

Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 7. The Family Neokoninckophyllidae Fomichev, 1953, with a preliminary revision of Moscovian taxa

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ABSTRACT:

Fedorowski, J. 2019. Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 7. The Family Neokoninckophyllidae Fomichev, 1953, with a preliminary revision of Moscovian taxa. *Acta Geologica Polonica*, **69** (1), 51–87. Warszawa.

The Family Neokoninckophyllidae and its type genus *Neokoninckophyllum* Fomichev, 1939 (type species: *N. tanaicum* Fomichev, 1939) are discussed and emended. In addition, the genera *Orygmophyllum* Fomichev, 1953 and *Yuanophylloides* Fomichev, 1953, originally included in the Families Campophyllidae Wedekind, 1922 and Lophophyllidae Grabau, 1928, respectively, are emended as well and transferred to the Neokoninckophyllidae. Two early Bashkirian species, viz. *Yuanophylloides rectus* (Vassilyuk in Aizenverg *et al.*, 1983) and *Y. inauditus* (Moore and Jeffords, 1945), and the Moscovian *Neokoninckophyllum* sp. nov. are described on the basis of new collections from the Donets Basin. *Neokoninckophyllum tanaicum*, *Yuanophylloides gorskyi* Fomichev, 1953 (both Moscovian in age) and *Y. cruciformis* Fomichev, 1953 (latest Bashkirian), are redescribed on the basis of peels taken from Fomichev's (1953) type specimens. Derivation of the Family Neokoninckophyllidae from the Subfamily Dibunophyllinae Wang, 1950 is postulated and phylogenetic links within the former are hinted at. The occurrence of *Yuanophylloides inauditus* in both the Donets Basin and the Western Interior Province of North America points to marine communication between those areas during the Bashkirian. The slightly earlier appearance of the oldest neokoninckophyllids in the Donets Basin, in comparison to North America (i.e., R₁ vs R₂ ammonoid biozones), documents the common roots and monophyletic development of the Neokoninckophyllidae in both areas.

Key words: Carboniferous (Pennsylvanian); Neokoninckophyllidae; Emendation; Phylogeny; Palaeogeographic implications.

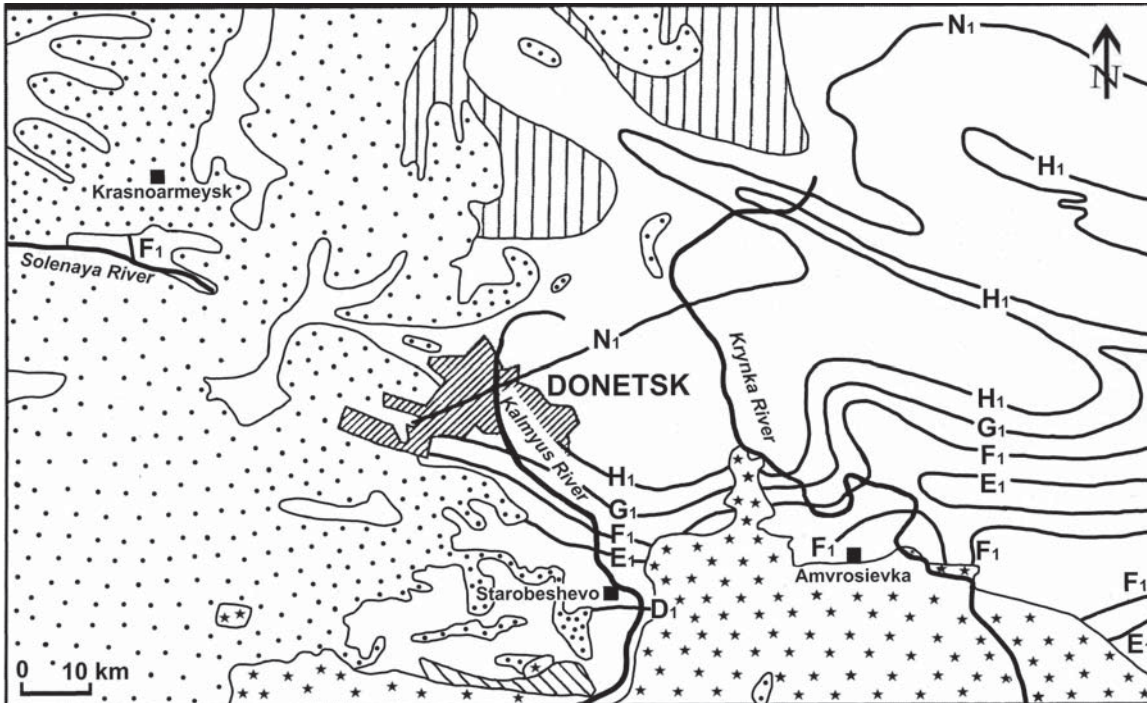
INTRODUCTION

Large, solitary, dissepimented Pennsylvanian rugose corals are common in several areas across the globe. Unfortunately, their diagnostic characters are weakly accentuated in many species and there is a great morphological similarity to Mississippian taxa. This has resulted in advanced subjectivity as far as taxonomic identifications at the species, genus and even family levels are con-

cerned (for details, see discussions below). The early Bashkirian Rugosa from the Donets Basin described in the present paper belong to this ambiguous group of corals. Diagnostic features resemble characteristics of four genera that have been recorded from that basin and assigned by Fomichev (1953) to three families, namely Campophyllidae Wedekind, 1922, Lophophyllidae Grabau, 1928, and Neokoninckophyllidae Fomichev, 1953. Those characteristics are incompatible with diagnoses of



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



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

the first two families as emended by Hill (1981), but are comparable to each other and match the diagnosis of the Family Neokoninckophyllidae. This discrepancy requires a comprehensive discussion, which is supported by new data wherever possible. Thus, the present paper is devoted mostly to discussions and preliminary emendations of the best-documented taxa. Those emendations, necessary for identifications of early Bashkirian specimens from the Donets Basin, are based on Fomichev's (1953) descriptions and illustrations, as well as on peels taken from his original material.

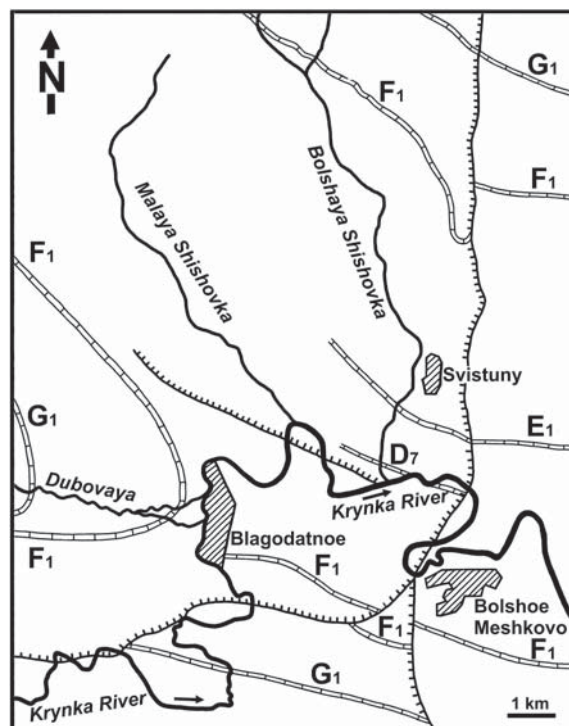
Following Hudson (1936) and Fedorowski (1997) only the cardinal and the counter major septa are considered as the protosepta that are derived from the axial protoseptum. As in my earlier papers, the term 'primary septa' used here refers to the innermost parts of septa, created within septal pockets prior to secretion of the sclerenchymal sheets. Such primary septa are described in the present paper under the microstructure of septa.

In order to avoid repetitions of the phrase "in Russian alphabet", all mentions of illustration numbers in cyrillic letters follow the original dictionary arrangement of that language (e.g., "v" follows "b" etc.).

Corals described in the present paper are housed in the collections of the Institute of Geology, Adam Mickiewicz University in Poznań (Poland) and bear the acronym UAM-Tc.Don.1. Specimens from Fomichev's collection are housed in the CNIGR Museum, Saint Petersburg, Russia, and bear the Museum collection number 5030.

GEOLOGICAL SETTING

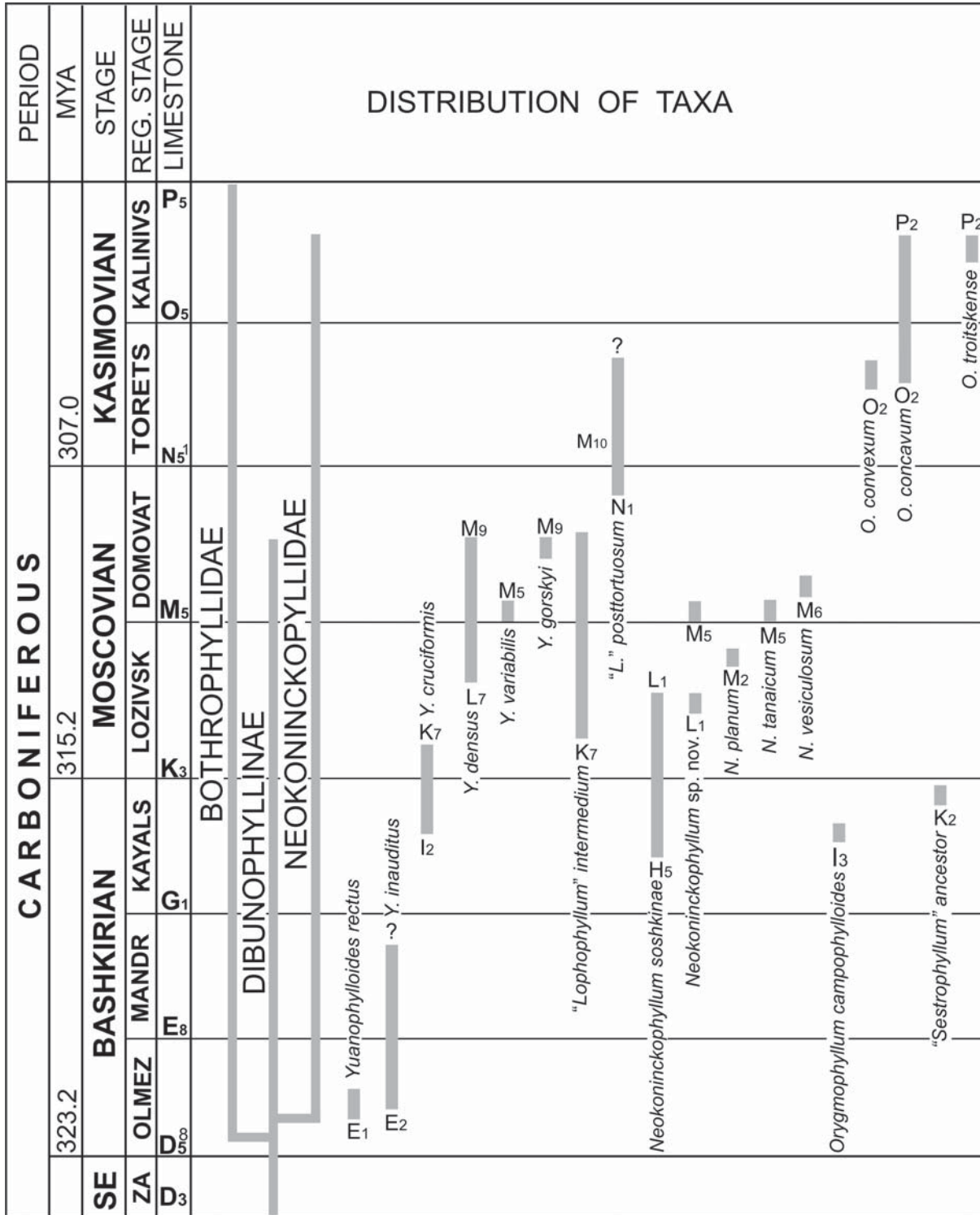
For an overview of the history of the Bashkirian Stage and its faunal content, reference is made to Fedorowski (2009). Poletaev *et al.* (2011) summarised the faunal content and provided numerous historical details on Mississippian, Pennsylvanian and lower Permian (Cisuralian) stratotypes in the Donets Basin. The comprehensive compendium edited by Gozhyk (2013) supplements the data summarised by Poletaev *et al.* (2011). A detailed description of the most important new locality of lowermost Bashkirian strata (at the Berestovaya River mouth) was published by Fedorowski and Ogar (2013). Some additional details concerning lower Bashkirian strata were discussed by Fedorowski (2017a). The stratigraphic position and geological context of all lower Bashkirian specimens described below can



Text-fig. 3. Outcrops east of the town of Donetsk. Krynka River Area. Tectonically affected Limestones D to G. (Provided by Dr. N.P. Vassilyuk, copied from Fedorowski 2009)

be referred to data available from the papers cited, making repetitions unnecessary. Text-figs 1–3 illustrate the provenance areas of the Bashkirian specimens recorded here.

Since the present paper is not a formal revision of Fomichev's (1953) taxa, reference is made to the papers listed above for details. However, it should be stated here that Poletaev *et al.* (2011) characterised the Moscovian strata as a single megacycle, divided into two cycles: Lozivskian and Domatovskian (Text-fig. 4), called Regional Stages. The megacycle started with Limestone K₃ and terminated with Limestone N₅⁰. The deposits encompassed are mostly terrigenous with sandstones prevailing. Limestone intercalations of both the K and M groups are numerous, yet thin (Poletaev *et al.* 2011, figs 17–20). However, they yield a diverse rugose coral fauna that becomes impoverished near the Moscovian/Kasimovian boundary (Fomichev 1953, appendix). The limestone intercalations of groups N and O decreased in number during deposition of Kasimovian strata, whereas the number and thickness of terrigenous levels with megafloal remains increased (Poletaev *et al.* 2011, figs 23–26).



Text-fig. 4. Derivation of Bothrophyllidae and Neokoninckophyllidae from Dibunophyllinae and distribution of taxa included herein in the Neokoninckophyllidae. Only ranges of described and/or revised taxa considered; may change when complete material is restudied. Letters with numbers at distribution lines – indices of Limestones. Abbreviations: Domat – Domatovskian; Kalinivs – Kalinivskian; Kayalsk – Kayalskiyan; “L.” – “Lophophyllum”; Lozivsk – Lozivskian; Mandr – Mandrikinskian; MYA – million of years ago; Olmez – Olmezivskian; Torets – Toretskian; N. – Neokoninckophyllum; SE – Serpukhovian; Y. – Yuanophylloides; ZA – Zapaltyubinskian. Radiometric ages after Menning et al. (2006)

MATERIAL AND METHODS

The specimens studied were collected by Dr. Nina P. Vassilyuk (Professor Emeritus of the Donetsk Polytechnic, Ukraine) during many years of field campaigns. They have been offered to me for study and repository. The specimens were originally labelled by Dr. Vassilyuk according to the indices of the limestone units from which they were collected. Thus, these limestone indices, used for many decades, have priority over horizons and suites. The limestone indices are supplemented by data derived from Nemyrovska's paper (1999) and from the stratigraphical summaries by Poletaev *et al.* (2011) and Gozhyk (2013).

As noted in the introduction, the brief redescrptions of and/or discussions on Fomichev's (1939, 1953) species are based on peels taken from his original material. However, numerous specimens listed by Fomichev (1953) when referring to occurrences of particular species, were not illustrated by him. In addition, many of those unfigured specimens were not available for peeling at the time of my restudy of his collection in 1969. Identifications of specimens that are not documented either by reliable illustrations (as published by Fomichev 1953) or by peels are treated here as not ascertainable and their stratigraphical data are not taken into account. Thus, the ranges of Fomichev's (1953) species, as listed by him, commonly differ from those indicated here in Text-fig. 4. The table refers solely to the stratigraphical positions of those specimens revised or at least discussed in the present paper. By doing so, quite a few of the specimens listed by Fomichev (1953) are omitted. However, this also does away with all doubts over the identifications and stratigraphical positions of specimens not studied in detail by Fomichev (1953) and not checked for the present paper.

All rugose corals described below are worn, fragmentary and/or slightly eroded during transport. In addition, they were subject to diagenetic changes following deposition which led to recrystallization precluding reliable reconstructions of the microstructure of septa. The external surfaces of some specimens, including those first investigated by Fomichev (1953), are corroded, and the skeletons of some others are deformed by sediment compaction.

Traditional methods of thin sectioning, peeling and polishing have been applied in most instances. Characters that could not be adequately demonstrated in the images have been supplemented by computer drawings based on high-magnification images.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
 Order Stauriida Verrill, 1865
 Suborder Aulophyllina Hill, 1981
 Family Neokoninckophyllidae Fomichev, 1953

GENERA INCLUDED: *Lophophyllum* Fomichev, 1953 non Milne Edwards and Haime, 1850, *Neokoninckophyllum* Fomichev, 1939, *Orygmophyllum* Fomichev, 1953, *Yuanophylloides* Fomichev, 1953.

EMENDED DIAGNOSIS: Solitary, dissepimented rugose corals; axial septum invariably present early in ontogeny, commonly divides into cardinal and counter septa during maturity; counter septum commonly elongated, may form monoseptal pseudocolumella; axial structure weak and irregular; may disappear in advanced maturity; rare septal lamellae may occur early in ontogeny; axial column absent; sclerenchymal sheets, when present, not differentiated distinctly in thickness by quadrants; tabularium normal, distabularium common.

REMARKS: For two reasons, emendation of the original diagnosis of the family (Fomichev 1953, p. 351) is called for. First, it had a descriptive character, listing some data that are not important for a family and, secondly, in view of the new content, as proposed herein. The latter, which is supported by a revision of the type genus *Neokoninckophyllum* Fomichev, 1939, differs considerably from the original concept. In turn, this revision allows many Pennsylvanian rugose coral taxa from Europe, Asia and North America to be taken into account, either as members or relatives of that family. The corals matching the new diagnosis are currently included in different genera and families, despite the fact that they reveal various combinations of similar morphological characters. Their taxonomic status is burdened by the subjective attitude of several authors to diagnoses of the various genera (see discussion on genera and synonyms of names below). This is complicated further by the common application of generic names of Mississippian taxa from western Europe to Pennsylvanian genera from elsewhere. As a result, over twenty generic names were used for species that potentially belong to the Family Neokoninckophyllidae, whereas only four genera are actually included herein in that family. The family content, as established here, is certainly incomplete as hinted at below. However, no new generic names are introduced, in spite of the fact that such are needed. I subscribe to the view that only

Genus	Neanic growth stage	Axial septum	Axial structure	Cardinal septum	Dissepiments	Remarks
<i>Neokoninckophyllum</i>	bilateral	lasting to early maturity	permanent with pseudocolumella	varies in length	herringbone, angular, lateral, grape-like, lonsdaleoid	perhaps two genera
			reduced in maturity	?shortened		
<i>Yuanophylloides</i>	bilateral	lasting to advanced maturity, interrupted	permanent, very simple, only axial septum in most species	varies in length or long	regular, herringbone, lonsdaleoid in some species	
“ <i>Lophophyllum</i> ”	bilateral	lasting to early maturity	simple, reduced in maturity	shortened	regular, herringbone	new genus or subgenus
<i>Orygmophyllum</i>	rotiphyllid	restricted to neanic growth stage	simple, interrupted, reduced in maturity	shortened	herringbone, grape-like, rare lateral	

Table 1. Distinguishing morphological characters of the genera *Neokoninckophyllum* Fomichev, 1953, *Yuanophylloides* Fomichev, 1953, *Orygmophyllum* Fomichev, 1953 and *Lophophyllum* Fomichev, 1953 non Milne Edwards and Haime, 1850

taxa supported by a complete analysis of the most important growth stages should be named.

The nomenclatorial confusion surrounding taxa that potentially belong to the Family Neokoninckophyllidae was added to by Fomichev (1953), who firstly included morphologically similar and most probably related corals into three different families, viz., Campophyllidae, Lophophyllidae and Neokoninckophyllidae. Secondly, he assigned unrelated genera to the Family Neokoninckophyllidae, and thirdly, his species content of *Neokoninckophyllum* Fomichev, 1939 was misleading. As a result, the Family Neokoninckophyllidae was subsequently synonymised with the Subfamily Dibunophyllinae (Hill 1981). This synonymy is rejected here and the full family status of the Neokoninckophyllidae is accepted and reinstated herein.

Fomichev’s (1953) views on the families Campophyllidae and Lophophyllidae and his application of the name *Lophophyllum* Milne Edwards and Haime, 1850 for dissepimented corals conflicts with recent interpretations of those taxa and is rejected here. Also, Hill (1981) restricted the Family Campophyllidae to a single Famennian genus, *Campophyllum* Milne Edwards and Haime, 1850, while the Family Lophophyllidae and the genus *Lophophyllum* exclusively comprise non-dissepimented rugose corals (see Hill 1981, pp. F306 and F333, respectively). Her emendations are followed in the present paper.

The taxonomic content of the Family Neokoninckophyllidae, as suggested by Fomichev (1953), requires comments that are more comprehensive than those concerning the families mentioned above. In addition to *Neokoninckophyllum*, the following genera were originally included by Fomichev (1953) in the Neokoninckophyllidae: *Caninella* Gorskiy, 1938, *Carinthiaphyllum* Heritsch, 1936, *Corwenia* Smith and Ryder, 1926, *Dibunophylloides* Fomichev, 1953, *Histiophyllum* Thomson, 1879, and *Sestrophyllum* Fomichev, 1953. None of these genera is accepted here as being directly related to *Neokoninckophyllum*.

Caninella, redescribed and reillustrated recently by Kossovaya *et al.* (2016), remains inadequately known because its early ontogeny has not been studied. The morphology of its mature growth stage tends towards the Family Bothrophyllidae, rather than the Neokoninckophyllidae. The early Permian genus *Carinthiaphyllum* has already been transferred to the Family Geyerophyllidae Minato, 1955 (Hill 1981, p. F407), a position accepted here. Based on the type species of *Corwenia*, i.e., *Lonsdaleia rugosa* McCoy, 1849, the genus is generally accepted as a fasciculate colonial Dibunophyllinae. However, only species that match exclusively the generic diagnosis (as based on the type species) belong to *Corwenia*. Some species placed in *Corwenia* by subsequent authors who had a subjective attitude to the genus in not properly considering the fundamental features of its diagnosis,

were excluded from *Corwenia* in my previous paper (Fedorowski 2017b).

Histiophyllum from the Viséan of Great Britain was synonymised with *Dibunophyllum* (Hill 1938–1941, p. 65), a view adopted here. However, “*H.*” *mediocarbonicum* Fomichev, 1953 is morphologically distant from that early Carboniferous taxon. Instead, it closely resembles *Neokoninckophyllum* in the morphology of the dissepimentarium, but differs from that genus in the occurrence of a *Dibunophylloides*-like axial structure that lasts up to the early mature growth stage (Fomichev 1953, pl. 26, fig. 8a; Text-fig. 5C herein). Whether that character suggests any close relationship to *Dibunophylloides* or should be classified as a homoeomorphy, remains to be determined (see also Considerations below). *Dibunophylloides* has recently been revised (Fedorowski 2017b); it is included in the Subfamily Dibunophyllinae. The indisputably solitary growth form of *Cyathoclisia symmetrica* Dobrolyubova, 1937, the type species of the genus, has been confirmed, settling the matter.

From the remarks above, it would appear that the Family Neokoninckophyllidae is monotypical, with “*Histiophyllum*” potentially belonging to it. However, revision of *Neokoninckophyllum tanaicum* Fomichev, 1939, the type species of the type genus, enables emendation of the generic diagnosis, as well as a much wider family content. The emended diagnosis of the family, as compiled from the main qualitative features of the type genus, allows the genera *Lophophyllum* Fomichev, 1953 non Milne Edwards and Haime, 1850 and *Orygmophyllum* Fomichev, 1953 to be transferred to it. Some specimens of *Sestrophyllum? ancestor* Fomichev, 1953 (see below for details) belong to that family as well.

In addition to the taxa from the Donets Basin mentioned above, many species (described under various generic names) from China and the United States (see below) are potential members of the family Neokoninckophyllidae, as are Gen. et sp. indet. 1 and 2 of Rodríguez (1984), *Skoleckophyllum triseptatum* Boll, 1985 and *Caninia ornata* Fomichev, 1953 of Boll (1985), all from the Pennsylvanian of Spain. The same holds true for *Neokoninckophyllum nipponense* Kato, 1959 from Japan and *Koninckophyllum ingavatae* Sugiyama in Sugiyama and Toriyama, 1981 from Thailand. However, detailed analyses of those taxa are beyond the scope of the present paper. Representatives of the Family Neokoninckophyllidae in North America are hidden under such generic names as *Dibunophyllum*, *Koninckophyllum*, *Neokoninckophyllum*, *Pseudozaphrentoides* and *Rhodophyllum* (e.g., Newell 1935; Moore and Jeffords

1945; Jeffords 1948; Ross and Ross 1962, 1963; Nations 1963; Rowett and Sutherland 1964; Cocke 1970; Cocke and Haynes 1973; Cocke and Molinary 1973). Again, detailed analyses of these North American genera are beyond the scope of the present paper. Merely the following features are noted here: 1. an axial septum occurs in all species included in those “genera”, and lasts at least to the late neanic growth stage or longer; 2. a continuous axial column is absent from the longitudinal sections of all those taxa, whereas that character is invariably present along the entire post-brephic ontogeny of all species of *Dibunophyllum* proper; 3. the differentiation by quadrants of the sclerenchymal thickening of major septa in the tabularium, typical of the Bothrophyllidae Fomichev, 1953 and some Cyathopsidae Dybowski, 1873, does not occur in those corals; 4. their dissepimentaria developed into two directions, both present in the Neokoninckophyllidae: a) the dominating variant characterised by a dissepimentarium that is loose and simple, with common small lonsdaleoid dissepiments, b) the rarely occurring variant with a very complex dissepimentarium, containing lateral and grape-like dissepiments¹. All four characters listed above point to the Neokoninckophyllidae. Some combinations of these characters suggest that new genera need to be erected; for the reasons outlined above, this is deferred to another occasion.

Potential members of the Family Neokoninckophyllidae are common in the Pennsylvanian strata of China. Unfortunately, the data available from the literature are commonly misleading. The monograph by Wu and Zhao (1989) is here briefly discussed as an example. The following taxa described by those authors are potential members of the Family Neokoninckophyllidae (all cited illustrations refer to that paper): *Complanophyllum densum* Wu and Zhao, 1989 (pl. 3, fig. 5a, b), *Bothrophyllum longiseptatum concentricum* Wu and Zhao, 1989 (pl. 7, figs 4a–e, 8a, b), *Timania damiauensis* Yu, 1980 (pl. 7, fig. 5a, b), *Timania planotabulata* Wu and Zhao, 1989 (pl. 8, fig. 4a–d only), *Bothroclisia sinensis* Wu and Zhao, 1989 (pl. 9, figs 8a, b, 9a–c, 11, 12a, b), *Eostrotion equiseptatum* Wu and Zhao, 1989 (pl. 22, figs 3a, b, 4a, b), *Yuanophylloides elegans* Wu and Zhao, 1989 (pl. 22, fig. 11a–e), and *Dibunophylloides irregularis* Wu and Zhao, 1989 (pl. 23, fig. 1a, b). The main characteristics of almost all species that were included in

¹ The term in English has been introduced by Fedorowski (2017b) for very small dissepiments, attached to septa at the corralite periphery in a way that imitates bunches of grapes.

the genera listed above conflict with their diagnoses. Only *Yuanophylloides elegans* matches the diagnosis of *Yuanophylloides* as emended here. However, that identification is only weakly supported and in need of a more comprehensive study.

The genus *Parazaphrophyllum* Wu and Zhao, 1989, originally placed in the Family Bothrophyllidae, bears some features that are characteristic of the Neokoninckophyllidae. However, it is not included in that family because of its provenance from the Bojiwan Formation of late Tournaisian–early Viséan age, its morphology that is more complex than that of its potential Bashkirian descendants and the fasciculate colonial growth form (Wu and Zhao 1989, p. 197), unlikely to give rise to solitary descendants.

The following generic names have been applied in the world's literature to species potentially belonging to the Family Neokoninckophyllidae (in alphabetic order): *Amandophyllum* Heritsch, 1941; *Arctophyllum* Fedorowski, 1975; *Bothroclisia* Fomichev, 1953; *Bothrophyllum* Trautschold, 1879; *Caninella* Gorskiy, 1938; *Caninia* Michelin in Gervais, 1840; *Caninophyllum* Lewis, 1929; *Carinthiaphyllum* Heritsch, 1936; *Complanophyllum* Wu and Zhao in Wu *et al.*, 1981; *Corwenia* Smith and Ryder, 1926; *Dibunophylloides* Fomichev, 1953; *Dibunophyllum* Thomson and Nicholson, 1876; *Eostrotion* Vaughan, 1915; *Gshelia* Stuckenberg, 1888; *Histiophyllum* Thomson, 1879; *Koninckophyllum* Thomson and Nicholson, 1876; *Lophophyllum* Milne Edwards and Haime, 1850; *Neokoninckophyllum* Fomichev, 1939; *Orygmophyllum* Fomichev, 1953; *Pseudozaphrentoides* Stuckenberg, 1904; *Rhodophyllum* Thomson, 1875; *Sestrophyllum* Fomichev, 1953; *Timania* Stuckenberg, 1895; and *Yuanophylloides* Fomichev, 1953 (see also synonyms and remarks to genera).

There is no need for detailed discussions of the genera listed above making reference to their type species as the fundamental source of diagnostic data. It is sufficient to make reference to Hill (1981) in order to establish that the characters of those genera do not match the diagnostic features of the Family Neokoninckophyllidae. For that reason, only selected genera and species, accepted here as members of that family, are briefly revised or discussed.

Genus *Neokoninckophyllum* Fomichev, 1939

(Type species *Neokoninckophyllum tanaicum* Fomichev, 1939; by subsequent designation of Fomichev 1953, p. 354).

SPECIES INCLUDED: *N. tanaicum* Fomichev, 1939; *N. soshkinae* Fomichev, 1953; *N. vesiculosum*

Fomichev, 1953; *N. planum* Fomichev, 1953; *Neokoninckophyllum* sp. nov.

EMENDED DIAGNOSIS: Neokoninckophyllidae with major septa amplexoid; in neanic growth stage major septa bilaterally arranged; axial septum in mature growth stage divided into cardinal and counter septa; counter septum commonly elongated, may form lath-like pseudocolumella in weak axial structure; rare septal lamellae occur at least in immature growth stage; length of cardinal septum commonly varies due to its amplexoid character; cardinal fossula indistinct or absent; dissepimentarium complex, grape-like at periphery with lateral dissepiments common and small lonsdaleoid dissepiments sporadic; tabularium normal, disstabularium common.

REMARKS: On several occasions, the generic name *Neokoninckophyllum* has been applied to a number of species of rugose corals (e.g., Moore and Jeffords 1945; Kato 1959; Nations 1963; Cocke 1970; Fedorowski 1971; Cocke and Haynes 1973; Cocke and Molinary 1973; Degtyarev 1979; Yu 1980; Yu and Zhu 1988; Yu in Fan *et al.* 2003). Most of the species described in those papers may possibly be included in the Family Neokoninckophyllidae. However, only *N. aff. tanaicum* Degtyarev, 1979 meets the three main criteria of the genus *Neokoninckophyllum*, established here on the basis of Fomichev's (1953) illustrations and descriptions, supplemented by images of peels taken from his original specimens. These data are completed by thin sections and peels taken from two Moscovian specimens from the Donets Basin available to me from Dr. Vassilyuk's collection.

The elongation of some major septa in the type species (Fomichev 1953, pl. 24, fig. 3b, v, g) vs the consistent presence of isolated septal lamellae is the first criterion. A comparison of three successive transverse sections of the holotype documents the amplexoid character of the major septa and suggests that, most probably, septal lamellae in the mature growth stage of that specimen were absent. However, septal lamellae occur in its early ontogeny (Fomichev 1953, pl. 24, fig. 3b), as they do in the early growth stage of *Neokoninckophyllum* sp. nov. (Text-fig. 6A, B), in which they are recognised as short protuberances of the pseudocolumella in the mature growth stage of that specimen (Text-fig. 6G). The bodies that are attached to sections of tabulae in the axial structure of another specimen of *Neokoninckophyllum* sp. nov., i.e., a topotype associated with the holotype of *N. tanaicum*, are also septal lamellae. They occur in the axial structure beneath the calice floor and continue

Species	Major septa	Minor septa	Cardinal septum	Counter septum	Axial structure	Median lamella	Dissepimentarium	Lateral dissepiments	n:d value [mm]	Limestone
<i>tanaicum</i>	3/4 corallite radius	≈1/2 dissepimentarium	amplexoid variable	elongated	weak continuous	commonly free	< 1/2 corallite radius	numerous	38-39:33-35	M-5
<i>soshkinae</i>	4/5 corallite radius	≈1/2 dissepimentarium	shortened	slightly elongated	simple discontinuous	discontinuous or reduced	2/3 corallite radius	almost absent	38-40:24-30	K-7 L-1
<i>planum</i>	≈1/2 corallite radius	1/3-1/2 dissepimentarium	= major septa	= major septa	absent	absent	1/3 corallite radius	very numerous	34:22.5	M-2
<i>vesiculosum</i> (holotype)	≈3/4 corallite radius	1/3-1/2 dissepimentarium	slightly shortened	elongated	weak continuous	joins counter septum	< 1/2 corallite radius	numerous	30-33:15-17	M-7
<i>vesiculosum</i> (small corallites)	≈3/4 corallite radius	1/3-1/2 dissepimentarium	slightly shortened	elongated	weak continuous	joins counter septum	≈ 1/2 corallite radius	rare	32:12.5	M-6
<i>sp. nov. 1</i>	≈2/3 corallite radius	enter tabularium	variable	elongated	weak continuous	free	1/3 corallite radius	rare	32:27	M-5
		reach tabularium	= major septa	= major septa					32:21	L-1

Table 2. Distinguishing mature morphological characters of *Neokoninckophyllum* species. Only ranges of described and/or revised taxa considered; may change when complete material is restudied. Data for *N. planum*, *N. soshkinum* and *N. vesiculosum* (proper and small corallites) compiled on the basis of Fomichev's (1953) descriptions and illustrations

in that structure to be elevated well above the calice floor (Text-fig. 7A, E, respectively). Thus, the presence of rudiments of septal lamellae is possible not only in the early ontogeny of *Neokoninckophyllum*, but also in the mature corallites of that genus. Such a skeletal structure is of special value for assessment of the relationships of the Family Neokoninckophyllidae (see Considerations below).

The inconsistent length of the cardinal septum in the holotype and in some paratypes of *N. tanaicum* is the second feature to be mentioned. In one transverse section of the holotype and in the sole transverse section of one of the paratypes illustrated (Fomichev 1953, pl. 24, figs 3g, 4), the length of the cardinal septum equals that of the adjacent major septa, whereas in two remaining transverse sections of the holotype (Fomichev 1953, pl. 24, fig. 3b, v) it is slightly shorter. A similar inconsistency is observed in the more completely preserved specimen described here as *Neokoninckophyllum* sp. nov. The shortened cardinal septum occurs in the early mature growth stage of that specimen (Text-fig. 6D), whereas it is almost indistinguishable from adjacent major septa in the advanced mature growth stage and in the lower part of the calice (Text-figs 6H, I; 7G). The cardinal septum in the second specimen, provisionally referred to that unnamed species, is shortened beneath the section of the tabula (Text-fig. 7A) and is short just above the calice floor (Text-fig. 7B). The shortened

cardinal septum occurs in individual transverse thin sections of some paratypes of *N. tanaicum* and in some "varieties" of that species (Fomichev 1953, pl. 23, figs 6a, 8a; pl. 24, fig. 10; Text-fig. 5A, B, corallite 'a' herein). However, it equals adjacent major septa in other thin sections illustrated by Fomichev (1953, pl. 24, figs 4, 7b). Data available to date are inadequate for a firm decision, but allow the following to be stated: 1. The variable length of the cardinal septum may result from its amplexoid character. Thus, its permanently great length may be apparent, resulting from random sections made above tabulae. The variable length, i.e., the amplexoid character of the cardinal septum is established in the holotype of the type species of *Neokoninckophyllum*, but that character is much weaker in other species. The cardinal septum may be shortened in *N. soshkinae* but the material restudied is inadequate for a firm solution. Thus, the variable length of the cardinal septum is typical of the type species, but not of the genus. 2. Shortening of the cardinal septum in the calice, high above the last tabula inserted, cannot be considered diagnostic until its non-amplexoid character has been documented, i.e., its shortening in a transverse section both above and beneath a tabula has been proven. 3. In some specimens, the amplexoid character of the cardinal septum may be more accentuated in an early mature growth stage of a corallite than in its advanced mature growth stage as documented above

(Text-figs 6A–H; 7G), but this is not true for most specimens investigated. The collection available for the present study does not allow a firm decision, but a variation in the length of the cardinal septum is provisionally accepted as being typical of the genus *Neokoninckophyllum*. However, its permanent shortening in the mature growth stage of some species (e.g., *N. soshkinae*) is possible.

The morphology of the dissepimentarium is the third important character of this genus. In the holotype of the type species and in all species closely comparable to the type species in morphology, the dissepimentarium constitutes a very complex net composed of various dissepiments: pseudo-herringbone, flat, concave, grape-like, lateral and and lonsdaleoid. The peripheral part of the dissepimentarium is invariably occupied by pseudonaotic structures and/or grape-like dissepiments. In addition, rare and small lonsdaleoid dissepiments may occur (Fomichev 1953, pl. 23, fig. 8a; Text-figs 5D, 7D herein). Thus, only specimens with a complex dissepimentarium are here considered to be members of *Neokoninckophyllum*.

Two new species introduced by Fomichev (1953) do not match the emended diagnosis of *Neokoninckophyllum* and are here excluded from that genus. *Neokoninckophyllum stepanovi* possesses a simple dissepimentarium and is here transferred to the genus *Yuanophylloides*, whereas ?*N. antipovi* from Limestone O₅ is excluded from the genus *Neokoninckophyllum* and the Family Neokoninckophyllidae. Specimens included in that species are morphologically variable and poorly preserved. Two of them (Fomichev 1953, pl. 25, figs 6a–v, 8a, b) resemble *Gshelia* Stuckenberga, 1888 rather than *Neokoninckophyllum* and belong perhaps to the former. The preservation of a third specimen (Fomichev 1953, pl. 25, fig. 7) is too poor to be assigned taxonomically.

The morphology of the dissepimentarium is rarely considered as diagnostic in taxa of supraspecific levels. However, an overview of potential members of the Family Neokoninckophyllidae as based on various criteria, documents the morphology of the dissepimentarium as a character that is important for differentiating some genera within that family. The dissepimentarium is very complex in the type species of the genus *Neokoninckophyllum* and in most of Fomichev's (1953) species included in that genus (see list above). In addition, it is complex in all species described by Fedorowski (1971) and Degtyarev (1979) and in *Neokoninckophyllum kansasense* (Miller and Gurley, 1893) of Cocke (1970). However, it is simple in all species described in the remaining papers listed in the first paragraph of these re-

marks. Most of those species may belong to the family Neokoninckophyllidae, but none of them can be assigned to the emended genus *Neokoninckophyllum*. Some of them are briefly discussed below under the genus *Yuanophylloides*. The species described by Fedorowski (1971) from the upper Viséan (Brigantian) strata of the Holy Cross Mountains in Poland and by Degtyarev (1979) from the Moscovian strata of the Urals in Russia, are briefly commented below because they have some value for the present paper. The remaining species described from outside of the Donets Basin are not discussed.

Polish specimens are the only taxa of the *Neokoninckophyllum*-like morphology known from the upper Viséan strata of the Western European Province. Thus, they are mentioned here as potential ancestors of neokoninckophyllids. Four species were identified, viz., *N. tanaicum* Fomichev, 1939, *N. soshkinae* Fomichev, 1953, *N. multiseptatum* Fedorowski, 1971 and *N. trifossulum* Fedorowski, 1971. The mature morphology of specimens assigned to Fomichev's (1939, 1953) species resembles that of the Donets Basin species in several characters. Only the dissepimentaria in the Polish species are less complex. The immature portions of the specimens referred to those two species are missing. However, the early ontogeny of the other species has been studied starting from the very early neanic growth stage and a strong axial septum has been well documented in both (Fedorowski 1971, fig. 42A, D_{2–6}; fig. 43A_{2–4}, C₃). The thin median lamella more closely connected to the cardinal than to the counter septum in the mature growth stage and the incomplete axial column present in the longitudinal section of *N. multiseptatum* (Fedorowski 1971, figs C, E, F_{1, 2, 4}) constitute the main distinguishing characters. The occurrence of alar fossulae, dipping slightly into the dissepimentarium, the thickening of the major septa in the tabularium and the minor septa that intersect the dissepimentarium in the late neanic/early mature growth stage are the prime differential characters of *N. trifossulum* (Fedorowski 1971, fig. 44A₁, B₁, C_{1, 2}). Two Polish species (*N. multiseptatum* and *N. trifossulum*) are here excluded from the genus *Neokoninckophyllum* and from the Family Neokoninckophyllidae on the basis of their morphological differences. All four Polish species are excluded from those Donets Basin taxa on the basis of palaeogeographic distribution (see Considerations below). Their taxonomic assignment is uncertain, but this matter is beyond the scope of the present paper.

Species from Moscovian strata in the southern Urals (Bashkirya) were identified by Degtyarev

(1979) as *Neokoninckophyllum* aff. *tanaicum*, *N. mediocarbonicum* and *N. soshkinae*. Unfortunately, neither the brief description nor the illustrations (both confined to the mature growth stage of a single specimen per each species) allow any reliable conclusions to be drawn. However, their assignment to Fomichev's (1953) species is contested here. The first of these specimens almost certainly belongs to *Neokoninckophyllum*, but not to the type species, *N. tanaicum*. The taxonomic position of the other two specimens cannot be determined more precisely on the basis of currently available data. One of the illustrations by Degtyarev (1979, pl. 50, fig. 1b) is worth attention as it clearly documents the distabularium in a longitudinal section. The picture (mounted upside down) demonstrates the smooth transition from small inner dissepiments to small, bubble-like peripheral tabellae, best seen on the right-hand side of the picture.

Neokoninckophyllum tanaicum Fomichev, 1953
(Text-fig. 5A, B, D)

e.p. 1939. *Neokoninckophyllum tanaicum* Fomichev, p. 58, pl. 8, fig. 2a–d only.

e.p. 1953. *Neokoninckophyllum tanaicum* Fomichev, p. 354, pl. 24, figs 3a–d, 4 only.

EMENDED DIAGNOSIS: *Neokoninckophyllum* with n:d value 38–39:33–35 mm; major septa amplexoid; minor septa reaching one-third of dissepimentarium width or less; length of amplexoid cardinal septum varying; weak, irregular axial structure permanent; cardinal fossula indistinct or absent; very complex dissepimentarium occupying half of corallite radius or more, transferring gently into distabularium; tabulae incomplete, sigmoidal in general shape, elevated towards section of elongated counter septum.

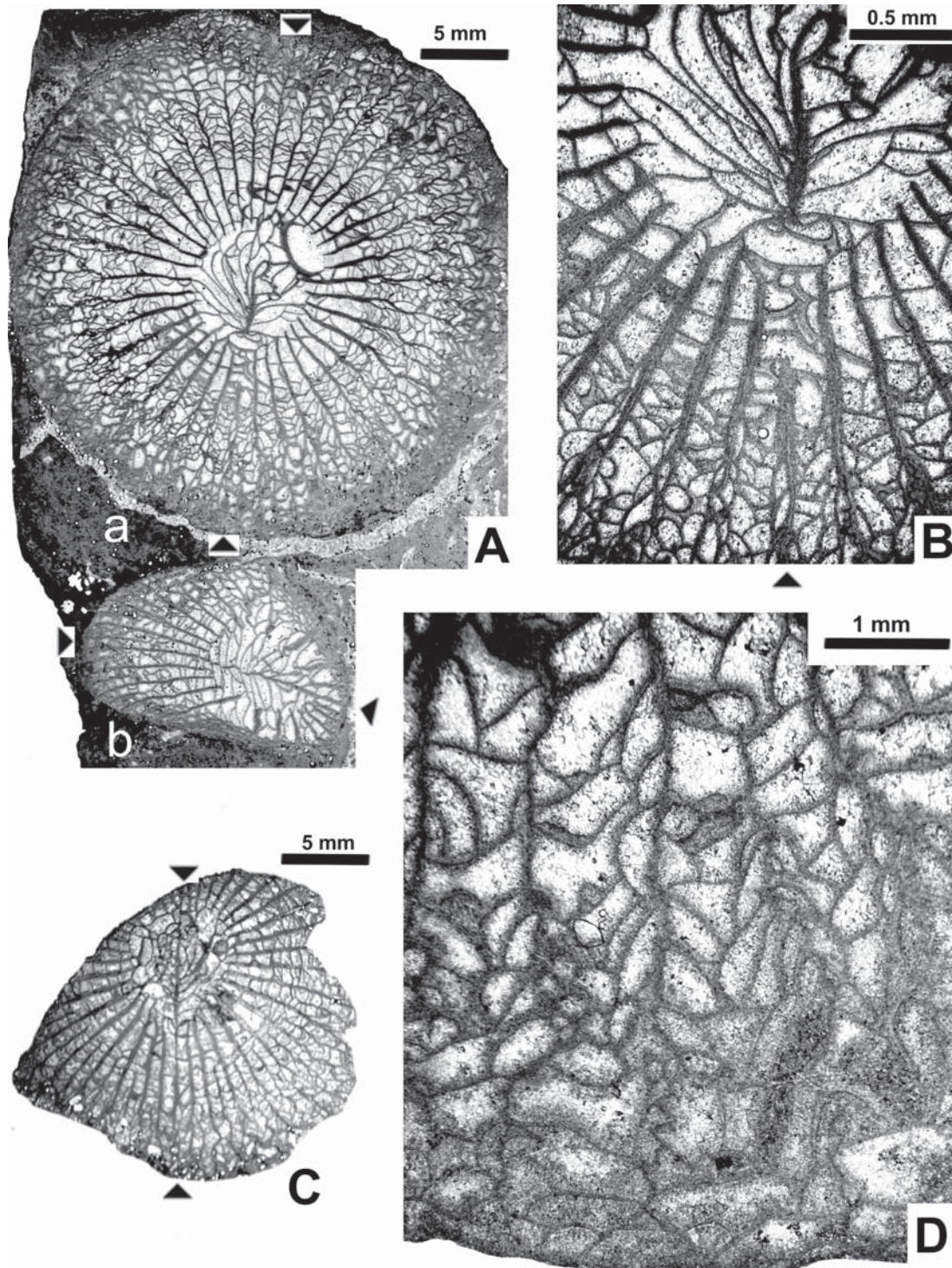
REMARKS: The illustrations provided by Fomichev (1953, pl. 23, figs 5–9; pl. 24, figs 1–10; pl. 25, fig. 1) for *N. tanaicum* and for two “varieties” and a “forma” of that species allow nothing more than a brief discussion on the genus and a preliminary emendation of the diagnosis of *N. tanaicum*. Those illustrations and supplementary peels of the paratypes of that species (Text-fig. 5A, B, D) have enabled the following observations: 1. the weak axial structure occurs throughout ontogeny and up to and including the calice floor; 2. the axial septum continues at least up to the late neanic/early mature growth stage (Text-fig. 5A, corallite ‘b’); 3. the counter septum is

permanently elongated to the corallite axis; 4. a free median lamella appears in the holotype and in one paratype (Fomichev 1953, pl. 24, fig. 3g; Text-fig. 5A, corallite ‘a’), but its continuous upward growth above the calice floor to form a pseudocolumella is not documented; 5. the median lamella is invariably mono-septal and thin, but its length differs. It is short in the holotype, but it approaches the cardinal fossula in the paratype (Text-fig. 5B). Also, isolation of the median lamella from the counter septum is temporary. Thus, the length, position and isolation of the median lamella are inconsistent; 6. the length of the cardinal septum varies depending of its position below or above a tabula, i.e., in a way typical of amplexoid major septa; 7. the major septa are slightly thickened in the tabularium, particularly in the early stage. That thickening is gently reduced towards the counter septum without a differentiation by quadrants of septa typical for Cyathopsidae and Bothrophyllidae; 8. the dissepimentarium is invariably wide and complex with grape-like dissepiments prevailing at the periphery, but small lonsdaleoid dissepiments have been established in the advanced mature growth stage of the paratype (Text-fig. 5D). Lateral dissepiments, which are an important morphological characteristic of *N. tanaicum* and the genus, are irregularly distributed within individual septal loculi.

The holotype of *N. tanaicum vesiculosum* Fomichev, 1953 and one paratype of that subspecies (Fomichev 1953, pl. 24, figs 9a–v, 10, respectively) resemble the characteristics of *N. tanaicum* closely enough to be included in the nominative species. The slightly lesser number of septa and smaller corallite diameters of those two specimens may be seen as intraspecific variation. This question is left open and for the time being the subspecies *vesiculosum* is raised here to species level. However, a new species name with a new holotype should be erected if the present type specimen of *N. vesiculosum* is assigned to *N. tanaicum*.

One of the specimens from Limestone M₁, identified by Fomichev as *Lophophyllum posttortuosum* (Fomichev 1953, pl. 16, fig. 2; Text-fig. 11B herein), resembles the early growth stage of the paratype of *N. tanaicum* in general morphology and *Neokoninckophyllum* sp. nov. in possessing the long minor septa. For that reason, it is identified here as a species of *Neokoninckophyllum*, but is left unnamed.

OCCURRENCE: Holotype and paratype No. 326. Churilina Balka (Ravine). Limestone M₅. According to Poletaev *et al.* (2011, p. 17): Sabivskian Horizon, lower upper Moscovian.



Text-fig. 5. **A, B, D** – *Neokoninckophyllum tanaicum* Fomichev, 1939. Transverse sections. Peels. Specimen No. 326. Paratype. Illustrations supplementary to Fomichev (1953, pl. 24, figs 2a, b, 4). **A** – Two corallites deposited in grainstone; **a** – mature growth stage, **b** – late neanic/early mature growth stage of another corallite; axial septum continuous; **B** – fragment of corallite with median lamella pointing to inconspicuous cardinal fossula and shortened cardinal septum; **D** – fragment of dissepimentarium enlarged to show lateral dissepiments and small lonsdaleoid dissepiments at periphery (**B, D** enlarged from **A**, specimen **a**). Martyshkina Balka (Ravine), Limestone M_5 (according to Fomichev 1953). **C** – *Histiophyllum mediocarbonicum* Fomichev, 1953. Specimen No. 345a. Holotype. Early mature growth stage. Upper part of Myus River near Edinoverchevskiyi Monastery. Limestone M_9 . After Fomichev (1953). Upper Moscovian, Domovatskian Regional Stage. Protosepta marked by black solid triangles

Neokoninckophyllum sp. nov.

(Text-figs 6 and 7)

MATERIAL: Two corallites, one near-complete with only the earliest ontogenetic stage missing and the second incomplete. The description is based on specimen UAM-Tc.Don.1/242 with supplementary data taken from specimen UAM-Tc.Don.1/243. Six transverse thin sections, one longitudinal thin section and three peels of transverse sections are available for the study.

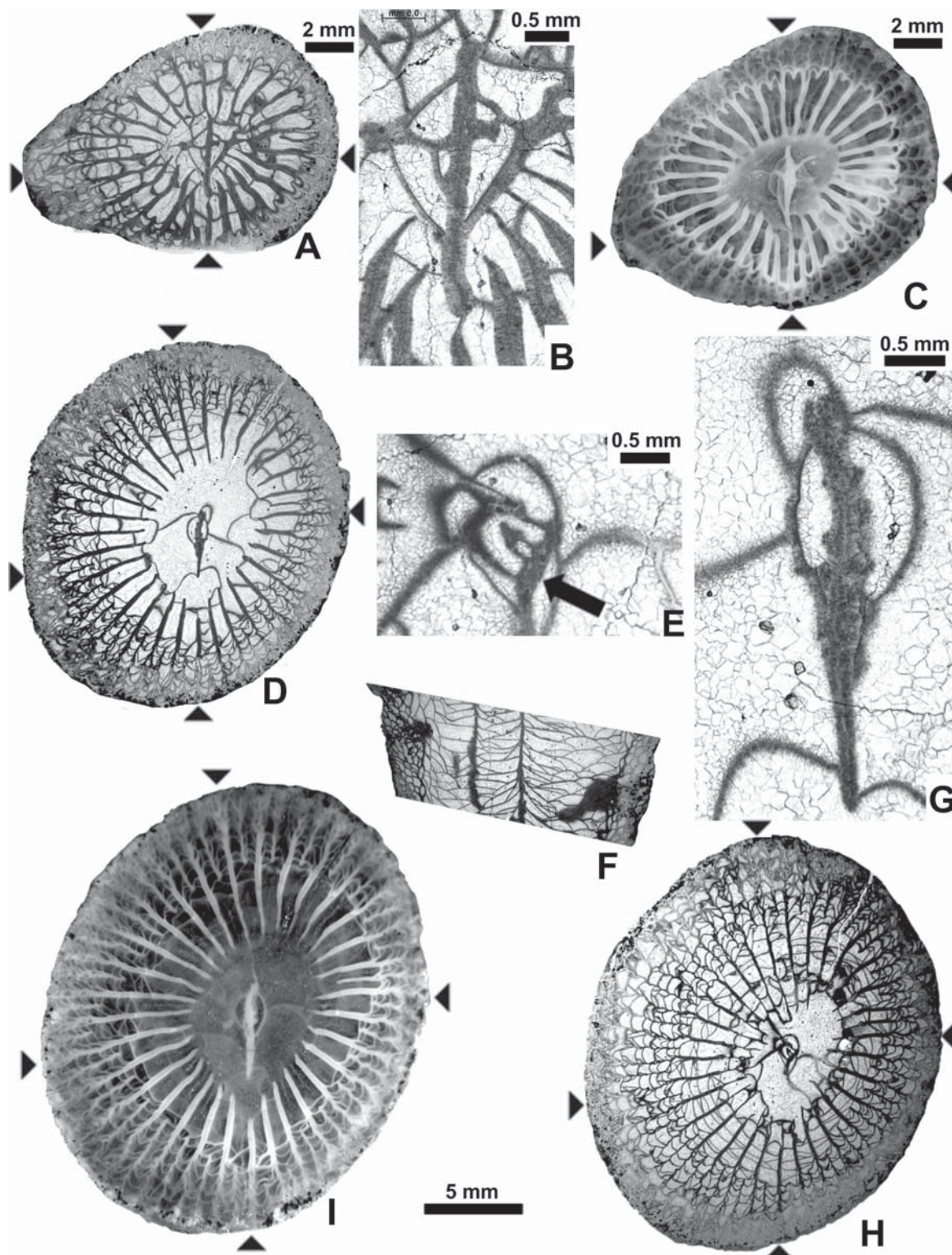
DESCRIPTION: Earliest growth stage preserved (Text-fig. 6A) with n:d value 27:13.5×9.0 mm, representing late neanic/early mature growth stage. Major septa radially arranged, thickened in tabularium, slightly more so next to cardinal septum; very thin and undulate in dissepimentarium. Last pairs of major septa inserted in counter quadrants thin and underdeveloped. Cardinal septum only slightly thinner than adjacent major septa in its peripheral part, thinning abruptly on its inner margin to meet median lamella. Median lamella slightly and equally thickened, extending to cardinal fossula, its opposite margin meeting thin inner margin of counter septum (Text-fig. 6B). Polished surface made 1.5 mm above thin section described above (Text-fig. 6C), with n:d value 29:15.0×11.3 mm, demonstrating relationship of tabula/inner margins of major septa. Most of major septa terminating in thickness of tabula. Some (Text-fig. 6C, lower left) extending axialwards with their very thin inner margins to document their amplexoid character and position of section immediately above tabula. Median lamella thickened in its median part, slightly isolated from both protosepta (Text-fig. 6I). Two septal lamellae and sections of axial parts of tabulae form weak axial structure in both thin section and polished surface of late neanic/early mature growth stage. Minor septa penetrating tabularium with their thickened inner margins, their peripheral parts being thin, similar to peripheral parts of major septa. Cardinal fossula shallow, dipping slightly into dissepimentarium that occupies slightly less than one-quarter of corallite radius. Dissepiments regular, irregular and pseudo-herringbone. Lateral dissepiments present already in some loculi (Text-fig. 6A, left) and first grape-like structures appear at periphery. Inner wall slightly thickened.

Number of major septa (32) in mature growth stage constant (Text-figs 6D, E, G, H; 6G), but corallite diameters differentiated (19.5×17.0 mm to maximum 22.0×18.5 mm). Amplexoid character of major septa hardly, if at all, recognised in thin transverse sections (Text-fig. 6D, H), with peripheral parts

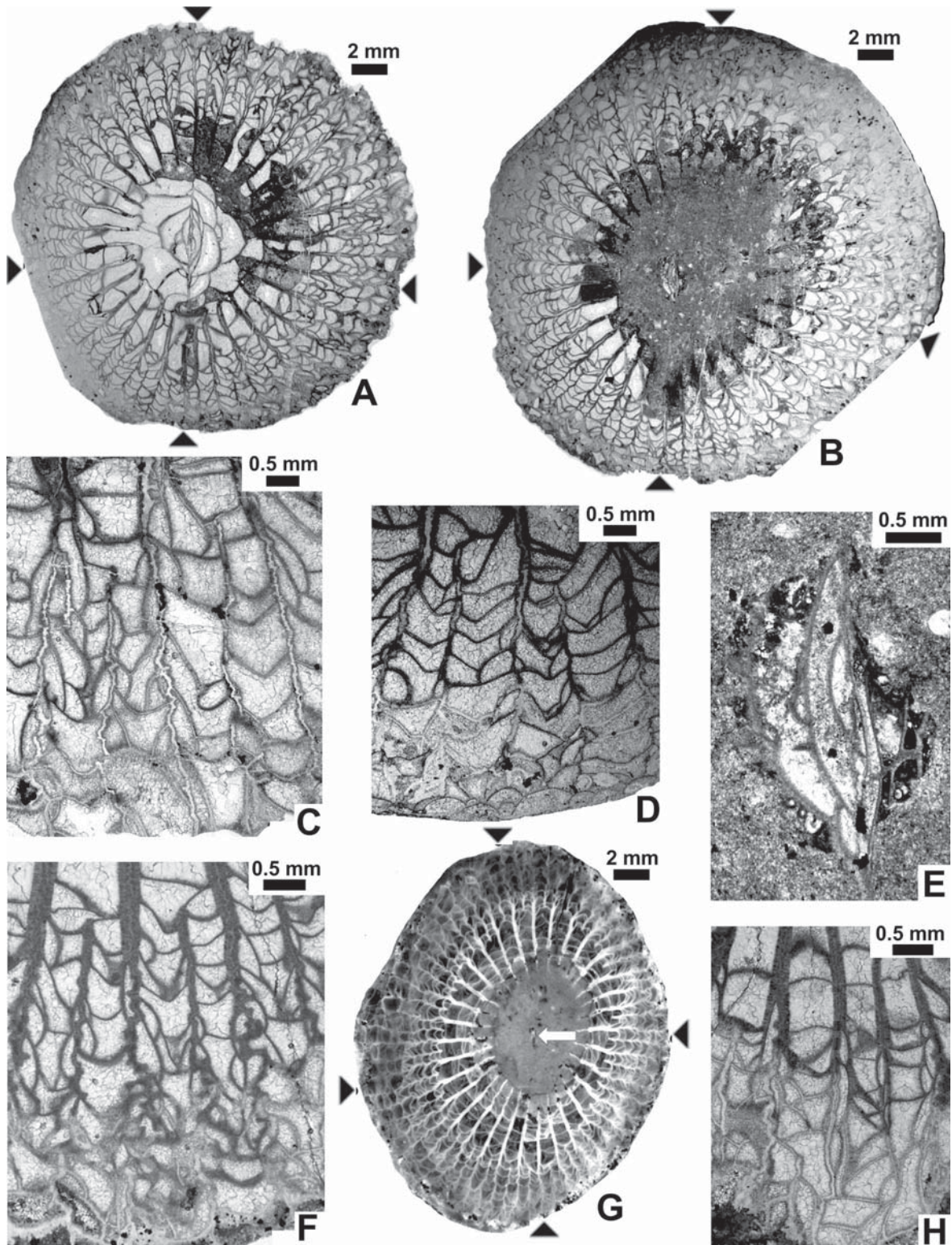
thin, undulate. Some twisted so much as to become disintegrated to form carina-like bodies (Text-fig. 7F). Cardinal septum in early mature growth stage slightly shortened (Text-fig. 6D). In more advanced growth stages indistinguishable from other major septa by length and thickness, but immediately above calice floor slightly shortened (Text-figs 6H, I and 7G, respectively). Minor septa identical to peripheral parts of major septa in morphology, intersecting dissepimentarium; inner margins of some slightly thickened in disstabularium. Pseudocolumella in early mature growth stage (Text-fig. 6C) free, long and slightly thickened at corallite axis, pointing towards cardinal septum. It consists of median lamella and six low protrusions sitting on and slightly dipping into thickness of median lamella (Text-fig. 6D, G). These bodies are here interpreted as rudiments of septal lamellae, as confirmed by their growth directed towards median lamella. Thus, pseudocolumella monoseptal as in *Dibunophyllum*, but not complex as in *Amygdalophyllum* Dun and Benson, 1920 or *Spirophyllum* Fedorowski, 1970. In late mature growth stage (Text-fig. 6E, H, I) pseudocolumella reduced to short, irregular plate; however, its thin upper margin extending into lower part of calice (Text-fig. 7G, arrow). Cardinal fossula shallow in early corallite growth (Text-fig. 6A, C), may disappear in advanced maturity as indicated by lack of its dipping into dissepimentarium (Text-figs 6H, I; 7G). Dissepimentarium slightly extending one-third of corallite radius in greatest width. Dissepiments variable with convex dissepiments towards periphery prevailing in some parts, whereas lateral and grape-like dissepiments common in other part of same transverse section (Text-figs 6D, H, I; 7F–H).

In longitudinal section (Text-fig. 6F), illustrating early mature growth stage, i.e., between Text-fig. 6C and 6D, dissepimentarium occupies one-quarter of corallite radius. Dissepiments small, globose, arranged in very steep and/or vertical rows. Tabularium of disstabularium type more clearly demonstrated at left-hand side of corallite. Tabulae incomplete. Peripheral tabellae dissepiment like, downsloping under various angles, steep at left-hand side of corallite. This area corresponds to densely packed sections of tabulae in outer tabularium of transverse sections, best seen in Text-fig. 6H, I. Tabellae in median part of tabularium flat or bubble like and almost horizontally arranged. They pass into inner tabellae, elevated under low angles towards pseudocolumella. Some short axial tabellae meet pseudocolumella steeply.

Second corallite (Text-fig. 7A–E) with n:d value 32:24.5×23.5 mm just below calice floor and 32:



Text-fig. 6. *Neokoninkophyllum* sp. nov. Specimen UAM-Tc.Don.1/242. Transverse thin sections except when stated otherwise. A-C – late neanic/early mature growth stage, B – enlarged from A to show axial structure, D-G, H, I – successive sections of mature growth stage, E – enlarged from H to document presence of short, simple pseudocolumella (arrow), G – enlarged from D to document rudiments of septal lamellae attached to pseudocolumella, F – longitudinal thin section between C and D (C, I – polished surfaces). Protosepta and alar septa marked by black solid triangles. Scale bar between I and H corresponds images D, F, I, H. For occurrence see description of species



Text-fig. 7. *Neokoninckophyllum* sp. nov. A-E – Specimen UAM-Tc. Don.1/243. Transverse thin sections except when stated otherwise. A – just beneath calice floor except for dark part in upper right, B – above calice floor except for axial structure and dissepimentarium, C, D – morphology of dissepimentarium, D – small lonsdaleoid dissepiments at periphery, E – axial structure (enlarged from B). F-H – Specimen UAM-Tc. Don.1/242. F – septa twisted so as to form carinae-like bodies, G – section through lower part of calice with rudiment of pseudocolumella (arrow), H – morphology of dissepimentarium. Protosepta and alar septa marked by black solid triangles. For occurrence see description of species

27.0×27.0 mm in lower part of calice, preserved only in its ontogenetically most advanced growth stage. Major septa in tabularium slightly thickened both beneath calice floor and just above it; in dissepimentarium thin and undulate. Minor septa slightly differentiated in length; most reach inner margin of dissepimentarium, but some shortened. Cardinal fossula dips slightly into dissepimentarium. Pseudocolumella remains connected to counter septum up to and including calice floor (Text-fig. 7A). That strongly elongated structure almost reaches cardinal fossula, but does not meet slightly shortened cardinal septum. Very thin pseudocolumella, accompanied by several sections of axial tabellae and few short, thorn-like bodies attached to tabellae elevated well above peripheral part of calice floor (Text-fig. 7B, E). Calcitic infillings present between sections of tabellae documenting extension of free axial structure above peripheral part of calice floor. Thorn-like bodies interpreted here as short septal lamellae. Morphology of dissepimentarium resembles that of previously described corallite, except for small and rare lonsdaleoid dissepiments (Text-fig. 7D).

REMARKS: The more complete specimen described above differs from all unquestionable members of *Neokoninckophyllum* by having long minor septa that permanently reach the distabularium. The dissepimentarium of both specimens resembles that in the type species, but is much narrower, being in that respect comparable to small specimens included by Fomichev (1953) in his “variety” *vesiculosa*, here elevated to species level. The differences mentioned are adequate for the erection of a new species for the more complete of the two specimens discussed, but formal naming of this specimen is deferred to another occasion.

The morphology of the incomplete, larger specimen, derived from Limestone M₅ and from the type locality of the holotype of *N. tanaicum* closely resembles that species. It differs from it in having a narrower dissepimentarium, longer minor septa, fewer major septa and a smaller diameter. However, its inclusion either in *N. tanaicum* or in *N. vesiculosum* is possible. The main characters in common of the specimens discussed and main features characteristic for each of them are summarised in Table 2, whereas their different stratigraphic positions are marked in Text-fig. 4.

OCCURRENCE: Specimen UAM-Tc.Don.1/242. Kalmyus River Area, Semenovka Village. Limestone L₁. According to Poletaev *et al.* (2011, p. 17): Marivskian

Horizon, upper lower Moscovian. Specimen UAM-Tc.Don.1/243. Churilina Balka (Ravine). Limestone M₅. According to Poletaev *et al.* (2011, p. 17): Sabivskian Horizon, lower upper Moscovian.

Genus *Yuanophylloides* Fomichev, 1953

(Type species *Yuanophylloides gorskyi* Fomichev, 1953, OD)

POSSIBLE SYNONYMY:

- ?e.p. 1938. *Lophophyllum* Milne Edwards and Haime, 1850; Gorskiy, pp. 74, 77 (*Lophophyllum infirmum* Gorskiy, 1938; *Lophophyllum* sp.).
1945. *Dibunophyllum* Thomson and Nicholson, 1876; Moore and Jeffords, p. 157.
- e.p. 1945. *Neokoninckophyllum* Fomichev, 1939; Moore and Jeffords, p. 158. (*N. arcuatum*, *N. gracilis*, *N. simplex*).
1953. *Yuanophylloides*; Fomichev, p. 278.
- e.p. 1964. *Koninckophyllum* Thomson and Nicholson, 1876; Rowett and Sutherland, p. 55 (*K. simplex*, ?*K. oklahomense*).
- e.p. 1970. *Neokoninckophyllum* Fomichev, 1939; Cocke, p. 26 (*N. petilum*, *N. perplexum*, ?*N. variabile*, ?*N. acolumnatum*).
- ?1976. *Bothrophyllum* Trautschold, 1879; Guo, p. 91.
- ?1978. *Lophophyllum* Milne Edwards and Haime, 1850; Wang, p. 142.
1981. *Koninckophyllum* Thomson and Nicholson, 1876; Sugiyama in Sugiyama and Toriyama, p. 5.
1983. *Pseudokoninckophyllum* Vassilyuk; Aizenverg *et al.*, pl. 28, fig. 7.
- ?1985. *Skoleckophyllum* Fomichev, 1953; Boll, p. 33.
- ?1985. *Yuanophylloides* Fomichev, 1953; Wu and Zhang, p. 135.
- ?e.p. 1985. *Caninia* Michelin, 1840; Wu and Zhang, p. 140 (non *C. wuqingnanensis*, *C. popovi*, *Caninia* sp.).
- ?1985. *Gshelia* Stuckenberg, 1888; Wu and Zhang, p. 141.
- ?1987. *Neokoninckophyllum* Fomichev, 1939; Yu and Wang, p. 79.
- ?1989. *Yuanophylloides* Fomichev, 1953; Wu and Zhao, p. 89.
- ?e.p. 1989. *Eostrotion* Vaughan, 1915; Wu and Zhao, p. 93 (*Eostrotion equiseptatum*).
1992. *Yuanophylloides* Fomichev, 1953; Wu and Lin, p. 87.
- ?e.p. 2003. *Neokoninckophyllum* Fomichev, 1939; Yu in Fan *et al.*, p. 300 (?*N. banagensense*, ?*N. jomdaense*).
- ?2003. *Yuanophylloides* Fomichev, 1953; Yu in Fan *et al.*, p. 304.

TEMPORARY SPECIES CONTENT (in alphabetic order by species names):

?*Neokoninckophyllum banagense* Yu in Fan *et al.*, 2003; ?*Bothrophyllum chengpoense* Guo, 1976; *Yuanophylloides cruciformis* Fomichev, 1953; ?*Yuanophylloides cylindricus* Wu and Zhang, 1985; *Yuanophylloides densus* Fomichev, 1953; ?*Yuanophylloides elegans* Wu and Zhao, 1989; ?*Eostrotion equiseptatum* (Yu, 1933) of Wu and Zhao 1989 (+ *E. equiseptatum simplex* Wu and Zhao, 1989 as a synonym); *Yuanophylloides gorskyi* Fomichev, 1953; *Neokoninckophyllum gracilis* Moore and Jeffords, 1945; ?*Neokoninckophyllum guizouense* Yu and Wang, 1987; *Dibunophyllum* (?) *inauditum* Moore and Jeffords, 1945 (+ *Neokoninckophyllum simplex* Moore and Jeffords, 1945 as a synonym); ?*Lophophyllum infirmum* Gorskiy, 1938; *Koninckophyllum ingavatae* Sugiyama in Sugiyama and Toriyama, 1981; ?*Neokoninckophyllum jomdaense* Yu in Fan *et al.*, 2003; ?*Yuanophylloides jomdaense* Yu in Fan *et al.*, 2003; *Neokoninckophyllum perplexum* Cocke, 1970; *Neokoninckophyllum petilum* Cocke, 1970; ?*Bothrophyllum pseudoconicum* Dobrolyubova, 1937 of Guo 1976; *Neokoninckophyllum stepanovi* Fomichev, 1953; ?*Lophophyllum subtilisum* Wu of Wang 1978, and of Guo 1980; ?*Skoleckophyllum triseptatum* Boll, 1985; ?*Gshelia xiangchengensis* Wu and Zhang, 1985 (+ *Caninia cf. vigilans* (Reed) of Wu and Zhang 1985

as a probable synonym); ?*Yuanophylloides zoganense* Wu and Zhang, 1985.

Notice. The literature data of all species with a question mark are insufficient for reliable identifications. Thus the list of some synonyms and the species content of the genus should be treated only as a suggestion.

EMENDED DIAGNOSIS: Neokoninckophyllidae with major and minor septa thin; in neanic growth stage major septa bilaterally arranged; axial septum commonly permanent; cardinal septum may be slightly shortened in advanced maturity and/or in calice; counter septum elongated when axial septum divided; cardinal fossula shallow, commonly indistinct or absent; tabulae incomplete, elevated towards axial septum; dissepimentarium simple, rare lonsdaleoid dissepiments may occur, but lateral and grape-like dissepiments absent.

REMARKS: According to ICZN rules, special letters (with diacritics), such as the German umlaut, cannot be used as such in biological names of animals. Thus, the original spelling by Fomichev (1953) is here given only in the synonymy.

Taxa here included in *Yuanophylloides* are fairly common in Bashkirian and Moscovian strata in Europe, Asia and North America. Corals possibly be-

Species	Major septa	Minor septa	Cardinal septum	Counter septum	Median lamella	Cardinal fossula	Dissepimentarium	Dissepiments	n:d value [mm]	Limestone/Formation
<i>gorskyi</i>	< 2/3 corallite radius	reach tabularium	slightly shortened	strongly elongated	not separated	indistinct	1/5-1/4 corallite radius	herringbone	26-27:10-12	M-9
<i>cruciformis</i>	many reach axial septum	spinelike	not shortened	strongly elongated	long, thin	indistinct	1/5-1/4 corallite radius	pseudo-herringbone and lonsdaleoid	28-31:10-12	K-7
<i>rectus</i>	amplexoid, long	variable, most short	permanent axial septum	permanent axial septum	permanent axial septum	distinct	1/5-1/4 corallite radius	regular and angular	32:15	E-1
<i>inauditus</i>	amplexoid, few to axia	short and spinelike	long above tabulae	interrupted axial septum	not separated	indistinct, triangular	1/4-1/3 corallite radius	regular and rare lonsdaleoid	38-40:16-21.5	E-1 and Hale Formation
<i>gracilis</i>	3/4 corallite radius	short and spinelike	slightly shortened	? equal to major septa	not separated	absent	1/4 corallite radius	regular and herringbone	31:12.5	Marble Falls Limestone
<i>perplexus</i>	1/2-3/4 corallite radius	short and spinelike	equal to major septa	elongated	temporary free	absent	1/7-1/5 corallite radius	regular and herringbone	26:15.5	Hertha Formation, Missourian
<i>petilum</i>	4/5 corallite radius	not observed	interrupted axial septum	interrupted axial septum	interrupted axial septum	absent	1/3-1/2 corallite radius	herringbone and lonsdaleoid	19-22:8	Cherryvale Formation, Missourian

Table 3. Distinguishing mature morphological characters of *Yuanophylloides* species. Only ranges of described and/or revised taxa considered; may change when complete material is restudied. Data for *Y. gracilis* compiled on the basis of Moore and Jeffords (1945), those for *Y. perplexus* and *Y. petilum* taken from Cocke (1970). Primary generic assignment of species: *gorskyi* and *cruciformis* assigned to *Yuanophylloides* (Fomichev 1953), *rectus* assigned to *Pseudokoninckophyllum* (Vassilyuk in Aizenverg *et al.* 1983), *inauditus* assigned to *Dibunophyllum* (Moore and Jeffords 1945), and the remaining assigned to *Neokoninckophyllum* (Moore and Jeffords 1954 and Cocke 1970)

longing to that genus and/or related genera have most commonly been recorded from China (see synonymy). Unfortunately, the level of studies of the latter is inadequate for a detailed analysis. Thus, most of these taxa can only tentatively be included in *Yuanophylloides*.

Eleven generic names have been applied by authors to species included here in a preliminary synonymy of *Yuanophylloides*. Such generic differentiation may have resulted from: 1. inconsistency of morphological characters during ontogeny. Superficial studies based on random thin sections, rather than series of sections, may have led to erroneous conclusions; 2. difficulties in selecting characters that are truly diagnostic of a given group of species; 3. subjectivity in evaluations of the main diagnostic characters of genera. The inconsistent approach by Fomichev (1953) to species described by him and the inclusion of the genus *Yuanophylloides* in the Family Lophophyllidae Grabau, 1928 worsened the taxonomic chaos. Hill (1981, p. F371) ignored Fomichev's (1953) concept of that family, included *Yuanophylloides* in the Subfamily Dibunophyllinae and suggested that this genus was possibly synonymous with *Yakovleviella* Fomichev, 1953. Her suggestion to exclude *Yuanophylloides* from the Lophophyllidae is accepted here, but the other statements are not subscribed to. Fomichev's (1953) concept of the Family Lophophyllidae has recently been discussed and rejected (Fedorowski 2017a).

Yuanophylloides gorskyi Fomichev, 1953

(Text-fig. 8A–E)

e.p. 1953. *Yuanophylloides gorskyi* Fomichev, p. 279, pl. 16, figs. 12, 13 only.

e.p. 1953. *Yuanophylloides gorskyi* forma *b* Fomichev, p. 281 and Atlas, p. 34, pl. 16, fig. 15 only.

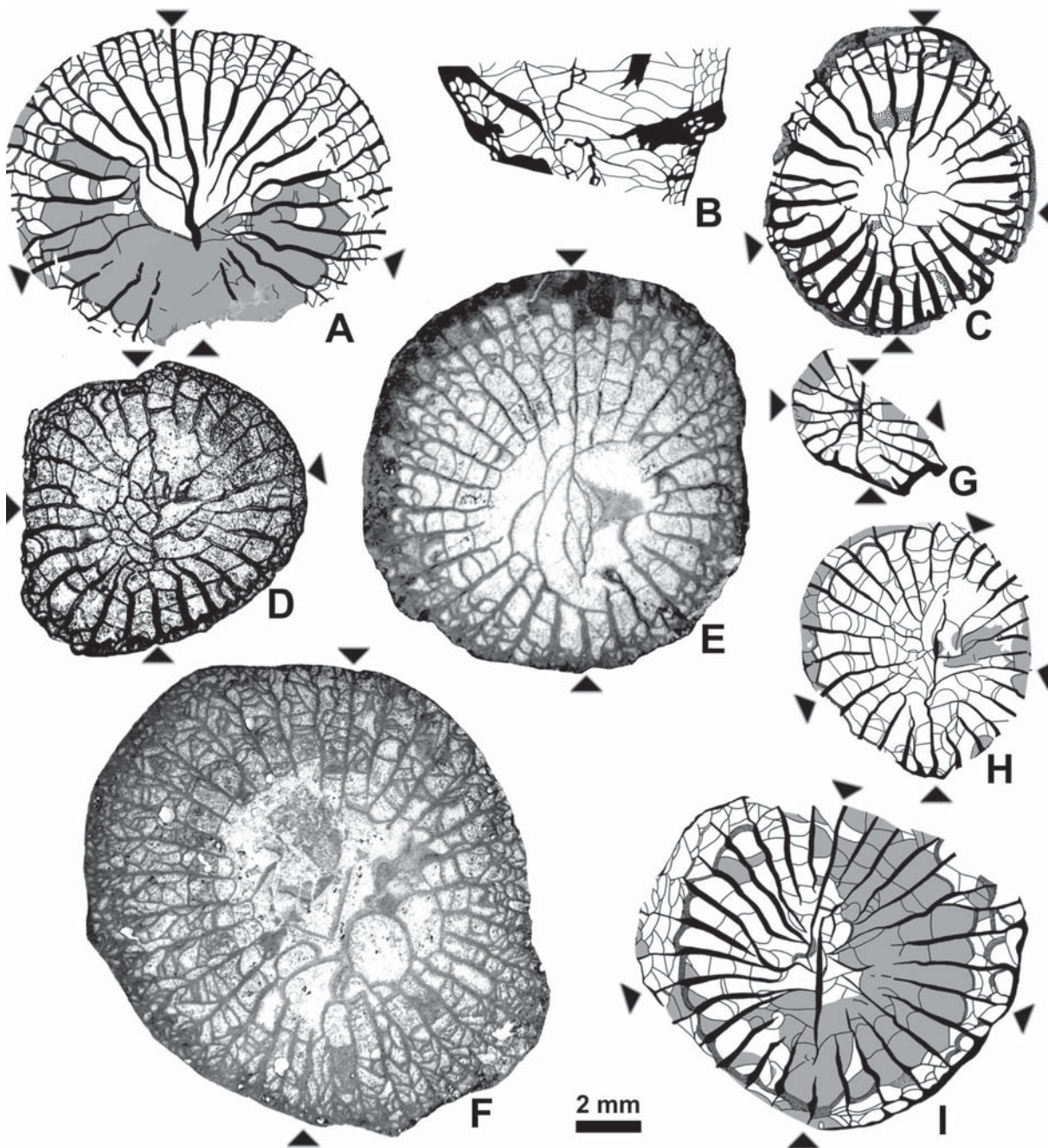
EMENDED DIAGNOSIS: *Yuanophylloides* with n:d value 26–27:10–12 mm; some major septa may approach axial septum or strongly elongated counter septum; minor septa intersecting dissepimentarium that occupies one-fifth to one-quarter of corallite radius; dissepiments in transverse sections herringbone and convex towards corallite periphery, in longitudinal section small, vertically arranged.

SUPPLEMENTARY DESCRIPTION: The morphology of the earliest growth stage of the holotype of *Y. gorskyi*, illustrated by Fomichev (1953, pl. 16, fig. 12a), is incomplete, but the axial septum is recognisable. Most major septa remain short of corallite axial area; some approach axial septum. One or two

rows of dissepiments and minor septa intersecting narrow dissepimentarium seen on right-hand side of corallite. Axial septum present up to mature part of specimen as illustrated by Fomichev (1953, pl. 16, fig. 12b). Mud infillings at cardinal side of axial septum either document original dipping of tabulae, i.e., presence of cardinal fossula, or reflect mechanical damage. The image of the holotype published here (Text-fig. 8A) shows a corallite morphology that is more advanced than that illustrated by Fomichev (1953). A large part of cardinal quadrants (grey in figure) infilled with mud, but rudiments of tabulae attached to inner parts of major septa remain recognisable within mud. Occurrence of those rudiments and arrangement of axial tabellae sectioned beneath calice floor (white in figure) suggest combination of both infilling with mud, resulting from mechanical damage of skeleton and dipping of calice floor towards dissepimentarium/tabularium border. Reduction in width of dissepimentarium (Fomichev 1953, pl. 16, fig. 12b; Text-fig. 8A herein, white in figure) towards cardinal septum, suggesting greatest depth of calice in cardinal septum area. Cardinal septum absent from transverse section illustrated here, perhaps eroded together with its immediate surroundings. Its probable shortening above calice floor suggested by rudiments of tabulae directed towards periphery in direction of former position of cardinal septum. Counter septum intersecting corallite axial area and extending into corallite part filled with mud. Inner margins of major septa thin and undulate. Several approach, some reach inner margin of slightly thickened counter septum. Thin minor septa reach inner border of dissepimentarium that consists of pseudo-herringbone and peripherally convex dissepiments.

In longitudinal sections (Fomichev 1953, pl. 16, fig. 12v; Text-fig. 8B herein) tabulae incomplete with peripheral tabellae either sinuous or convex and axial tabellae elevated towards axial septum at low angle. Only rare, short tabellae adjacent directly to axial septum, elevated steeply. Morphology of tabularium resembles that in *Neokoninckophyllum* and can perhaps be considered typical of the family Neokoninckophyllidae.

INTRASPECIFIC VARIABILITY: Only paratype No. 331a, specimen No. 716 (holotype of “forma *b*”) and an unnumbered specimen, labelled “forma *b*”, all from Fomichev's collection, are here accepted as conspecific with the holotype of *Y. gorskyi*. The mature growth stage of paratype No. 331a was not available for study. The early mature growth stage studied (Text-fig. 8C) confirms the occurrence of an indis-



Text-fig. 8. **A-C** – *Yuanophylloides gorskyi* Fomichev, 1953. **A, B** – Specimen No. 331. Holotype. **A** – transverse section, below calice floor when in white; **B** – eccentric longitudinal section. Rodnikovaya Balka (Ravine), Limestone M₉; **C** – Specimen No. 331a. Paratype. Transverse section, early mature growth stage (all drawings on images of peels). **D-F** – *Yuanophylloides gorskyi*, forma *b* Fomichev, 1953. Transverse sections. **D** – Specimen No. 716. Holotype. Late neanic/early mature growth stage (peel); **E** – unnumbered specimen. Mature growth stage (peel). Likhaya River Area, Kalinovaya Balka (Ravine), Suite C₃²; **F** – Specimen No. 732. Paratype; here excluded from the species and genus. Mature growth stage (peel). Volchaya River Area, Limestone M₁. **G-I** – *Yuanophylloides cruciformis* Fomichev, 1953. Specimen No. 408. Holotype. Transverse sections. **G** – neanic growth stage; **H** – mature growth stage; **I** – partly above (grey), partly below (white) calice floor (all drawings on images of peels). Petrovskoye Village, Orlovaya Balka (Ravine), Limestone above coal seam V. All occurrences after Fomichev (1953). Protosepta and alar septa marked by black solid triangles where recognisable. Scale bar between **F** and **I** corresponds to all images and drawings

tinct cardinal fossula and continuous axial septum. The smaller diameter and lower number of septa (n:d value 26:9.5×8.5 mm), thicker major septa in tabularium and the narrower dissepimentarium distinguish that specimen from the holotype, but those differences may result from its immature growth stage.

The early growth stage of specimen No. 716 (Fomichev 1953, pl. 16, fig. 15a, b), perhaps late neanic/early mature, lacks a continuous axial septum. Its destruction by diagenesis is highly probable, but cannot be confirmed. The growth stage illustrated here (Text-fig. 8D) corresponds to the most advanced growth stage illustrated by Fomichev (1953, pl. 16, fig. 15v) (n:d values 26:10.0×8.0 mm vs 26:10.5×8.5 mm). The morphology of that advanced growth stage is comparable to the late neanic/early mature growth stage characterised above. Some major septa attached to axial septum. Minor septa enter tabularium in most loculi. Dissepimentarium very narrow, one eighth of corallite radius at most. A peel of an unnumbered specimen in Fomichev's (1953) collection (not mentioned by him; Text-fig. 8E) with n:d value 27:12.6×12.0 mm, illustrates a growth stage that is closely comparable to the mature growth stage of the holotype. Very long counter septum approaches slightly shortened cardinal septum. Major septa almost equal in length, leaving wide axial area free. Minor septa approaching, some entering tabularium. Cardinal fossula indistinct, dipping slightly into dissepimentarium. Reduction in width of dissepimentarium in cardinal quadrants enlarged by erosion. Better-preserved part of corallite suggest increase of dissepimentarium width towards counter septum. Dissepiments either herringbone or convex towards periphery.

REMARKS: The description of the holotype and remarks on the specimens included here in *Y. gorskyi* supplement the detailed description by Fomichev (1953, pp. 279–281). They are here introduced for three reasons: 1. to add new data lacking from the original description; 2. to emphasise the main characters of that species as the type species of the genus; 3. to document arguments for assigning *Y. gorskyi*, and thus the genus *Yuanophylloides*, to the Family Neokoninckophyllidae. The number of specimens available for this preliminary revision is inadequate for documenting intraspecific variability reliably. Besides, one paratype illustrated by Fomichev (1953, pl. 16, fig. 14a, b) remains unsectioned and is excluded from consideration until sectioning and confirmation of its morphology are accomplished. The holotype of “forma *b*” closely resembles the holotype, as pointed out above. Thus, that “forma” is included in the syn-

onymy of the species. One specimen identified by Fomichev (1953, pl. 16, fig. 16a, b; Text-fig. 8F herein) as “forma *b*”, is excluded from both *Y. gorskyi* and the genus *Yuanophylloides*. Its complex dissepimentarium and the thin and shortened major septa liken it to *Neokoninckophyllum campophylloides*, to which it may perhaps be assigned. Peels of *Y. variabilis* were not available for the present study. The illustrations of Fomichev (1953, pl. 16, figs 20, 21) hint at the conspecificity of that species and *Y. gorskyi*, but this cannot be proved without more detailed data.

Fomichev (1953, p. 321) mentioned several specimens as either belonging to “forma *b*” or questionably included in *Y. gorskyi*. Those specimens were not illustrated, nor are peels of them available. Thus, their potential value for a more comprehensive characterization of *Y. gorskyi* remains elusive.

OCCURRENCE: Holotype and paratype No. 331a from Rodnikovaya Balka (Ravine), Limestone M₉ (after Fomichev 1953, p. 281). Sanzharivskian Horizon, upper Moscovian (after Poletaev *et al.* 2011, p. 17). ?Specimen No. 716 from Kalinovaya Balka (Ravine). Suite C₃². (after Fomichev 1953, p. 34, Atlas).

Yuanophylloides cruciformis Fomichev, 1953
(Text-fig. 8G–I)

1953. *Yuanophylloides cruciformis* Fomichev, p. 284, pl. 17, figs 1–3.

EMENDED DIAGNOSIS: *Yuanophylloides* with n:d value 28–31:10.0–12.0 mm; major septa slightly undulate, most approaching, some reaching axial septum and/or long, thin median lamella; last pair of major septa in cardinal quadrants remaining underdeveloped up to advanced maturity; cardinal septum above calice floor shortened; minor septa very short, from several loculi absent; dissepimentarium one-fifth to one-quarter of corallite radius in width; dissepiments irregular; rare lonsdaleoid dissepiments may occur at periphery.

SUPPLEMENTARY DESCRIPTION OF HOLOTYPE: Ontogenetically earliest growth stage preserved, with incomplete diameter 3.8×2.0 mm (Text-fig. 8G), not illustrated by Fomichev (1953). Major septa differentiated in length, arranged in distinct quadrants; 18 preserved, perhaps 22 when broken part included. Axial septum thickened in its median part. Alar septa and median major septa in quadrants joining axial septum. Last pair of major septa in car-

dinal quadrants underdeveloped, marking position of cardinal septum. Minor septa and dissepimentarium absent from part of corallite preserved.

Underdevelopment of last pair of major septa in cardinal quadrants and continuous axial septum lasting up to mature growth stage (Fomichev 1953, pl. 17, fig. 1a; Text-fig. 8H herein). Major septa remaining differentiated in length, but only some of them approaching and/or reaching thin, undulate axial septum. In transverse section, made partially below (white in figure) and partially above calice floor (grey in figure, Text-fig. 8I), not illustrated by Fomichev (1953), major septa slightly thickened in tabularium, semi-radially arranged, differentiated in length, most long, approaching and/or reaching median lamella. Counter-lateral major septa shorter than other major septa in counter quadrants. Axial septum divided into cardinal septum, counter septum and median lamella. Counter septum elongated beyond corallite axis with its inner margin parallel to median lamella. Axial part of median lamella slightly thickened; its thin margin almost meeting short cardinal septum. Very short break between those two skeletal elements suggesting presence of axial septum up to and including calice floor. Minor septa very short, from some septal loculi either totally reduced or restricted to thickness of external wall. Dissepimentarium approximately one-fifth of corallite radius wide. Dissepiments mostly irregular in shape and size, pseudo-herringbone in some loculi; sporadic lonsdaleoid dissepiments present.

REMARKS: The description and illustrations of the holotype of *Y. cruciformis*, supplementary to the data published by Fomichev (1953), are included in the present paper because of a cognitive value of this species as a morphologically intermediate between the Moscovian *Y. gorskyi* and the late early Bashkirian *Y. rectus* (see Considerations below). It resembles *Y. gorskyi* in the n:d value but differs in possessing longer major septa, commonly approaching the axial septum, very short minor septa and most dissepiments irregular. Paratypes closely resemble the holotype in the particular growth stages illustrated by Fomichev (1953, pl. 17, figs 2, 3a, b). However, those very restricted illustrations and lack of peels of paratypical specimens preclude a more comprehensive discussion of the species.

OCCURRENCE: Holotype and one paratype, Kharkov Region, Petrovskoe Village, Orlovaya Balka (Ravine). Limestone overlying coal seam V (according to Fomichev 1953, p. 36, Atlas) = Lime-

stone K₇ (Professor V.V. Ogar, written information), Kamyanskian Horizon, lowermost Moscovian. Paratype 312, Khutor Bogdanov, Nizhnaya Kamyshvakha River, Limestone I₂ (according to Fomichev 1953, p. 36, Atlas) = Krasnodonskian Horizon, uppermost Bashkirian.

Yuanophylloides rectus (Vassilyuk
in Aizenverg *et al.*, 1983)
(Text-fig. 9)

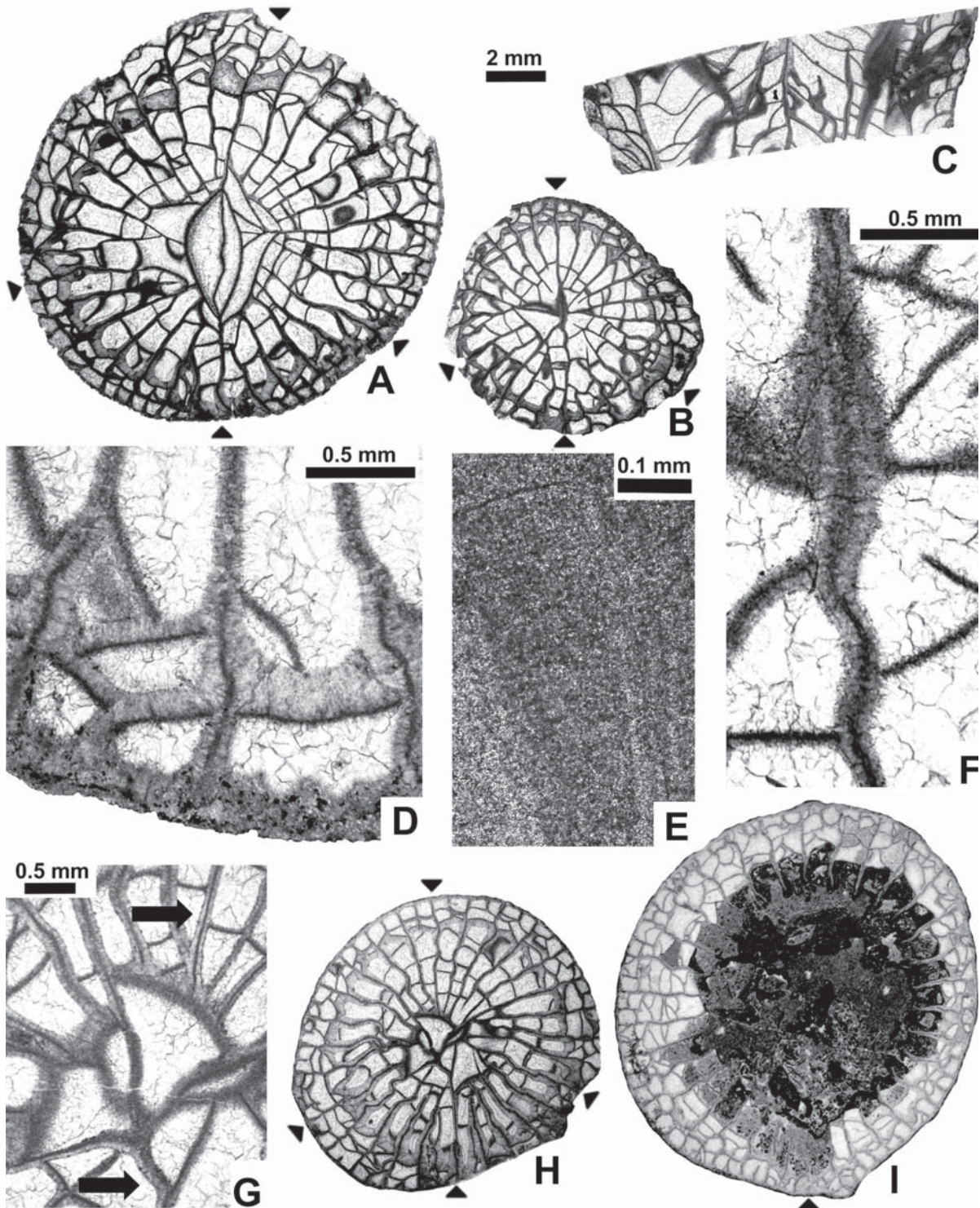
1983. *Pseudokoninckophyllum rectus* Vassilyuk in Aizenverg *et al.*, p. 142, pl. 28, fig. 7 (no description).

MATERIAL: Holotype UAM-Tc.Don.1/244; two transverse and one longitudinal thin section; remainder of sample missing. Possible paratype UAM-Tc.Don.1/245; two thin sections and three peels, only mature growth stage and calice preserved.

DIAGNOSIS: *Yuanophylloides* with n:d value 32:15.0 mm in holotype; major septa slightly thickened in peripheral tabularium; most staying short of permanent axial septum; cardinal fossula dipping slightly into dissepimentarium; minor septa varying in length; rare ones reaching inner limit of dissepimentarium that occupies one-fifth to one-quarter of corallite radius; dissepiments interseptal, herringbone and regular.

DESCRIPTION: External wall 0.2–0.4 mm thick, smooth. Septa dip into it with their triangular bases. Septa-like protrusions of external wall in some loculi (Text-fig. 9D), median one illustrated being underdeveloped minor septum. In late neanic/early mature growth stage of holotype (Text-fig. 9B) with n:d value 25:9.5 mm, major septa differentiated in length; those in middle of quadrants longest, some reaching axial septum. Last pairs of major septa in quadrants and counter-lateral septa shortest. Middle part of axial septum thickened (Text-fig. 9B, F). Short minor septa appearing in some loculi. Dissepimentarium in 1–3 rows of regular and irregular dissepiments. Inner wall slightly thickened.

In mature growth stage of holotype (Text-fig. 9A) major septa slightly undulate, thickest in peripheral tabularium, free axially. Last pairs of major septa in quadrants shortened, making alar pseudofossulae and cardinal fossula recognisable. Axial septum thin, slightly undulate. Minor septa in most septal loculi of cardinal quadrants well developed, almost reaching inner limit of dissepimentarium. In remaining septal loculi short; close to counter septum shortest.



Text-fig. 9. *Yuanophylloides rectus* (Vassilyuk in Aizenverg *et al.*, 1983). A-F – Specimen UAM-Tc.Don.1/244. Holotype. Transverse thin sections except C and E. A – mature growth stage; B – late neanic/early mature growth stage; C – longitudinal thin section; D – peripheral part of corallite with septa-like protuberations at external wall in right septal loculus; E – rudiments of growth lines and tiny trabeculae in longitudinal section; F – axial septum with median part thickened (enlarged from B). G-I – Specimen UAM-Tc.Don.1/245. Possible paratype. G – enlarged from H to show cardinal septum (lower arrow) connected to major septum of counter quadrant; counter septum indicated by upper arrow; H – late neanic/early mature growth stage; I – lower part of calice. Protosepta and alar septa marked by black solid triangles where recognisable. Scale bar between A and C corresponds to all images except D-G. For occurrences see description of species

Cardinal fossula shallow, dipping slightly into dissepimentarium. Dissepimentarium in cardinal quadrants narrow, composed of 2–3 rows of regular dissepiments; widest next to counter septum. Dissepiments in transverse section mostly herringbone, in longitudinal section convex (Text-fig. 9C), arranged in 2–3 vertical rows. Tabulae incomplete, elevated towards axial septum at approximately 45°. Remnants of microstructure preserved in restricted fragments of major septa in holotype (Text-fig. 9E). Very tiny bodies, < 0.01 mm in diameter, arranged perpendicular to growth lines and passing through several of them, are interpreted as rudiments of trabeculae.

Morphology of specimen interpreted as possible paratype (Text-fig. 9G–I) resembles holotype in most main characters except axial septum. Cardinal septum united with longest major septum of left counter quadrant, but not with counter septum that terminated on tabula (Text-fig. 9G, upper arrow). Unfortunately, only thin section with n:d value 30:10.8 mm and calice with n:d value 33:13 mm available for study.

REMARKS: Vassilyuk (in Aizenverg *et al.* 1983, pl. 28, fig. 7) illustrated the mature transverse section of the holotype and described it in the figure captions as follows: “*Pseudokoninckophyllum rectus* gen. et sp. nov. Amvrosievskiy r-n, khut. Svistuny, izv. E₁”, meaning “Amvrosievskiy region, Svistuny Village, Limestone E₁”. She did not indicate the specimen illustrated as being the holotype, did not provide generic and specific diagnoses and did not describe her new species and genus. However, the specimen has been illustrated, the type area and the stratum have been indicated and the specimen has been specified as belonging to the new genus and species. Thus, the main formal ICZN requirements were met. This allows the specimen in question to be accepted as representing a new species and to designate it formally as the intended holotype. However, all the main diagnostic characters of *Pseudokoninckophyllum* correspond to the diagnosis of *Yuanophylloides*, which is why the former is synonymised herein with the latter.

Yuanophylloides rectus differ from *Y. gorskyi* in that the major septa are longer and thicker at the dissepimentarium/tabularium boundary, the minor septa are much shorter, the cardinal fossula is better developed, the inner wall is slightly thickened and the n:d value is different. Its immature morphology resembles the early mature growth stage of *Y. cruciformis*, but mature growth stages of those two species differ considerably in the length of the major and minor septa and in lonsdaleoid dissepiments that are present in *Y. cruciformis*.

OCCURRENCE: Krynka River Area, Amvrosievskiy Region, Svistuny Village, Limestone E₁. Svita C₂^b_a^{nizhn}, Feninian Substage, *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiogmathodus sinuosus* conodont Biozone, *Reticulocebras*–*Bashkortoceras* (R₁) ammonite Biozone. Early Bashkirian.

Yuanophylloides inauditus (Moore and Jeffords, 1945)
(Text-fig. 10)

1945. *Dibunophyllum?* *inauditum* Moore and Jeffords, p. 157, text-fig. 148.

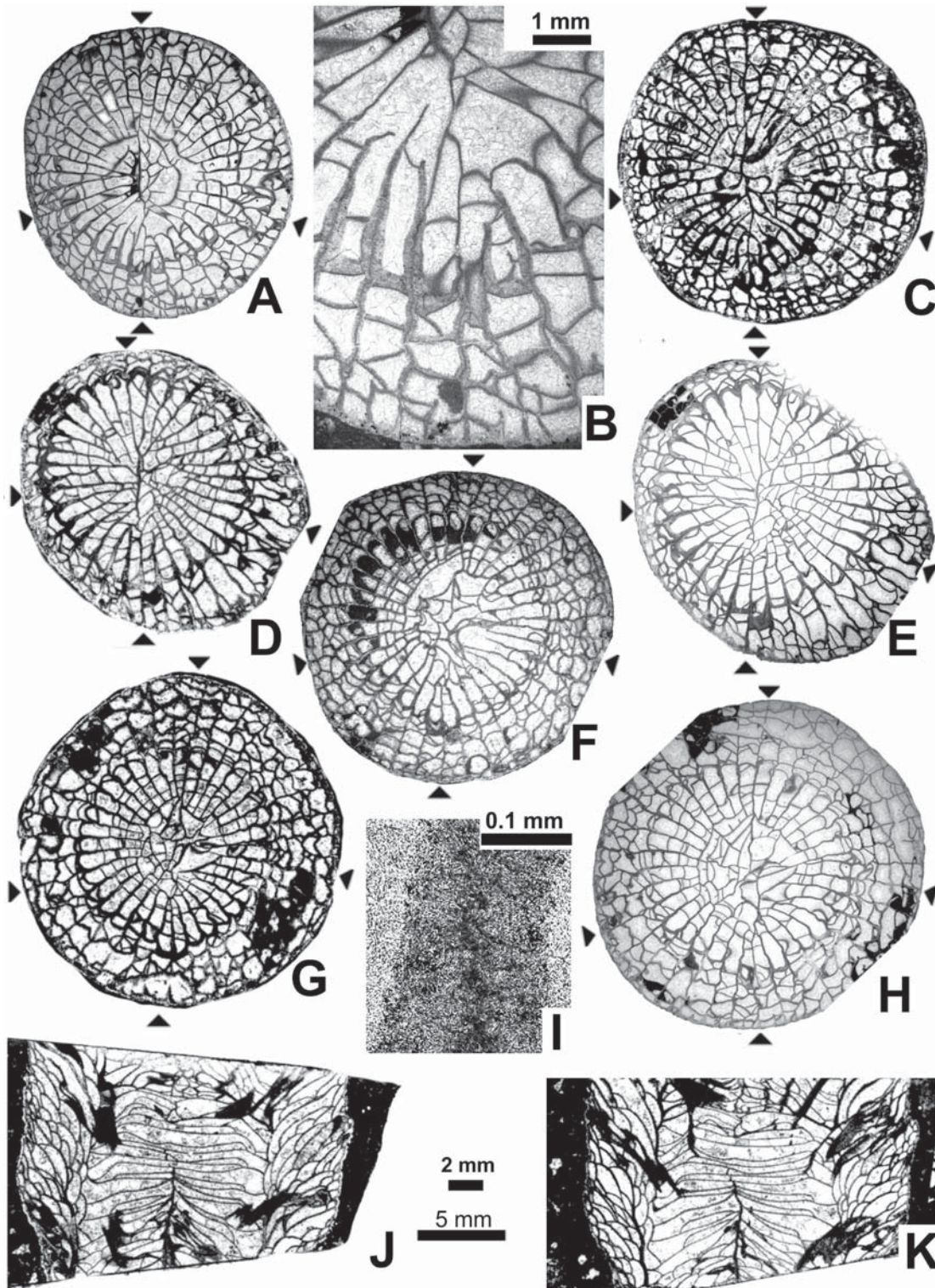
1945. *Neokoninckophyllum simplex* Moore and Jeffords, p. 159, text-figs 149, 150, 156.

non 1964. *Koninckophyllum simplex* (Moore and Jeffords); Rowett and Sutherland, p. 55, pl. 7, figs 1, 2; pl. 8, figs 4–6.

MATERIAL: Three fragmentary specimens, UAM-Tc.Don.1/246–248, all mature growth stages and all sectioned. Internal structure well preserved, but microstructure of septa altered by diagenesis. Three thin sections and 12 peels available for the study.

EMENDED DIAGNOSIS: *Yuanophylloides* with n:d value 40:16.0 mm (holotype) and 38:19.5 mm to 40:21.5 mm in other specimens; several major septa approaching corallite axis, some joining axial septum that may be temporarily interrupted; minor septa restricted to peripheral dissepimentarium; cardinal fossula indistinct, in maturity marked by triangular arrangement of last pair of major septa; dissepimentarium one-quarter to one-third of corallite radius in width; dissepiments irregular; rare lonsdaleoid dissepiments may occur.

DESCRIPTION OF DONETS BASIN SPECIMENS: N:d values: UAM-Tc.Don.1/246 : 38:19.5, 38:16.5; UAM-Tc.Don.1/247: 36:19.6, 32:14.0; UAM-Tc.Don.1/248: 40:21.6. Internal wall thin, almost smooth. Major septa amplexoid. In earliest mature growth stage studied (Text-fig. 10A, D, E) major septa long, several approaching or meeting thin axial septum, irrespective of their position against tabulae, i.e., below or above tabula surface. In more advanced growth stage amplexoid character of major septa recognisable. Their marked shortening beneath tabulae may result in temporary appearance of weak, partially isolated axial structure (Text-fig. 10A, F, H). Major septa above tabulae surfaces long, slightly differenti-



Text-fig. 10. *Yuanophylloides inauditus* (Moore and Jeffords, 1945). Transverse thin sections except when stated otherwise. A-C – Specimen UAM-Tc.Don.1/246. A, C – mature growth stage (C – peel); B – enlarged from A to show extremely thin cardinal septum elongated towards thickened margin of counter septum. D-K – Specimen UAM-Tc.Don.1/247. D-G, H – mature growth stage; I – microstructure of septum altered diagenetically with probable rudiments of trabeculae; J, K – longitudinal section; two surfaces of cut, approximately 0.6 mm apart (F, G, J, K – peels). Protosepta and alar septa marked by black solid triangles. Scale bars between J and K corresponds to all images except B, I. For occurrences see description of species

ated in length, most approaching corallite axis. Their slight thickening in peripheral tabularium better accentuated in cardinal quadrants. Axial septum thin, temporarily divided into cardinal and counter septa. Isolated median lamella not developed. Cardinal septum very thin ended, varying in length: restricted to cardinal fossula in some sections (Text-fig. 10F, G), elongated to corallite axis (Text-fig. 10C, H) or forming part of axial septum (Text-fig. 10D, E). Counter septum thin, permanently long. Minor septa very thin, rarely extending up to one third of dissepimentarium width; commonly restricted to part of dissepimentarium closest to periphery; in some septal loculi unrecognisable. Cardinal fossula indistinct, dipping slightly into dissepimentarium, parallel walled in earliest growth stages studied (Text-fig. 10A, D, E), triangular in advanced mature growth stage (Text-fig. 10C, F, G). Dissepimentarium one quarter to almost half of corallite radius in width. Widest dissepimentarium in transverse sections resulting from curvature of corallite and local obliqueness of section. Most dissepiments interseptal, large and slightly irregular, some herringbone. Lonsdaleoid dissepiments rare, restricted to small parts of peripheral dissepimentarium. In longitudinal section (Text-fig. 10J, K) dissepiments highly differentiated in size and shape from small, bubble-like to flat, occupying most of dissepimentarium width. Tabulae complete and incomplete; at periphery slightly downturned with rare, downsloping peripheral tabellae; in median part elevated towards axial septum when present or flat, slightly sagging when axial septum temporarily interrupted. Long, flat periaxial tabellae attached to both kinds of tabulae.

REMARKS: Moore and Jeffords (1945, pp. 158 and 161) sectioned only four specimens and assigned them to two different genera and species. None of those specimens was investigated for all growth stages. The ontogenetically earliest stage illustrated in an oblique thin section (Moore and Jeffords 1945, fig. 149a) corresponds to a late neanic/early mature growth stage and documents the morphology typical of the genus *Yuanophylloides*. The mature morphology of the specimens illustrated differ only in small details. Thus, both are here synonymised, with the common species name *inauditum* having page priority.

Corallites from the Donets Basin are similar to the type and other North American corallites in all the main characters of mature morphology, including rare appearances of lonsdaleoid dissepiments. Small differences in the $n:d$ value among the Donets

Basin and between them and the North American specimens are best interpreted as intraspecific variability. The dissepimentaria of the Donets Basin and North American specimens are strikingly similar in the longitudinal sections, but the tabulae differ. Periaxial tabellae in North American specimens are shorter and more numerous (Moore and Jeffords 1945, figs 148d, 150c) than those in the material from the Donets Basin. The overwhelming similarities in other characters prevail over such a small difference and both groups of specimens are assigned to the same species.

OCCURRENCE: USA, Oklahoma, near and in Keough Quarry near Fort Gibson, Hale Formation, Praire Grove Member, upper *Reticuloceras*–*Bashkortoceras* (R_2) perhaps to G_1 ammonoid Biozone (Dr. Alan Titus, personal communication in letter of 3rd July, 2017), Lower Morrow. Donets Basin, Krynka River Area, Ambrosievskiy Kupol: UAM-Tc. Don.1/246; Bolshaya Shishovka Ravine, UAM-Tc. Don.1/247 and 248, Limestone E_2 . All Donets Basin specimens from the Feninyan Substage, lower (R_1) *Reticuloceras*–*Bashkortoceras* ammonite Biozone, *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathodus sinuatus* conodont Biozone, Suite $C_2^{b_{a\ n\ izh}}$ (Suite after Poletaev *et al.* 2011). Lower Bashkirian.

REMARKS ON SOME OF FOMICHEV'S GENERA

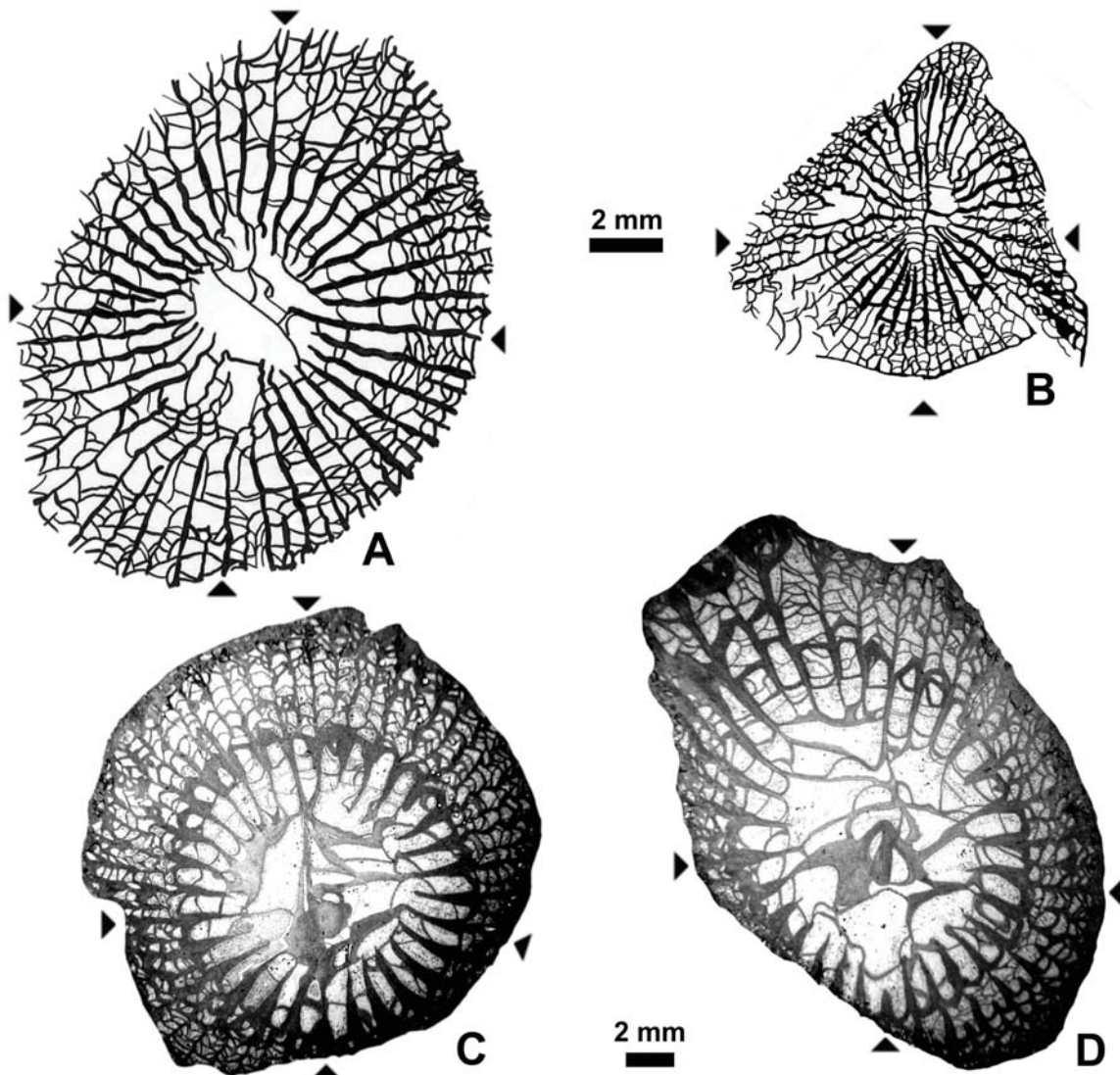
Three genera, namely *Lophophyllum* Milne Edwards and Haime, 1850, *Orygmophyllum* Fomichev, 1953, and *Sestrophyllum* Fomichev, 1953, require some attention within the context of the present paper. Some, if not all, species of the two first genera and one species of *Sestrophyllum* are assigned here to the Family Neokoninckophyllidae despite having been included by Fomichev (1953) in three different families. The documentation of those species in Fomichev's paper (1953) and supplemented by peels taken by me from his original material are differentiated in their cognitive value. Thus, the remarks that follow below differ in detail, with some being restricted to short comments and illustrations supplementary to those published by Fomichev (1953). They are given here in order to make the early Pennsylvanian Donets Basin rugose coral fauna better understood and more easily utilised in phylogenetic studies of the Rugosa and assessments of their palaeogeographic distribution.

Genus *Lophophyllum* of Fomichev, 1953 non Milne Edwards and Haime, 1850
(Text-fig. 11A–D)

REMARKS: Most comments on the Family Lophophyllidae and the genus *Lophophyllum* are included above in remarks on the Family Neokoninckophyllidae. The comments below are added in order to draw attention to the morphological variety of four new species, one species identified as *conformis*, one species (with a question mark) left in open nomenclature and one

“forma” identified by Fomichev (1953, pp. 261–274, pl. 15, figs 10–15; pl. 16, figs 1–5) as *Lophophyllum*. All the main characteristics of those specimens match the diagnosis of the Family Neokoninckophyllidae, to which all should be assigned.

Lophophyllum intermedium (but not forma *elongata*) and *L. posttortuosum* (but not specimens illustrated by Fomichev 1953 in pl. 16, figs 2, 3a, b) are included here in *Yuanophylloides*, possibly forming a separate subgenus. The two specimens excluded from the species cited closely resemble



Text-fig. 11. *Lophophyllum* Fomichev, 1953 non Milne Edwards and Haime, 1850. Transverse sections. Images of peels taken from remnants of Fomichev's (1953) specimens **A, B** – *L. posttortuosum* Fomichev, 1953. **A** – Specimen No. 686. Perhaps surface above that illustrated by Fomichev (1953, pl. 16, fig. 3b). Ryazantseva Balka (Ravine), Limestone N₁. **B** – Specimen No. 469. Surface beneath that illustrated by Fomichev (1953, pl. 16, fig. 2). Shiryayeva Balka (Ravine), Limestone M₁. **C, D** – *L. topschiense* Fomichev, 1953. Specimen No. 52a/38. Holotype. Dyadinaya Balka (Ravine). Limestone K₉. Peels taken from surfaces supplementing thin sections illustrated by Fomichev (1953, pl. 15, fig. 15a, b). All occurrences after Fomichev (1953, Atlas, pp. 32, 33). Protosepta and alar septa marked by black solid triangles. Scale bars between two images correspond to both

Neokoninckophyllum. Specimen No. 469 (Fomichev 1953, pl. 16, fig. 2; Text-fig. 11B herein) may belong to *N. tanaicum*, whereas specimen No. 686 (Fomichev 1953, pl. 16, fig. 3a, b; Text-fig. 11A herein) belongs perhaps to *N. soshkinae* as documented by a reduced median lamella, a slightly shortened cardinal septum, and a complex dissepimentarium, with lateral dissepiments present in some loculi.

Lophophyllum topshiense Fomichev, 1953, which is represented solely by an incomplete holotype (Fomichev 1953, pl. 15, fig. 15a–v; Text-fig. 11C, D herein), may belong to *Neokoninckophyllum*, but its poor documentation allows only a tentative assignment. The corallite, identified as *L. intermedium* forma *elongata* (Fomichev 1953, pl. 15, fig. 12a–v), resembles *Orygmophyllum* and may belong to that genus. The remaining specimens identified by Fomichev (1953)

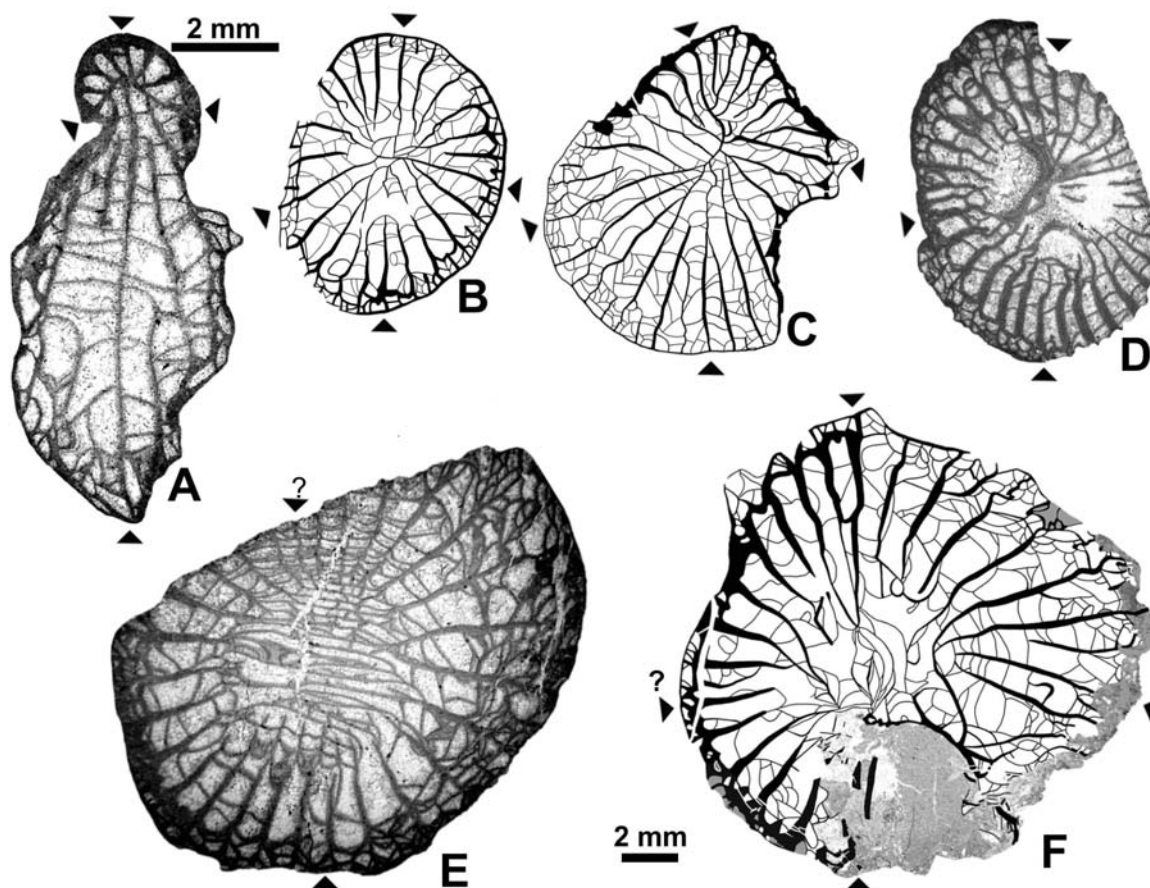
as *Lophophyllum* were illustrated by him in such an inadequate way that comments cannot be made.

Genus *Orygmophyllum* Fomichev, 1953
(Text-fig. 12)

TYPE SPECIES: *Orygmophyllum convexum* Fomichev, 1953, OD.

SPECIES INCLUDED: *O. convexum* Fomichev, 1953, *O. concavum* Fomichev, 1953, *O. troitskense* Fomichev, 1953, ?*Neokoninckophyllum campophylloides* Fomichev, 1953.

EMENDED DIAGNOSIS: Solitary, dissepimented rugose corals; major septa, including protosepta, am-



Text-fig. 12. *Orygmophyllum* Fomichev, 1953. Transverse sections with peels. **A, B** – *Orygmophyllum concavum* Fomichev, 1953, specimen No. 394a. Holotype. **A** – oblique section, neanic growth stage; **B** – early mature growth stage. Both beneath thin section illustrated by Fomichev (1953, pl. 118, fig. 8b). Left bank of Kalitva River, Limestone O₂, coal seam VII-31. **C, D** – *Orygmophyllum troitskense* Fomichev, 1953. Two corallites bearing specimen No. 379, but different from specimen with the same number illustrated by Fomichev (1953, pl. 18, fig. 7a, b). Probably Kalinovskoe Village, Limestone P₁, coal seam IV-22. **E, F** – *Orygmophyllum convexum* Fomichev, 1953. Paratypes. **E** – Specimen No. 394c, mature growth stage (not illustrated by Fomichev 1953). **F** – Specimen No. 394b, mature growth stage. Above thin section illustrated by Fomichev (1953, pl. 18, fig. 13). Left bank of Kalitva River, Limestone O₂, coal seam VII-31. (All occurrences after Fomichev 1953, p. 38, Atlas). Protosepta and alar septa marked by black solids triangles where recognisable. Scale bar between E and F corresponds to all images except A

plexoid; their rotiphyllid arrangement with long cardinal septum lasting up to late neanic growth stage; in maturity cardinal septum slightly shortened, axial area free except close to upper tabulae surfaces when major septa, including counter septum temporarily elongated; dissepimentarium complex; lateral dissepiments sporadic; tabularium normal; disstabularium may develop; tabulae incomplete, flat and/or sagging axially when major septa short.

REMARKS: Fomichev (1953, pl. 18, figs 3–14; pl. 19, figs 1, 2) erected five new species (two questionably) as members of his new genus *Orygmophyllum*, which he assigned to the Family Campophyllidae. However, a corallite axial area that is temporarily free of major septa, is the only feature in common between *Orygmophyllum* and the late Famennian genus *Campophyllum* Milne Edwards and Haime, 1850, i.e., the only genus included in that family by Hill (1981). Thus, Fomichev's assignation is not followed in this paper.

The morphology of particular species of *Orygmophyllum* differs to such a degree that the congeneric nature of some of them is doubtful. Unfortunately, inadequate documentation in Fomichev's (1953) paper and lack of peels of some of Fomichev's (1953) species in my present collection preclude comprehensive comments on the doubtful species. *Orygmophyllum altschevskianum* Fomichev, 1953 is not commented upon. Pictures published by Fomichev (1953, pl. 18, figs 3a–v, 4a, b) suggest that it might be referable to the Family Neokoninckophyllidae, but nothing more.

Two specimens were illustrated by Fomichev (1953, pl. 19, figs 1a–d, 2a–v) under the name of ?*O. marjevkense*. The questionable status of that species, established by Fomichev (1953), is expanded on here. The earliest known growth stage of its holotype and the mature growth stage of the paratype closely resemble the corresponding growth stages of members of the Family Bothrophyllidae (Fomichev 1953, pl. 19, figs 1a and 2b, g, respectively). The mature growth stage of the holotype (Fomichev 1953, pl. 19, fig. 1b, v) resembles either *Orygmophyllum convexum* or some specimens of *Lophophyllum* Fomichev, 1953 non Milne Edwards and Haime, 1850. Immature growth stages of the paratype (Fomichev 1953, pl. 19, fig. 2a, b) closely resemble *O. troitskense*. V.D. Fomichev appears to have mixed sections of different specimens; for that reason, this species is not considered further here.

Particular growth stages of *O. troitskense* illustrated in Fomichev (1953, pl. 18, figs 5–7) and Text-fig. 12C, D herein, and those of the holotype of ?*O.*

concaevum Fomichev, 1953 (his pl. 18, fig. 8a–v; Text-fig. 12A, B herein) document their close relationship or even conspecificity. Both species differ from the holotype of *O. convexum* in having the mature growth stage short septal. The arrangement of the major septa in the early mature growth stage of *O. concaevum* (Fomichev 1953, pl. 18, figs 5, 6a, 8b; Text-fig. 12B herein) and the paratype of *O. convexum* (Fomichev 1953, pl. 18, fig. 12a), is here accepted as typical of *Orygmophyllum*. That growth stage is lost from the holotype of *O. convexum* as suggested by the great difference in morphology, in the number of septa and in the corallite diameter between its two successive transverse sections (Fomichev 1953, pl. 18, fig. 11a vs 11b).

The morphology of two specimens included by Fomichev (1953) in *O. convexum* (Text-fig. 12E, F) and two specimens of *O. troitskense* (Text-fig. 12C, D) exceed the margins of individual variation acceptable for a species, but new names are not proposed here for these specimens (for further discussion see Considerations below).

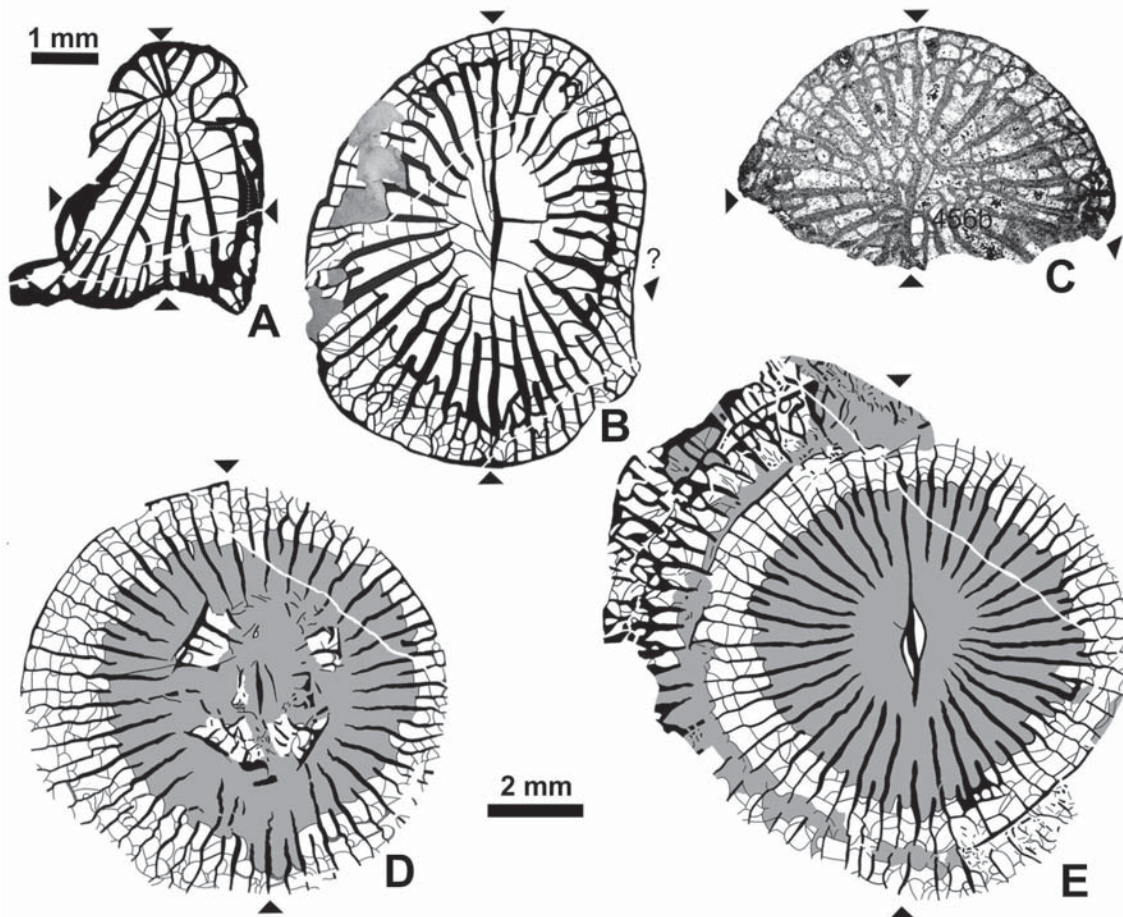
Sestrophyllum Fomichev, 1953

(Text-fig. 13)

TYPE SPECIES: *Sestrophyllum astraeforme* Fomichev, 1953, OD.

REMARKS: The type specimen of *Sestrophyllum* and most specimens included in that genus by Fomichev (1953, pl. 26, figs 7–16) represent a new, distinct family as suggested previously (Fedorowski 2017b). The holotype of *Sestrophyllum? ancestor* Fomichev, 1953 may also belong to that unnamed family, provided that its everted calice (Fomichev 1953, pl. 26, fig. 16a–v) is proved. However, the main characters of the paratypes of that species (Fomichev 1953, pl. 26, fig. 17; Text-fig. 13A–C herein) and of *S.? ancestor* forma *complexa* (Fomichev 1953, pl. 26, fig. 18; Text-fig. 13D, E herein) differ distinctly from the type species of the genus.

All specimens questioned here as members of *Sestrophyllum* possess sharp-ended calices. All dissepiments are interseptal and either rectangular or herringbone, but more irregular dissepimentaria with rare lateral dissepiments occur in some septal loculi. The cardinal and counter septa are permanently united with the slightly thickened median lamella to form the axial septum that lasts up to the mature growth stage (Text-fig. 13A–C). The cardinal septum is slightly shortened



Text-fig. 13. **A-C** – *Sestrophyllum? ancestor* Fomichev, 1953. Transverse sections with peels. A, B – Specimen No. 456d, not illustrated by Fomichev. A – early neanic growth stage; B – mature growth stage; C – specimen No. 456b. Mature growth stage. Probably above thin section illustrated by Fomichev (1953, pl. 26, fig. 17a); **D, E** – *Sestrophyllum? ancestor* forma *complexa* Fomichev, 1953, pl. 26, fig. 18. Specimen No. 456a. Mature growth stage with axial (D) and peripheral (E) rejuvenation. All from Malaya Nesvetaya River bank, Limestone K₂? (after Fomichev 1953, p. 54, Atlas). Protosepta and alar septa marked by black solid triangles where recognisable. Scale bar between D and E corresponds to all images except A

above the calice floor, but the free medial lamella is not isolated from the counter septum up to the lower part of the calice (Text-fig. 13E). The cardinal fossulae dip slightly into the dissepimentaria. All those characters point towards the Family Neokoninckophyllidae, to which these specimens are transferred herein. Peculiar structures observed in one specimen (Text-fig. 13D, E) are the result of rejuvenation.

Sestrophyllum pumilum Fomichev, 1953 (pl. 27, fig. 1a–v) from Limestone P₂ is the next taxon unrelated to *S. astraeforme* as documented by the arrangement of peripheral dissepiments in longitudinal section. Some of its characters point towards the genus *Dibunophylloides*. However, data provided by Fomichev (1953) are inadequate for a firm decision.

CONSIDERATIONS

Family derivation

Inclusion of the Family Neokoninckophyllidae into the synonymy of the Subfamily Dibunophyllinae (Hill 1981) forms a good starting point to the discussion, whereas the incompleteness of the literature data reduces the following remarks to mere suggestions rather than solutions. Important characters in common to both Dibunophyllinae and Neokoninckophyllidae are: 1. the axial septum lasting at least to the late neanic growth stage; 2. the division of the axial septum into the cardinal septum, the counter septum and the monoseptal median lamella;

3. the shortening of the cardinal septum; 4. the appearance of septal lamellae; 5. the total reduction of the axial structure at advanced maturity of rare species; 6. the tabularium normal; 7. the microstructure of septa very finely trabecular.

The following exceptions from those general similarities are established: 1. In most of the Viséan *Dibunophyllum*, the median lamella is separated from the axial septum early in ontogeny. It remains connected with the cardinal septum longer than with the counter septum. In Serpukhovian and early Bashkirian species of *Dibunophyllum* and *Dibunophylloides* of the Donets Basin, the continuous axial septum lasts long in the ontogeny. The latter character is here suggested to be an expression of neoteny or paedomorphosis. It makes the early ontogeny of those genera similar to that of the earliest Bothrophyllidae (Fedorowski 2017a, b) and the earliest Neokoninckophyllidae, i.e., *Yuanophylloides*. The early ontogeny of *Orygmophyllum* differs in that respect from both families. 2. The median lamella commonly constitutes a constant and fundamental part of the axial structure in the Dibunophyllinae, connected to or elongated towards the cardinal septum. The counter septum is rarely elongated towards and meets the median lamella. In contrast to the Dibunophyllinae, the isolated median lamella rarely appears in the Neokoninckophyllidae. In the latter the axial septum becomes divided into two unequal segments: the long counter septum and the much shorter cardinal septum. The median lamella, if present, is cut off from the inner part of the counter septum. A permanent axial septum or elongated counter septum with median lamella not isolated prevails in the simplest Neokoninckophyllidae such as *Yuanophylloides*. 3. The cardinal septum in the Dibunophyllinae shortens early in the ontogeny and remains short, whereas its length in the Neokoninckophyllidae may either vary due to its amplexoid character, or becomes slightly and permanently shortened, but only at an advanced adult growth stage. 4. The septal lamellae are fundamental skeletal elements in the axial structure of all Dibunophyllinae other than *Koninckophyllum* and coral genera morphologically similar to it. The latter taxa may form a different subfamily as already suggested by Wang (1950). Septal lamellae in the Neokoninckophyllidae are rare, being commonly replaced by continuous, amplexoid major septa, elongated above tabulae surfaces. 5. A total reduction of the axial structure appears only in *Turbinatocania* of the Dibunophyllinae, if *Koninckophyllum interruptum* Thomson and Nicholson, 1876 is not considered, whereas such a morphology appears in most genera

that are here included in the Neokoninckophyllidae. 6. The normal tabularium present in both families is commonly replaced by the disstabularium in the Neokoninckophyllidae, whereas such a structure is absent from the Dibunophyllinae. 7. The microstructure of septa is poorly documented in both families, precluding a detailed comparison.

Four options of derivation of the Neokoninckophyllidae are possible when similarities and differences listed above are taken into consideration: 1. derivation directly from Brigantian taxa, such as those described from Poland and included in the genus *Neokoninckophyllum* (Fedorowski 1971); 2. derivation either from *Lophophyllum infirmum* Gorskiy, 1938 (uncertain Viséan–Namurian strata of Novaya Zemlya, Russia) or a species morphologically similar to it; 3. derivation from simplified Chinese Viséan and Serpukhovian Dibunophyllinae, such as those included by Yu (1937, pl. 5, fig. 9a–c; pl. 6, figs 6a–c; 7a, b) in *Lophophyllum (Arachnolasma)* Grabau, 1922; 4. derivation from the early Bashkirian *Dibunophylloides* of the Donets Basin.

The first option is attractive on account of the morphological similarity of Polish specimens to Moscovian representatives of the Neokoninckophyllidae and by differentiation in length of their protosepta: either the cardinal septum or, more commonly, the counter septum prevails in length in those specimens (Fedorowski 1971, fig. 42F₁ vs figs 41A–C, 42E, 43A–C). *Mira prima* (Fedorowski 1971, fig. 52), renamed *Mirka* Fedorowski, 1974, with its axial septum present early in the ontogeny, with a dense dissepimentarium including lateral dissepiments and with an inconsistent axial column may support that option. However: 1. taxa morphologically similar to the Polish species have never been described from Brigantian and Serpukhovian strata, either in the Western European Province or in the Eastern European Province, including the Donets Basin, 2. the Sudetic Orogeny uplifted most of the western and central European terrains, including the territory of present-day Poland, 3. the uplift created an impassable barrier for Serpukhovian rugose corals. Thus, the notion of a direct derivation by descendants of Bashkirian and younger neokoninckophyllids from taxa like those of the Polish Brigantian strata, is rejected.

The second option, i.e., Novaya Zemlya, is more likely for two reasons. First of all, a direct link between that area and the Sverdrup Basin in North America, the Far East and eastern European basins is very probable. Secondly, that area has already been considered as a probable refugium for *Dibunophyllum*

(Fedorowski *et al.* 2012). Thus, Novaya Zemlya could well be treated as both a refugium of some late Mississippian taxa and an origination area of some Pennsylvanian rugose corals including the Neokoninckophyllidae. However, more indisputable data are called for in order to accept that option.

The third option, i.e., derivation of the Neokoninckophyllidae from one of the simple Chinese Dibunophyllinae is possible as well. Unfortunately, that option is not considered possible at present, because the taxa are not documented well enough. Moreover, some of the Chinese species included here in the genus *Yuanophylloides* are stratigraphically older than other taxa included in the emended family Neokoninckophyllidae. However, those species, as well as other potential ancestors of the Neokoninckophyllidae, such as *Arachnolasma* mentioned above, require a thorough restudy prior to be considered in earnest further.

The fourth option, i.e., derivation of the Neokoninckophyllidae from morphologically simplified Serpukhovian/earliest Bashkirian Dibunophyllinae of the Donets Basin is the most probable option, which is best supported by data available today. Representatives of the subfamily Dibunophyllinae are common and continuously present in Viséan, Serpukhovian and Bashkirian strata of that basin (Vassilyuk 1960, 1964; Fedorowski 2017b). The paralic character and cyclic accumulation of the deposits in the Donets Basin do not contradict the continuous development of the coral fauna. The deposits of late Viséan to early Bashkirian age are mostly marine, belonging to the progressive part of the cycle (Poletaev *et al.* 2011; followed by Fedorowski 2017b).

In my attempt to reconstruct the phylogeny of Serpukhovian–Bashkirian Dibunophyllinae (Fedorowski 2017b), I still consider a direct phylogenetic link between *Dibunophyllum medium* Fedorowski, 2017b and *Dibunophylloides paulus* Fedorowski, 2017b. Consequently, the disappearance of the axial column and simplification of the axial structure has been accepted as the main trend in the development of middle Bashkirian and younger descendants of the earliest Bashkirian Dibunophyllinae. Derivation of the Family Bothrophyllidae from those descendants has already been discussed (Fedorowski 2017a, b). It forms one phylogenetic lineage that originated from *Dibunophylloides* near the Serpukhovian/Bashkirian boundary. A second phylogenetic lineage, i.e., the Family Neokoninckophyllidae, is suggested here (Text-fig. 4). At the start this lineage is characterised by a continuous presence of the axial septum in ontogeny, as observed in *Yuanophylloides rectus*

(Vassilyuk in Aizenverg *et al.*, 1983), the stratigraphically oldest species of the Neokoninckophyllidae found in the Donets Basin to date. Also, in that species the median part of the continuous axial septum is thickened in the late neanic/early mature growth stage, the cardinal fossula is developed during the entire ontogeny and the dissepimentarium is narrow, simple and clearly distinguishable from the tabularium. The latter character means that the dissepimentarium, common in advanced neokoninckophyllids, is absent from *Y. rectus*. The list of similarities to the early Bashkirian Dibunophyllinae on the one hand and to the slightly younger representatives of *Yuanophylloides* on the other, suggest an intermediate position of *Y. rectus* between two families. Thus, it is accepted here as ancestral to the family Neokoninckophyllidae until a better candidate is found.

The phylogeny within the neokoninckophyllid lineage, summarised in Text-fig. 4, includes the following features: 1. Differentiation in the development of the cardinal and counter septum. The former may be temporarily or permanently shortened at different growth stages. As a rule, the latter is elongated, but exceptions such as length equal to adjacent major septa do occur. The median lamella, if present, is invariably derived from the axial part of the counter septum, but that separation is commonly temporarily. 2. The major septa amplexoid and differentiated in length with the counter septum permanently long, are characteristic of *Yuanophylloides* and occur in most species of *Neokoninckophyllum*. This means that the acolumellate growth stage is absent from the former genus during its entire phylogeny, inclusive of its Moscovian species. The acolumellate growth stage occurs in some species of *Neokoninckophyllum* and commonly appears in *Orygmophyllum*. Thus, a kind of a sequence in the appearance and development of that character is recognised among the Donets Basin species. “*Neokoninckophyllum*” *acolumellatum* Cocke, 1970 (his pl. 4, figs 13, 14) is not taken into account because the early growth stage of that species remains unknown. 3. The appearance of septal lamellae, a character fundamental for the axial structure in *Dibunophyllum*, *Dibunophylloides* and closely related genera, such as *Arachnolasma*. In contrast to those Dibunophyllinae, the major septa in the Neokoninckophyllidae are most commonly amplexoid. The shape and length of such septa in transverse sections taken just above and just below tabulae surfaces are discussed in the systematic part of the paper (see above). The amplexoid character of the major septa means that skeletal bodies attached to sections

of tabulae are not always true septal lamellae, i.e., skeletal structures permanently separated from the inner margins of the major septa. However, such true septal lamellae may temporarily occur in most genera included here in the family Neokoninckophyllidae. As mentioned in the systematic part of the paper, their best development is observed in the Moscovian “*Histiophyllum*” *mediocarbonicum* Fomichev, 1953. However, they also occur in the early Bashkirian *Yuanophylloides inauditum* (Moore and Jeffords, 1945). This character does not form any sequence in the occurrence, but its random occurrences are treated here as rudiments pointing to the Dibunophyllinae as the closely related and ancestral taxon. 4. Variety in the development of the dissepimentarium. This feature remains simple in *Yuanophylloides*, but grape-like dissepiments appear at the periphery in *Orygmophyllum* and the dissepimentarium is very complex in *Neokoninckophyllum*. Thus, that character can perhaps be accepted as generic and discussed as important for intrageneric phylogeny.

Derivation of the Donets Basin Neokoninckophyllidae and Bothrophyllidae from the Dibunophyllinae by descent is very probable when all of the remarks listed above are considered. Data published by Fomichev (1953), Vassilyuk (1960, 1964, and in Aizenverg *et al.* 1983), Fedorowski and Ogar (2013), and Fedorowski (2017a, b) allow one to consider that thesis well supported. Whether or not that relationship can be extended to all species across the globe that have characters of the Neokoninckophyllidae remains to be determined.

The North American species included here in the Neokoninckophyllidae can be accepted as related to the Donets Basin taxa. This observation is supported by three facts: 1. The appearance of the simplest and oldest neokoninckophyllid in the Donets Basin slightly earlier (Limestone E₁ = R₁ biozone) than the oldest North American representative of that family (Hale Formation = R₂ to G₁ biozones). 2. The absence of *Dibunophyllum* and *Dibunophylloides*, i.e., genera potentially ancestral to the neokoninckophyllids, in the Western Interior Province of North America. 3. The close morphological similarity of some of the oldest North American specimens to the Donets Basin specimens. That close similarity allows to place them in the same species, i.e., *Yuanophylloides inauditus* (Moore and Jeffords, 1945).

In summary the following can be stated. Although the phylogeny suggested above is the most probable when the existing data are considered, Novaya Zemlya and China cannot be excluded as potential areas of the ancestor of the Neokoninckophyllidae.

Thus, future thorough and well-documented studies on corals from those areas may result in modification of the phylogenetic reconstruction above, but all other conclusions would be premature.

Some probable phylogenetic lineages within the family Neokoninckophyllidae

Yuanophylloides

Three species, i.e., *Y. gorskyi*, *Y. rectus* and *Y. inauditus* require special attention. The first named, originating from Limestone M₉ (Donets Basin, upper Moscovian), is the reference taxon as the type species of the genus. The second is of importance in being the stratigraphically oldest and morphologically simplest representative of the genus, whereas the last-named species forms the direct connection between the Donets Basin and basins in Oklahoma and southwest Texas (USA).

Comparison of the morphology of all species described from the Donets Basin and the southwestern United States and included here in the genus *Yuanophylloides*, allows some preliminary phylogenetic reconstructions. *Yuanophylloides rectus* plays a key role in this comparison: it either is the taxon that is intermediate between the Dibunophyllinae and Neokoninckophyllidae or is closely related to such intermediate species as postulated above. Also, its morphology (Text-fig. 9A–I) allows the connection of morphologically distant species such as *Y. gorskyi* (Fomichev 1953, pl. 16, fig. 12a–v; Text-fig. 8A–E herein) and *Y. inauditus* (Moore and Jeffords 1945, figs 148–150; Text-fig. 10A–K herein). A comparison of the three species mentioned above, plus *Y. cruciformis* and North American “neokoninckophyllids”, allows one to assume two main phylogenetic lineages within the genus *Yuanophylloides* and its probable descendants:

1. Lineage *Y. rectus* → *Y. cruciformis* → *Y. gorskyi*. The species listed are treated only as milestones. Arrows between their names signify only a general direction of phylogenetic development, but not a direct derivation of one species from another. Two species assigned by Fomichev (1953) to *Lophophyllum*, i.e., *L. subtortuosum* and *L. intermedium*, form an offshoot of that lineage. The median lamella distinct, commonly separated to form a pseudocolumella, the cardinal fossula well developed and the dissepimentarium simple are the main characters of this offshoot, classified here as an unnamed subgenus. *Yuanophylloides cruciformis* with its septal lamella isolated from both protosepta in maturity, may stay close to a species ancestral to that offshoot. Limited data available to date (see remarks

on *Lophophyllum* above) preclude a more specific reconstruction of that offshoot.

2. Lineage *Y. rectus* → *Y. inauditus* → *Y. simplex* → *Y. gracilis* (the latter three named by Moore and Jeffords 1945) morphologically more advanced North American species. Species names between arrows are only milestones, although the relationship between some of them (e.g., *Y. rectus*–*Y. inauditus*) appears to be a close one. This lineage, originating in the Donets Basin, flourished in the North American Interior Province where three phylogenetic offshoots may have developed: 1. The morphologically simplest offshoot, actually restricted to “*Pseudozaphrentoides*” *lepidus* and “*P.*” *spatiosus*, both named by Moore and Jeffords (1945). The characters of that lineage are reminiscent of cyathopsid or bothrophyllid corals in that the major septa are slightly thickened at the tabularium/dissepimentarium border, a corallite axial area is free except for the elongated counter septum present in some transverse sections and the cardinal fossula well developed. The similarity mentioned was already recognised by Moore and Jeffords (1945), as is demonstrated by the generic name given by them. A new generic name should be applied to those corals when more detailed studies have been carried out. However, their large size and simple morphology may indicate relationships other than to the Neokoninckophyllidae. Cyathopsid corals present in the Mississippian strata of North America should be indicated as an alternative.

The second offshoot includes taxa such as *Koninckophyllum oklahomense* Rowett and Sutherland, 1964 and, perhaps, the North American “*Dibunophyllum*” of several authors (e.g., Newell 1935; Jeffords 1948; Ross and Ross 1962, 1963; Nations 1963; Cocke 1970; Cocke and Haynes 1973; Cocke and Molinary 1973). The dissepimentarium is simple in most representatives of that offshoot, but an introductory development of grape-like dissepiments appears in some species (e.g., *Dibunophyllum arcuatum* Moore and Jeffords, 1945; *D. exiguum* Jeffords, 1948). The cardinal septum and cardinal fossula are barely distinguishable in most, whereas the counter septum is elongated. The comparatively complex axial structure present in the transverse section of species included in this offshoot and the lack of an axial column in the longitudinal section are the most important characters. Species belonging to this offshoot are in need of one or two new generic names.

The third offshoot is represented by *Neokoninckophyllum kansasense* Cocke, 1970 and its two variants. The dissepimentarium is extremely complex with many small lateral dissepiments. The cardinal sep-

tum indistinguishable from adjacent major septa, the cardinal fossula absent and the corallite axial area free from major septa in the mature growth stage are the main distinguishing characters of that offshoot, as is an ability for offsetting. It remains uncertain whether this ability led to the formation of protocolonies or true colonies. Similar to the previously listed offshoots, this one also requires a new generic name and more detailed studies of early ontogeny, offsetting and septal microstructure.

The distinction of all offshoots or phylogenetic lineages mentioned above are no more than suggestions supported by very superficial reinvestigations of the Donets Basin collections and most of the United States collections. Such a preliminary restudy is inadequate for the formal erection of new generic names.

Neokoninckophyllum

A precise reconstruction of the relationships of the Donets Basin species of the genus *Neokoninckophyllum* cannot be presented for two reasons: the morphological variety of species included in that genus by Fomichev (1953, pl. 23, figs 5–9; pls 24, 25, 26, figs 1–4) and the incomplete documentation in some instances. Three species, i.e., ?*N. antipovi*, *N. campophylloides* and *N. stepanovi* have already been excluded from that genus (see above). In addition, several specimens included by Fomichev (1953) in the species accepted here as members of *Neokoninckophyllum* have been illustrated inadequately for firm conclusions to be drawn. Nevertheless, two groups of species or possible phylogenetic lineages can be distinguished within that genus.

The first group consists of the following species described so far: *Neokoninckophyllum tanaicum* (Limestone M_{5, 6}), the holotype of *N. vesiculosum* (Limestone M₇; maybe conspecific with *N. tanaicum*), small specimens (Limestone M_{6, 7}), excluded herein from *N. vesiculosum* as a possibly new species, and *Neokoninckophyllum* sp. nov. (Text-figs 6, 7; Limestones L₁ and M₅, respectively). The permanent elongation of the counter septum, a possible development of the pseudocolumella documented in *Neokoninckophyllum* sp. nov. (Text-fig. 7B, E, G) and the very complex dissepimentarium are the most important characters of this group of species. The width of their dissepimentaria differs, but no sequence is recognised in that and other characters.

Two species, represented by several specimens illustrated, i.e., some specimens of *N. soshkinae* and the holotype of *N. tanaicum* var. *plana*, elevated

herein to species level, form the second of those possible lineages. The amplexoid character of the major septa is doubtful or weakly marked, if present. A corallite axial area is either free from any kind of axial structure or a simple, short median lamella appears temporarily. The counter septum is equal in length to the adjacent major septa, although its elongation in the early growth stage is proven by longitudinal sections at least in some specimens (Fomichev 1953, pl. 23, figs 5g, 6b; pl. 25, fig. 2v). The comparison of width and complexity of the dissepimentaria, superimposed on the stratigraphical positions of particular specimens forming this lineage, allows some phylogenetic suggestions to be made. The two stratigraphically oldest paratypes of *N. soshkinae*, derived from Limestones H₅¹ and K₆ (Fomichev 1953, pl. 25, figs 3a–v, 4a, b, respectively) possess long minor septa, penetrating the tabularia, weakly accentuated disstabularia and a ‘caninoid growth stage’ appearing early in the ontogeny. They belong perhaps to a separate new species. The holotype and remaining paratype of *N. soshkinae*, both originating from Limestone L₁ (Fomichev 1953, pl. 25, figs 2a–v, 5), are here considered as *N. soshkinae* proper. Their minor septa are restricted to one-third to one-half of the peripheral part of the wide dissepimentaria and the disstabularia are well developed. The sequence of this possible phylogenetic lineage ends with the occurrence of the holotype of *N. planum* (Limestone M₂, upper part of lower Moscovian). The concept of that species, as established by Fomichev (1953, p. 360, pl. 23, figs 5–9), is not adopted here. The illustrated paratypes differ morphologically from the holotype to such an extent that their conspecificity is doubtful. Thus, the name *N. planum* is here restricted to the holotype. Its major septa are slightly amplexoid, the minor septa are short, the cardinal septum is almost equal to the adjacent major septa in length and its dissepimentarium is very complex with numerous, long lateral dissepiments attached along the major septa (Fomichev 1953, pl. 23, fig. 5a–g).

The differences between the two groups of species of *Neokoninckophyllum* distinguished here are sufficiently substantial for the distinction of separate genera or subgenera, not introduced here for reasons outlined above.

Orygmophyllum

The immature growth stage of *Orygmophyllum* differs from that of both *Yuanophylloides* and *Neokoninckophyllum* by the rotiphyllid arrangement of the major septa, lasting up to the appearance of

first dissepiments. That arrangement is also radial in more advanced growth stages, whereas a bilateral symmetry is typical of the early growth stages of both *Neokoninckophyllum* and *Yuanophylloides*. Such a difference results from the morphology of the axial septum that is thickened in its median part and long lasting in the latter two genera, whereas in *Orygmophyllum* it is thin all along and divides into the cardinal and the counter septum early in ontogeny.

The morphological and ontogenetic features of *Orygmophyllum* discussed allow us to accept it as a separate genus within the family Neokoninckophyllidae. It resembles *Yuanophylloides* in possessing a narrow dissepimentarium. However, in *Orygmophyllum* this is complex like that in *Neokoninckophyllum vesiculosum*, with rare lateral dissepiments developed. Shortening of the major septa in the mature growth stage of *Orygmophyllum* and reduction in length of the counter septum to the length of the adjacent major septa resembles the situation seen in *Neokoninckophyllum planum*. Thus, a closer relationship of *Orygmophyllum* with *Neokoninckophyllum*, rather than with *Yuanophylloides*, is slightly better supported. Unfortunately, the restricted documentation available to date precludes any adequately supported views about the position of that genus within the phylogenetic lineage of the Family Neokoninckophyllidae.

Neokoninckophyllum campophylloides Fomichev, 1953 (Limestone I₃, upper Bashkirian), provisionally assigned here to *Orygmophyllum*, developed some characters that can be interpreted as leading towards the stratigraphically younger representatives of that genus on the one hand, but resembling remaining neokoninckophyllids on the other. Its axial septum occurs in the early growth stage, like in *Neokoninckophyllum* or *Yuanophylloides*, but it becomes divided into the cardinal and the counter septum soon after, as in *Orygmophyllum* (Fomichev 1953, pl. 26, figs 3a, b, respectively). Also, the arrangement of its major septa is closely comparable to the late neanic and late neanic/early mature growth stages of *Orygmophyllum* (Fomichev 1953, pl. 18, figs 11a, 12a). In the short septal mature growth stage of *N. campophylloides* the dissepimentarium consists of regular dissepiments in a part of the transverse thin section, but is complex with rare lateral dissepiments in the other part of the same thin section (Fomichev 1953, pl. 26, fig. 3d). The similarities listed and the early stratigraphical position of *Neokoninckophyllum campophylloides* speak in favour of both its intermediate phylogenetic position and its closer relationship to *Orygmophyllum* as suggested herein.

Acknowledgements

My warmest thanks are first of all directed to Dr. N. P. Vassilyuk, Professor Emeritus of the Donetsk Polytechnic, who offered her collection for the series of papers on the Bashkirian Rugosa from the Donets Basin. My thanks are also extended to Professor V.V. Ogar, Kyiv University, for his help in clarifying some stratigraphic questions and to Drs. C.H. Stevens, San Jose University, California and Alan Titus, Grand Staircase-Escalante National Monument, Utah for their help in establishing the stratigraphic correlation between the lower Bashkirian in the Donets Basin and the Hale Formation in Oklahoma. Professors Sergio Rodríguez, Ciudad Universitaria, Madrid, Spain and Ian D. Somerville, University College Dublin, Ireland own my sincere thanks for their careful revision of the paper and the important suggestions. I also wish to express my thanks to Marta Bartkowiak M.Sc., Institute of Geology, Adam Mickiewicz University for her excellent technical assistance. The accomplishment of this paper was possible due to the support of the Adam Mickiewicz University in Poznań, Poland.

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Manuscript submitted: 14th November 2017

Revised version accepted: 23rd May 2018