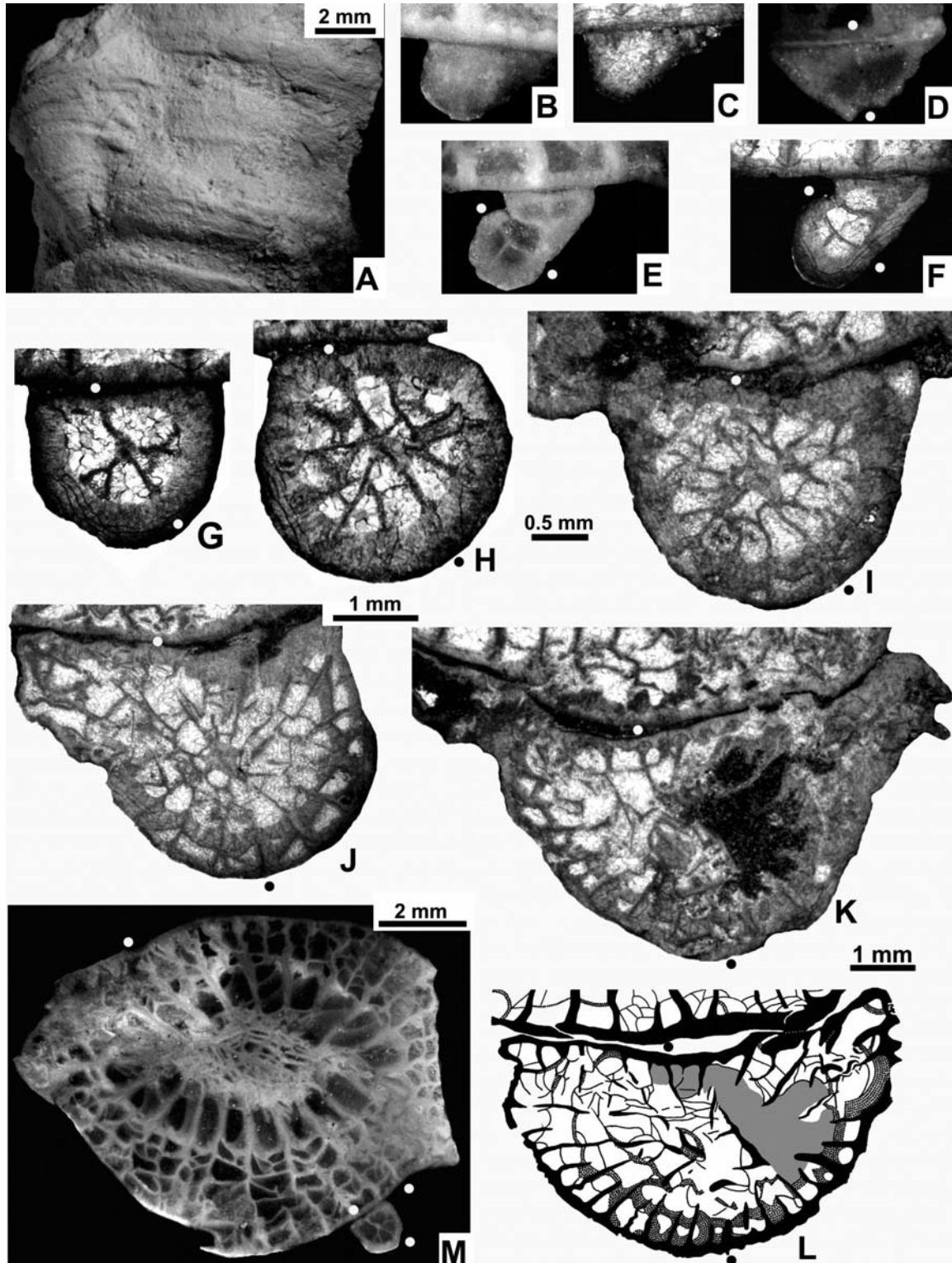
Text-fig. 10. *Cordibia pumila* sp. nov. A–C, E–M – UAM-Tc.Don.1_114. Paratypes. The common number for the host and attached corallite. Transverse thin sections, except when stated. A – side view of a young protocorallite attached to the mature protocorallite, B, C – the earliest postlarval skeleton; B – polished surface, E, F – brephic growth stage; E – polished surface, G – earliest neanic growth stage, H – neanic growth stage, I, J – late neanic growth stage, K, L – late neanic/early mature growth stage; rejuvenation at right side, M = G of attached protocorallite and mature morphology of the host protocorallite. D – UAM-Tc.Don.1_98 early postlarval skeleton attached to the holotype. Scale bar in the middle corresponds to pictures B–I – enlargement of remaining pictures as indicated separately. Dots around the margin of specimens indicate position of cardinal (up) and.counter septum

rect orientation of the longitudinal section. The axial structures in transverse sections are very similar in both corallites compared (Text-fig. 8K *vs* 8I, J).

The early ontogeny of a protocorallite, was studied in a single, almost complete, 6.8 mm long corallite attached to the mature specimen (Text-fig. 10A). The upper 1.8 mm of the protocorallite studied, corresponding to its calice, was diagenetically destroyed. Seven thin sections taken from the lower 5 mm of the corallite (Text-fig. 10C, F–K) spaced approximately 0.6–0.8 mm apart, and a peel with a drawing taken from the upper fragment (Text-fig. 10L) were available for this study. Polished surfaces (Text-fig. 10B, E, M) supplemented by thin sections allowed a comparison between those two sources of data.

The earliest growth stage (Text-fig. 10B, C) corresponds to the post-larval, probably aseptal cup, filled in with the sclerenchyme. Two larvae may had settled next to one another as documented by the next thin section made at the distance of 0.6 mm and in the corresponding polished surface (Text-fig. 10E, F). The right skeleton belongs to a specimen that did not continue to grow, and was only able to grow short protosepta opposite to one another along its wall. That image was recognizable in the polished surface, but is not seen in the thin section (Text-fig. 10E, F, respectively; upper right). Similar position and size of the protosepta is documented by another corallite (Text-fig. 10D) attached to the holotype. The much larger size of the latter may have resulted from the suppression of the former by a stronger young polyp that continued to develop.

That earliest septogenesis of the stronger and more complete corallite was destroyed by the cutting wire. In the brephic growth stage, illustrated by the polished surface and the thin section (Text-fig. 10E, F, lower left, respectively), the thin axial protoseptum and the left counter-lateral septum are developed. A shadow opposite to the counter-lateral septum, seen only in the thin section (Text-fig. 10F, right) may correspond to the second counter-lateral septum destroyed during the process of recrystallization. Alar septa are not yet developed. An acceleration in the increase of the major septa in the counter quadrants continues during the next 0.8 mm of the corallite growth (Text-fig. 10G) when two counter-lateral septa and two next major septa appear in those quadrants, whereas only short bodies, slightly extending from the external wall are present next to the cardinal septum. Those bodies may belong to the alar septa. The cardinal quadrants otherwise lack septa. This is the growth stage when the axial septum became thickened in its middle part to form the initial part of the pseudo-columella. Such a thickening lasts for a few millimetres of corallite growth (Text-fig. 10H–K). The

comparatively well preserved part of the host protocorallite and the early neanic growth stage of the protocorallite attached, is illustrated to demonstrate their proportions (Text-fig. 10M).

The insertion of septa in the cardinal quadrants (Text-fig. 10H) is rapid and took place during 0.8 mm of the corallite growth destroyed during cutting and grinding. The left alar septum is long, but the opposite one is either broken or divided into two fragments (Text-fig. 10H, left and right respectively). The counter-lateral septa are shorter than the next pair of the metasepta, and remain that way during the following growth stage (Text-fig. 10I, J). The middle metasepta in the counter quadrants remain the longest. Their inner sectors perhaps become septal lamellae of the axial structure. Unfortunately, this cannot be confirmed with certainty, because the corallite skeleton of this and the next corallite growth stage was partly destroyed by compaction (Text-fig. 10I–L).

The median lamella is not isolated from the protosepta until the late neanic/early mature growth stage (Text-fig. 10L). Thinning of that skeletal element is accompanied by its disconnection from the counter septum. It may remain attached to the cardinal septum, as suggested by broken septal fragments (Text-fig. 10L, upper left).

The number of septa become almost equal in all quadrants at the corallite growth level corresponding to the insertion of the first dissepiments (Text-fig. 10I). Their incomplete ring appears in the counter quadrants and extends step by step into the first inserted major septa of the cardinal quadrants. Dissepiments remain absent next to the host corallite during growth of the protocorallite studied (Text-fig. 10J-L). The minor septa remain unrecognizable during early corallite growth (Text-fig. 10B-J), but they appear in all quadrants close to the end of the corallite growth (Text-fig. 10K, L) giving the impression of cyclic insertion. Such a simple interpretation is not accepted. Only their elongation into the corallite lumen was more or less simultaneous, but not their insertion. The minor septa were perhaps hidden in the thickness of the corallite external wall and camouflaged by the diagenesis.

The distal corallite growth exhibits a partial rejuvenation (Text-fig. 10K, L, right, black and shadowed). The polyp secreted a new external wall (neotheca) close to its axial area, whereas its peripheral-most parts around the atavotheca remained connected to the main part of the body. That interpretation is suggested by the continuous secretion of the sclerenchyme and by the absence of a strange fabric between septa that always appear in septal loculi emptied by a polyp.

The comparison of the ontogeny (Text-fig. 10A–L),

based on the immature protocorallite described above, to the blastogeny based on serial sections with peels and drawings taken from the holotype protocorallite (Text-fig. 7A–L) and on the serial polished surfaces taken from one well preserved paratype protocorallite (Text-fig. 9A–J), shows several similarities in those processes. Thus, a separate description of the blastogeny is omitted. The appearance of the axial septum early in the ontogeny (Text-fig. 10E–G) and blastogeny (Text-figs 7A, B; 9A–J, right offset) points directly to the early ontogeny of *Dibunophyllum* (Fedorowski 1971, figs 19:A^1–A^8; 22:A^1–A^3; 28:A^1–A^5). The inheritance of the cardinal septum by the offset and some other major septa attached to the atavotheca at the offset's periphery, are important as an early blastogenetic feature. Only the inherited major septa are well developed at the earliest blastogeny, whereas the inherited minor septa are reduced to short, thin slats at the external wall (Text-fig. 7A–D). This character points to the absence of the minor septa in the early ontogeny described above (Text-fig. 10E–H). The paratype exhibits a similar relationship of the major and minor septa inherited by the offsets (Text-fig. 9D–J). All major septa at the parent's side of the offsets are short, thick and relatively few in number. In the holotype, their number increases rapidly (Text-fig. 7A, B) and their shape changes, quickly achieving the early mature character (Text-fig. 7C–E). This feature is again comparable to the characters described in the early ontogeny, which is characterized by a rapid increase in septa Text-fig. 10G, H).

The median lamella in the holotype's offset appeared at the n:d ratio 16:5.4 mm (Text-fig. 7B) by means of thickening of the inner margin of the cardinal septum. Its very early disconnection from the counter septum in the holotype may be a diagenetic feature, but its disconnection soon after (Text-fig. 7C) is real, being documented by sections of tabulae attached to the inner margin of the counter septum. The strong thickening in the middle part of the axial septum, i.e., formation of the pseudocolumella-like structure comparable to that seen in the ontogeny, is much better demonstrated both in the parent protocorallite of the paratype (Text-fig. 9A–D) and in its left offset (Text-fig. 9G–I). Also the median lamella is longer and more clearly united with the elongated cardinal septum in that paratype than in the holotype. The counter septum became disconnected from the median lamella in both offsetting specimens, whereas either the direct connection of the cardinal septum to the pseudocolumella, or elongation of the latter skeletal element towards the cardinal septum is observed in all specimens studied. Thus, the leading role of the cardinal septum in the formation of the median

lamella is obvious in both processes. Septal lamellae are absent at the early growth stages in both the ontogeny and the blastogeny. In the blastogeny of the holotype's offset they appear irregularly (Text-fig. 7A–E). Their shape and number, always small, is established only after the complete separation of the offset from its parent (Text-fig. 7F). The appearance of the septal lamellae in the blastogeny differs from that observed in the ontogeny in that they are isolated from the inner margins of the major septa very early. As in the case of the young protocorallite described above, septal lamellae in the lost structures are very short and not numerous.

The morphology of the completely isolated offset (the lost structure) closely resembles that of the parent protocorallite in several details. All major septa are equally developed and isolated from the simple axial structure which consists of a thin median lamella elongated towards the cardinal septum and 2–3 septal lamellae at each side. The minor septa increase in length, but in contrast to the parent protocorallite, most of them are restricted to the dissepimentarium which forms a narrow ring of mostly interseptal dissepiments. The cardinal fossula is probably absent from the offset (Text-figs 7E–J; 9D–J, left offset). Concluding the comparison of the blastogeny and ontogeny we want to stress a great value of the blastogeny for the reconstruction of the main ontogenetic characteristics of both colonial and protocolonial rugose corals.

The morphology in the longitudinal sections was not established with adequate detail because most specimens are crushed. The following options are possible: 1. The complexity of axial structures in this view depends upon the advancement in the blastogeny. That option is suggested by the different diameter in a small (ontogenetically younger) transverse section and much wider longitudinal section of one paratype (Text-fig. 8 K, L, respectively). 2. That difference in the morphology between the early and the advanced mature growth stage reflects differences between protocorallites and lost structures. 3. The difference in the complexity of axial structures reflects a wide intraspecific variability. None of those three options is proven.

The microstructure of septa in most specimens was diagenetically altered precluding its identification. Poorly preserved structures seen in some transverse and longitudinal sections (Text-fig. 6A, B) however, suggests the presence of fine trabeculae.

REMARKS: A need for the separate generic position of *Cordibia pumila* was discussed in remarks to the genus. For three reasons we decided to describe and name that species despite the poor preservation of

specimens: 1. Specimens are common in the Limestone E_1^{up} and in the underlying mudstone and marly limestone. Rare specimens occur in the Limestone E_1^1. They have not been found yet either below or above those strata. Also, they are easily distinguishable from other rugose corals of approximately the same age by their protocolonial growth form. Thus, they may serve as an auxiliary taxon for the identification in the field of the Limestones mentioned. 2. Very early Bashkirian rugose corals are rare on the global scale, making every species of that age important for the transition between coral faunas of the Lower and Upper Carboniferous. 3. Corals described represent the protocolonial growth form, a very rare feature in the Rugosa.

'Dibunophyllum' cylindricum is the only species known to us that possesses the main characteristics of the new genus Cordibia. However, it is larger than C. pumila (maximum n:d value 32:17×22 mm), possesses much longer major septa in the immature growth stage, is more strongly amplexoid, has minor septa shorter in comparison to both the length of the major septa and the width of the dissepimentarium, and its axial structure in the transverse section is more irregular and weaker than C. pumila. Those differences and the much earlier occurrence of C. pumila in the stratigraphic column suggests it may be ancestral to 'D.' cylindricum.

OCCURRENCE: Left bank of circumferential channel near Starobeshevo power plant. Limestone E_1^{up} and underlying mudstone and marly limestone, Limestone E_1^1. Reticuloceras-Bashkortoceras Zone.

CONSIDERATIONS

Growth form is consistent in the overwhelming majority of the Rugosa and is generally accepted as an important diagnostic character at the generic level. Specimens of some solitary taxa can produce either lateral or peripheral offsets (see the Nomenclatorial note above) becoming protopolyps in a general sense. Offsets of such protopolyps either die at a very early growth stage or continued to grow long enough to develop morphological features characteristic of the early mature growth stage of a protopolyp. However, such offsets do not reach diameters, numbers of septa and other morphological features characteristic of their parental polyps, and are incapable of offsetting a third generation of polyps. Thus true colonies are never initiated by these protopolyps. Fedorowski (1978) introduced the term "lost structures" to distinguish between the offsets capable of reproduction and

those that cannot. Intriguingly, a process of formation of the lost structures is identical to that culminating in fully maturated clones in regular colonies. The ability of some polyps of otherwise solitary species to offset but the inability of their progeny to produce their own clones is considered genetically controlled (Fedorowski 1978 and here). That interpretation is proven by the offsetting of many "lost structures" in a given species, but mechanism of that genetic control remains unknown.

Two ways of offsetting were observed in protocorallites producing lost structures: lateral and peripheral. Both of those ways also are known in fully developed colonies, and both were discussed by Fedorowski and Jull (1976), who interpreted and/or introduced some ideas used in this discussion. Lateral offsetting is more obvious and is better known in the protocolonies because of the early description of the new genus and species "Craterophyllum" verticillatum by Barbour (1911). Cordibia pumila offsets in the lateral manner.

Peripheral offsetting was first discussed in detail by Fedorowski (1970) who informally introduced the name protocolony (p. 603), re-introduced here in a formal manner. He pointed to several details characteristic of that type of coloniality in the Rugosa. He also compared his colony, Spirophyllum geminum Fedorowski, 1970, to those of some fully colonial specimens of Lithostrotion sp. of Jull (1965) from the Lower Carboniferous of Australia. Fedorowski (1970, p. 603) suggested a similarity and possible relationship between those two taxa, but eventually left that question open. Now we realize that these two species are similar only in having peripheral offsetting and that there is no faunal relationship between the two taxa. Fedorowski and Jull (1976, p. 47) considered peripheral increase as being a "multiple form of rejuvenation" and we agree with that interpretation. It is characteristic for some genera, but may also appear to be a polyp's response to unfavourable extrinsic factors. Moreover, it may appear in laterally offsetting colonies, as those in the Australian "Lithostrotion" mentioned above. Such an incidental appearance in regular colonies has not yet been interpreted.

The growth form of the here described specimens, intermediate between the solitary and the fully colonial ones, is especially intriguing when the occurrence at the same time and in the same province of solitary Dibunophyllum is taken in mind. Morphologically similar, typical, solitary dibunophylla both slightly older and of the same age occur in the Donets Basin. Some were described by Vassilyuk (1960) as Dibunophyllum finalis the others will be described in a detailed study by the senior author later. Also, morphologically similar, small

and simple dibunophylla occur in the Bug River Basin (eastern Poland) (Fedorowski and Musiał, in preparation). Those non yet described corals rather than *D. finalis* with its highly simplified axial structure and much larger size should be considered as related to *C. pumila*. This question is not developed here in order to avoid an inclusion of *nomina nuda*. The close morphological similarity, geographic co-occurrence and restriction to the Donets Basin suggest that *Cordibia pumila* is perhaps endemic and that it was derived either from one of the Donets Basin or other eastern/central European species of *Dibunophyllum*.

Acknowledgements

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