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Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 10. The Family Krynkaphyllidae fam. nov.

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ABSTRACT:

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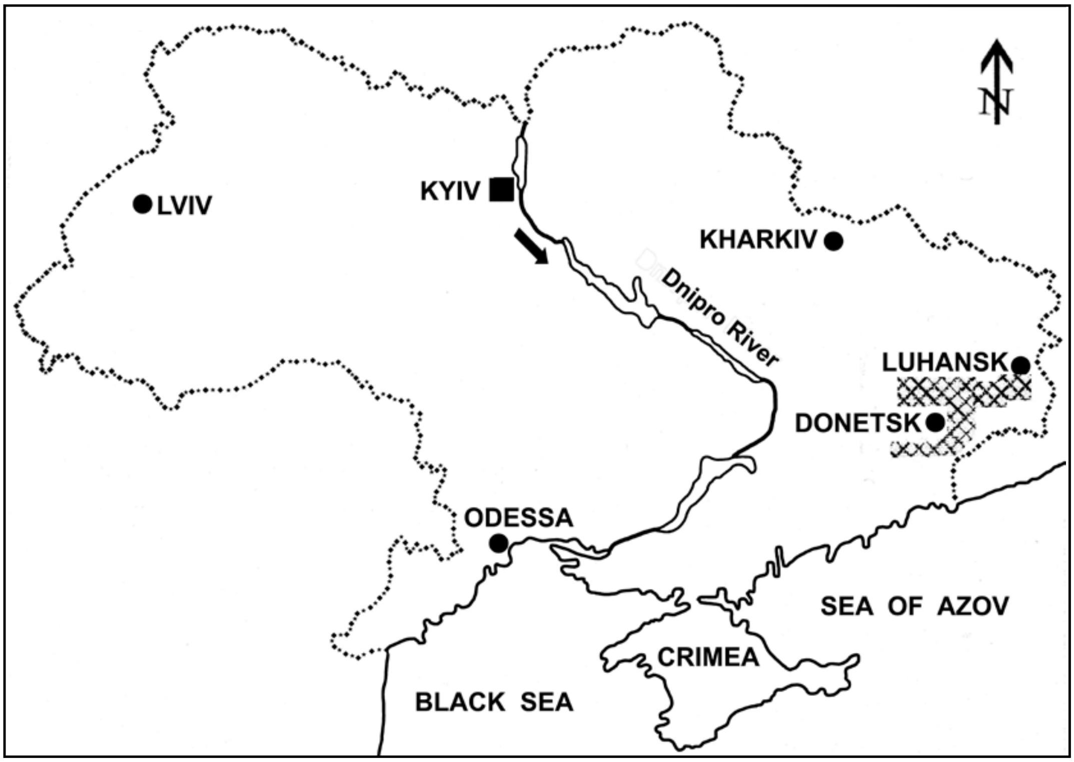
The known occurrence of corals distinguished here in the new Family Krynkaphyllidae varies at the subfamily level. Those of the Subfamily Krynkaphyllinae subfam. nov. are so far almost unknown from outside of the Donets Basin. In contrast, those of the Subfamily Colligophyllinae subfam. nov. are common, possibly ranging from the lower Viséan *Dorlodotia* Salée, 1920, a potential ancestor of the family, to the Artinskian *Lytvophyllum tschernovi* Soshkina, 1925. They bear different generic names, but were all originally described as fasciculate colonial. A detailed study of *Lytvophyllum dobroljubovae* Vassilyuk, 1960, the type species of *Colligophyllum* gen. nov., challenges that recognition in that at least some of those taxa are solitary and gregarious and/or protocolonial. As such, solitary, protocolonial and, probably, fasciculate colonial habits are accepted in the Colligophyllinae subfam. nov., whereas the Krynkaphyllinae subfam. nov. contains only solitary taxa. The resemblance to the Suborder Lonsdaleiina Spasskiy, 1974 led to the analysis of families included in that suborder by Hill (1981) in the context of their relationship, or homeomorphy, to Krynkaphyllidae fam. nov. This question primarily concerns the Family Petalaxidae Fomichev, 1953; a relationship with the Family Geyerophyllidae Minato, 1955, is more distant, if one exists. The distinct, parallel stratigraphic successions of taxa within two subfamilies of the Krynkaphyllidae fam. nov. document their probably common roots and early divergence. However, a lack of robust data precludes an interpretation or treatment of those successions as phylogenetic. The absence of key stratigraphic and morphologic data meant that eastern Asiatic taxa have not been considered in these successions; however, morphological similarities allow for their tentative inclusion within the Krynkaphyllidae fam. nov. The following new taxa are introduced: Krynkaphyllidae fam. nov., Krynkaphyllinae subfam. nov., Colligophyllinae subfam. nov., *Krynkaphyllum* gen. nov., *Colligophyllum* gen. nov., *Protokionophyllum feninoense* sp. nov., *Krynkaphyllum multiplexum* sp. nov., *Krynkaphyllum validum* sp. nov., and three species of *Protokionophyllum* Vassilyuk in Aizenverg *et al*., 1983 left in open nomenclature.

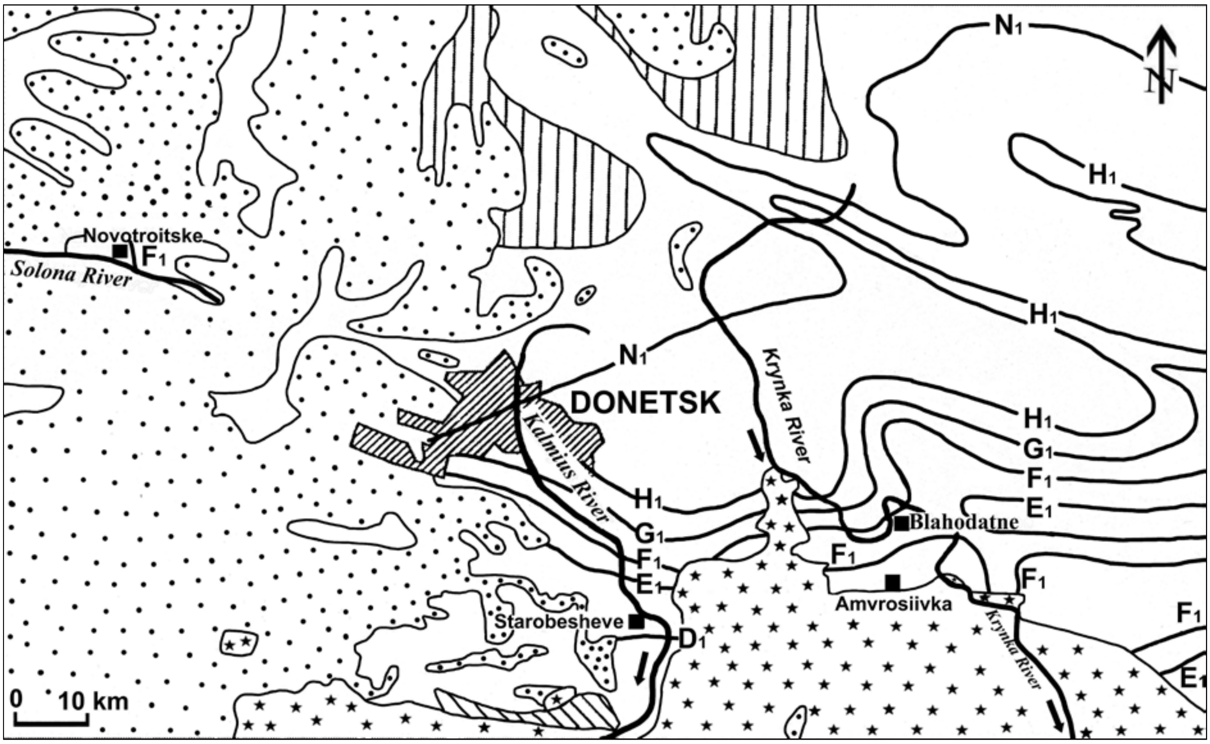
Key words: Rugosa (Anthozoa); Taxonomy; Relationships; Bashkirian; Donets Basin.

INTRODUCTION

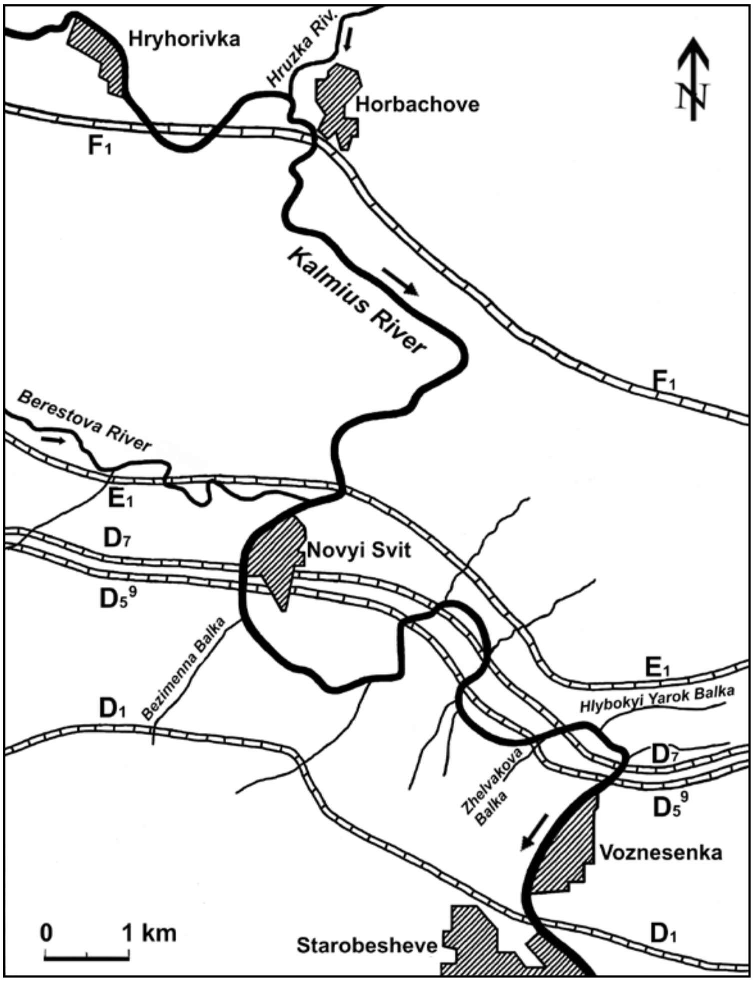
This paper constitutes part ten of a series of papers devoted to Bashkirian rugose corals from the Donets Basin, Ukraine (Text-fig. 1). These earlier papers should be consulted for introductory data on this region (Fedorowski 2009), including the stratigraphic nature of the Limestone Groups D, E, and F (Fedorowski 2017), which have yielded many rugose coral taxa, including these described here. The reader is kindly referred to those papers, to summaries by Poletaev *et al*. (2011) and Gozhyk (2013) and to the paper by Nemyrovska (2017) for geological and stratigraphic details. Only those sketches that illustrate the region in detail are reproduced here (Text-figs 2−4).



Text-fig. 1. General map of Ukraine showing the approximate position of the study area (after Fedorowski 2009a, supplemented with geographical names in Ukrainian).



Text-fig. 2. Location of individual limestones D_1 to N_1 in the vicinity of Donetsk. Carboniferous deposits left in white (after Fedorowski 2009a, with geographical names in Ukrainian).

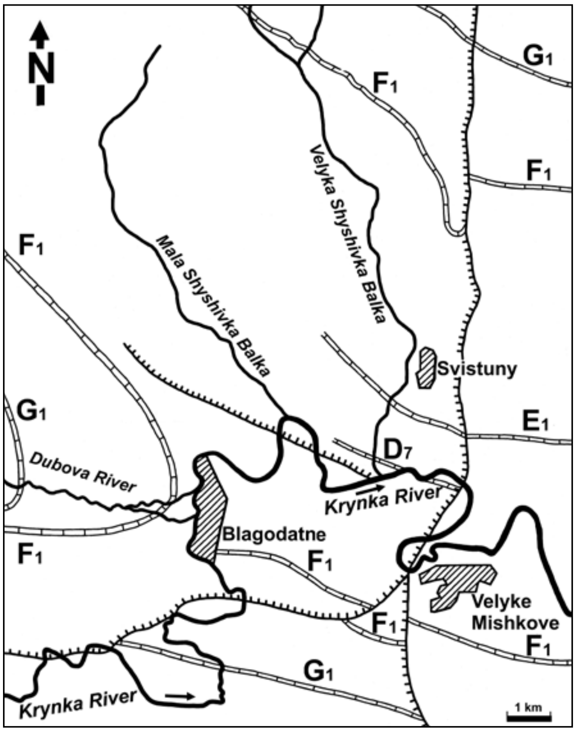


Text-fig. 3. Outcrops of Limestones D to F in the Kalmius River Area (after Fedorowski 2009a with geographical names in Ukrainian).

The herein described taxa of the Family Krynkaphyllidae fam. nov. bear certain characters typical of the families Axophyllidae Milne Edwards and Haime, 1851, Petalaxidae Fomichev, 1953, and Geyerophyllidae Minato, 1955, and these taxa are therefore discussed as potential relatives to the Krynkaphyllidae fam. nov. The available data document a dearth of Krynkaphyllinae-like taxa outside the Donets Basin. Specimens described by Yoshida and Okimura (1992) from the uppermost Serpukhovian–lowermost Bashkirian Omi Limestone in Japan, included by those authors in the genus *Amygdalophylloides* Dobroljubova and Kabakovich, 1948, form the only potential exception known to me.

Specimens resembling and/or related to the Subfamily Colligophyllinae subfam. nov. are much more common in Eastern Europe and Asia (e.g., Soshkina 1925; Soshkina *et al.* 1941; Minato 1955; Vassilyuk 1960, 1974; Kozyreva 1976, 1978; Gorskiy 1978; Vassilyuk and Zhizhina 1978; Wang *et al.* 1978; Degtyarev 1979; Yu 1985; Yu and Wang 1987; Wu and Zhao 1989; Xu and Poty 1997; Fan *et al.* 2003; Kossovaya 2009). Inadequate knowledge and/or misidentification of growth form, a lack of indisputable data concerning morphology in subsequent ontogenetic growth stages, and the unknown septal microstructure of most taxa described in the papers listed above prevent their firm identification in the majority of cases. However, their close similarity in some important morphological details makes the relationship of those taxa very probable, as discussed below in detail. The stratigraphic distribution of the discussed species is presented in Text-fig. 5.

Following Hudson (1936) and Fedorowski (1997), only the cardinal and the counter major septa are considered protosepta. As in my earlier papers, the



Text-fig. 4. Outcrops of Limestones D to G in the Krynka River Area (after Fedorowski 2009a with geographical names in Ukrainian).

microstructure of septa, if recognisable, is described on the basis of the so-called 'dark lines': i.e., the primary septa created within septal pockets prior to secretion of the sclerenchymal covers.

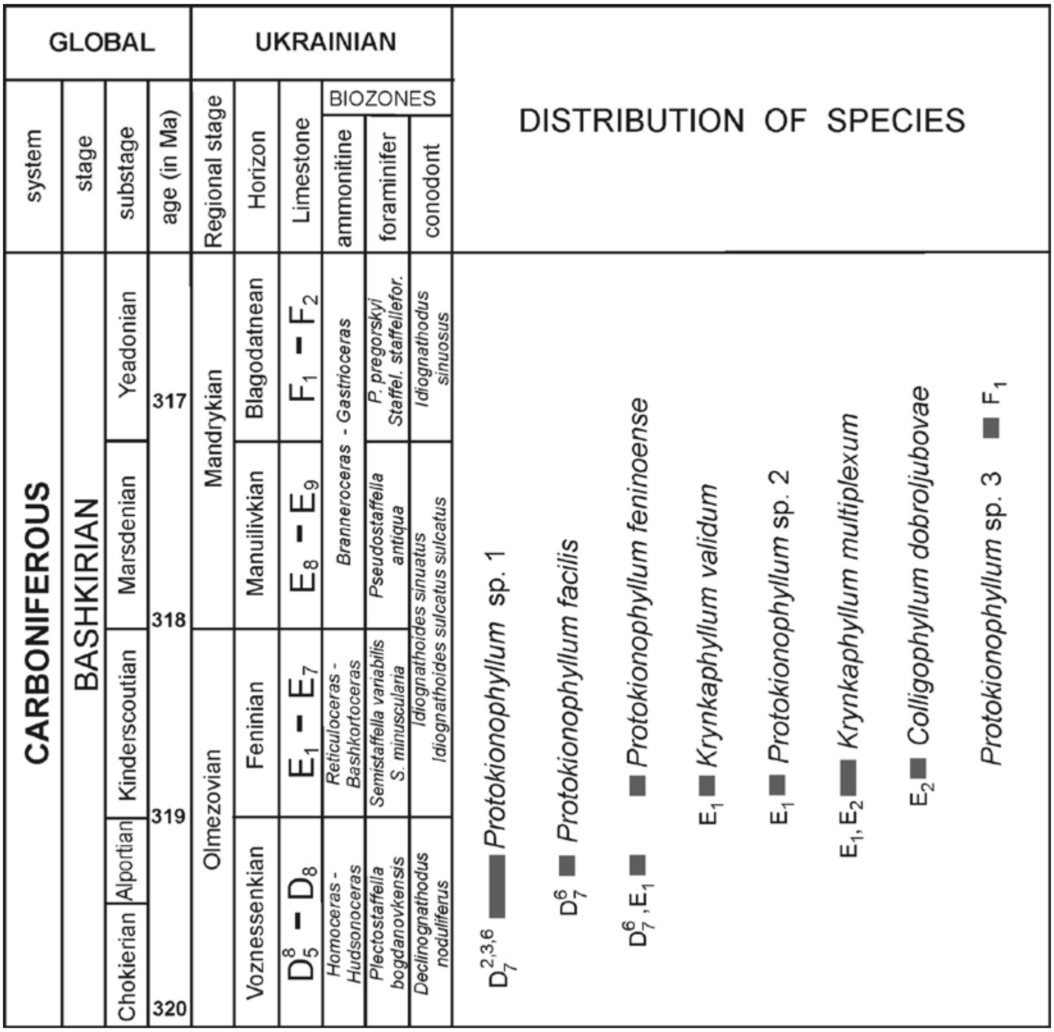
The term 'pseudocolumella' is employed here to describe the axial skeletal structure derived from either protosepta. It replaces the commonly applied term 'columella'. The latter name, typically applied to the genus *Cyathaxonia* Michelin, 1847, should be restricted to the solid axial structure formed by the inner margins of tabulae being elevated steeply and resting on each other, as demonstrated by Fedorowski and Vassilyuk (2011).

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

MATERIAL AND METHODS

The specimens described in the present paper belong to the collection donated to me by the late Dr N.P. Vassilyuk, former professor of the Donetsk Polytechnic, Ukraine. Twenty four free-living corallites and two gregaria, all incomplete and diagenetically altered, have been examined. Their restricted representation, incompleteness, and considerable morphological variability render their studies incomplete and taxonomic identifications difficult and, in certain cases, insufficiently documented. The brephic growth stage is missing from all free living representatives of the Family Krynkaphyllidae fam. nov., but one broken specimen of that growth stage is found in the holotype gregarium of *Colligophyllum dobroljubovae* (Vassilyuk, 1960). That gregarium contains a few specimens restricted to a very variable neanic growth stage, described below. The neanic growth stage preserved in one free-living specimen offers the possibility of a limited comparison to *C. dobroljubovae*. Nevertheless, their ontogenetic and microstructural data are incomplete. Furthermore, the number of free-living specimens that are similar enough to be included in a common species is restricted to a limited number of corallites. The limited representation of particular groups of specimens and their extensive morphological variability prompts a dilemma in treating the material. One can either consider almost all of the free-living corallite specimens as one or two enormously variable species, or split the collection into many poorly documented taxa. The first approach – i.e., grouping specimens that bear qualitatively different characters into a single species – violates the standard rules for treating rugosan taxonomy, whereas inordinate splitting may lead to taxonomic chaos. A third option is to simply leave the small, incomplete specimen fragments undescribed; however, this approach has been rejected due to the phylogenetic value of those specimens. Almost all of them were derived from lower Bashkirian deposits, including some from the limestones deposited close to the base of the Bashkirian. This interval is characterised by the near-complete absence of rugose corals worldwide, rendering every known specimen critical in understanding the nature of the basal Bashkirian Rugosa. Thus, all better-preserved and/or better-represented specimens are named, whereas all remaining specimens are mentioned, illustrated, and left in open nomenclature. Some of the species left in open nomenclature are obviously artificial: i.e., they group together specimens morphologically distant in certain characters. However, this consciously artificial grouping reduces potentially unwarranted splitting, without losing a demonstration of morphological variability within certain rugose corals at the onset of the late Carboniferous rugosan evolutionary phase (Fedorowski 1981).

All specimens of the collection were cut using



Text-fig. 5. Litho- and biostratigraphic schemes of the lower and middle Bashkirian Stage in the Donets Basin with reference to Western European standards and the vertical ranges of taxa studied. Abbreviations: *P.* – *Pseudostaffella*, *S.* – *Semistaffella*, *Staffel. staffellefor.* – *Staffelleformes staffelleformis*.

a cutting machine equipped with a 0.03 mm wire. Subsequently, they were either thin-sectioned, acetate-peeled, or both. Almost all studied specimens are illustrated to allow the reader his own taxonomic determinations. Images of poorly preserved corallites are augmented by computer drawings based on highly enlarged images.

Repetitions of the family name in the diagnosis of the subfamily, etc., mean the occurrence in the lower rank taxa of all the main diagnostic characters of a higher level taxon. This approach reduces redundancy in diagnoses, limiting them to the distinguishing characters of the subfamily, genus or species being described.

The corals described in this paper, like all other rugose corals described in the series of papers devoted to the Bashkirian corals from the Donets Basin, are housed in the Institute of Geology, Adam Mickiewicz University in Poznań (collection UAM-Tc.Don.1).

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder ?Lonsdaleiina Spasskiy, 1974
Family Krynkaphyllidae fam. nov.

DIAGNOSIS: Solitary, protocolonial and possibly fasciculate colonial, dissepimented rugose corals;

major septa in premature growth stage arranged bilaterally, commonly radial in maturity; cardinal septum elongated and predominant; counter septum, elongated in early corallite growth, either remain long, or reduced to length of remaining major septa; pseudocolumella simple or complex, derived from inner margin of cardinal septum; cardinal fossula absent; tabularium normal or weakly biform; tabulae mostly complete, but vary in position, commonly elevated gently towards pseudocolumella; dissepiments interseptal and lonsdaleoid; external wall as septotheca; microstructure of septa finely trabecular.

CONTENT OF SUBFAMILIES: Krynkaphyllinae subfam. nov.; Colligophyllinae subfam. nov.

REMARKS: The suborder affinity of the Family Krynkaphyllidae fam. nov. is questionable. Some of its characters point towards Aulophyllina Hill, 1981, whereas others are indicative of Lonsdaleiina, but neither can be accepted as decisive. Its resemblance to the Aulophyllina is weakest, as it is restricted to similarities in particular characters. *Protokionophyllum feninoense* sp. nov. resembles the Mississippian genus *Koninckophyllum* Thomson and Nicholson, 1876 in possessing a simple pseudocolumella free in the mature growth stage from either both protosepta or only the counter septum. One specimen included in *P. feninoense* sp. nov. (see below in Text-fig. 9A–C) and the species of *Krynkaphyllum* gen. nov. resemble the genus *Voragoaxum* Fedorowski, 2017 in that the protosepta expands to meet the pseudocolumella laterally. All of the remaining characters of the taxa mentioned differ considerably from the genera of the Suborder Aulophyllina. Thus, the similarity in pseudocolumellae morphology should be considered homeomorphic.

The development of lonsdaleoid dissepiments, formation of the septotheca, and pseudocolumella derived from the cardinal septum, all features characteristic of both the Family Krynkaphyllidae fam. nov. and well known genera included by Hill (1981, p. *F*398) in the Family Axophyllidae point towards the Suborder Lonsdaleiina. However, both the cardinal and the counter septum dominate in at least the premature ontogeny of both genera included here in the Subfamily Krynkaphyllinae subfam. nov. and appear in some corallites of *Colligophyllum dobroljubovae*. The pseudocolumella/protosepta relationship and the inner morphology of the pseudocolumella in the Family Krynkaphyllidae fam. nov. is of fundamental taxonomic value, enabling distinction from taxa included in the Suborder Lonsdaleiina thus far. Nevertheless, some morphological similarities of the Family Krynkaphyllidae fam. nov. to the families included by Hill (1981) in the Suborder Lonsdaleiina suggest the distant relationship of at least some of those taxa. Thus, the Families Axophyllidae, Petalaxidae, Geyerophyllidae, and Koninckocariniidae Dobroljubova in Soshkina *et al.*, 1962 (if not synonymous with Geyerophyllidae) are briefly discussed.

The similarity of all four families include: (i) the derivation of the pseudocolumella from the cardinal septum (except perhaps in *Dorlodotia* as discussed below); (ii) the dissepimentarium comprising both interseptal and lonsdaleoid dissepiments; and (iii) the septotheca built of the peripheral margins of both septa cycles exclusively, or supplemented by subordinated sclerenchyme. Moreover, the pseudocolumellae in the Family Krynkaphyllidae fam. nov. are either monoseptal, attributed by Minato and Kato (1975b) to the Koninckocariniidae, or complex, attributed by Minato and Kato (1975a) to the Geyerophyllidae (see description of *Krynkaphyllum*). In the Petalaxidae that character "varies from simple median lamella formed by thickening of cardinal septum to complex structure" (Bamber and Fedorowski 1998, p. 19). With all these similarities, the question of the relationship between these families remains open as a result of doubts concerning the Geyerophyllidae and Koninckocariniidae, discussed below, and the extremely broad generic content attributed by various authors to the Petalaxidae.

The composition of the Axophyllidae suggested by Hill (1981), although doubtful to me, is not a subject treated here. Only *Axophyllum* Milne Edwards and Haime, 1850, the type genus for the family, and *Dorlodotia* Salée, 1910 (included by Hill 1981 in the Family Lithostrotionidae d'Orbigny, 1852) are briefly discussed due to their value for the present paper. The solitary growth form, stratigraphic position, worldwide distribution, and certain characters of the genus *Axophyllum* – that is, well developed lonsdaleoid dissepiments and septotheca present in many species – may suggest its ancestry in the Family Krynkaphyllidae fam. nov. An offsetting corallite illustrated by Somerville *et al.* (2012, fig. 4A) slightly reduces the validity of that supposition. That corallite, illustrated in only a single thin section, requires comprehensive study prior to consideration in a phylogenetic context. It may contain only a lost structure *sensu* Fedorowski (1978), and it is not colonial. However, it is not the modestly doubtful growth form of the genus *Axophyllum*, but its very complex and variegated axial structure, well documented by

Semenoff-Tian-Chansky (1974), which renders a potential *Axophyllum* ancestry for the taxa described here unacceptable to me.

The taxonomic position of *Dorlodotia* remains disputable. In contrast to Hill (1981), Poty (1981, p. 65) included that genus in the Subfamily Lonsdaleiinae Chapman, 1893 of the Family Axophyllidae. Denayer (2011, p. 1437) placed *Dorlodotia* in an uncertain suborder and family. Here, I consider it to be probably ancestral to Krynkaphyllidae fam. nov. As a consequence of this suggestion, *Dorlodotia* should be reluctantly placed into that family: this solution is conditionally accepted here as possible. A comparison of the characters of *Dorlodotia* to the characters of the various genera included in the Family Krynkaphyllidae fam. nov. is suggestive of the closer affinity of *Dorlodotia* with the Krynkaphyllidae fam. nov., rather than with the genus *Lonsdaleia* McCoy, 1949 that gave its name to the suborder. In this framework, the suborder status of both *Dorlodotia* and Krynkaphyllidae fam. nov. is uncertain, although the Suborder Lonsdaleiina should be pointed out as probably the phylogenetically closest from among the existing suborders.

The synonymy of *Dorlodotia* suggested by Poty (2007) is only partially accepted here. The poor knowledge of certain genera, including *Kwangsiphyllum* Grabau and Yoh, 1931 and *Pseudodorlodotia* Minato, 1955, included by Poty (2007) in the list of synonyms, are grounds to reject their synonymy. Moreover, some doubts remain in the case of *Dorlodotia* itself, despite the many studies on that genus published so far on the basis of specimens from Western Europe, as synonymised by Denayer (2011, p. 1438). The major concerns include: (i) The septal microstructure is omitted from the papers listed above. The remarks by Poty (1975, p. 94) on the columella (= pseudocolumella) and his hand drawing in figure 2 do not clarify this question. (ii) The details of offsets formation: i.e., the sequence in the insertion of major septa remains unknown, and the formation of the pseudocolumella is not firmly established (see below). (iii) The microstructure of the external wall remains uncertain. The expression ‘festooned’ wall (Poty 2007) is general and misleading. It may be applied to the deep septal furrows of both cycles of septa with unincorporated rudiments of septal skeletons, but it may also imply both a complete septotheca – i.e., composed entirely by only the wide bases of major and minor septa – and an incomplete septotheca – i.e., partially formed by a sclerenchyme. Moreover, that sclerenchyme may be either original or false, that is, resulting from diagenetic recrystallization. The cathodoluminescence study of the Belgian specimen of *Dorlodotia briarti* Salée, 1920 documents its external wall as not being recrystallised (Prof. Edouard Poty, written communication, 6 April 2020). An indisputable septotheca derived from both septal cycles is well documented in some corallites (e.g., Poty 1975, pl. 1, figs 1, 2), but is not in several other corallites (e.g., Poty 1993, fig. 11:1). (iv) Derivation of the pseudocolumella. Both Poty (1975, 1981, 2007) and Denayer (2011) described the pseudocolumella (in their nomenclature, columella) as being merely connected to the counter septum, with rare connection to the cardinal septum. However, that connection, its origin in the course of early hystero-ontogeny, and differentiation in the mature growth stage, if it truly occurs, is not clear. Poty (1993, p. 148) wrote: “The cardinal septum and the counter septum are in connection and affected by a thickening of the axis of the corallite which is the first stage in the development of a columella.” This important statement means that an axial septum was present in an early growth stage of a corallite, and that the pseudocolumella was formed prior to the disconnection of the protosepta. Unfortunately, the occurrence of such an axial septum is not documented in either a series of drawings or in their interpretation (Poty 1975, figs 3, 4, respectively), or in any offset in a hystero-brephic growth stage illustrated by Poty (1975, 1981, 1993) and Denayer (2011). All of the very young offsets illustrated in these papers appear to be short-septal with an axial septum absent; the earliest growth of an offset is perhaps acolumellate. A thin or axially thickened, long protoseptum appeared only in the offsets of a slightly more advanced growth stage (Poty 1975, 1981, 1993; Denayer 2011). Some of those elongated structures seem to be attached to two opposite major septa, most probably the protosepta. However, the mutual relationship of those three skeletal elements – i.e., the protosepta and the pseudocolumella – remains uncertain. A true axial septum, by definition, occurs only when the ‘middle dark lines’ of both protosepta and the pseudocolumella are in direct contact and form an uninterrupted line. Such a connection is not clearly documented in *Dorlodotia*. That being said, one young corallite illustrated by Poty (1975, pl. 22, fig. 6) may demonstrate the formation of an axial septum, if the break between the ‘middle dark line’ of the counter septum and that ‘line’ in the pseudocolumella is diagenetic. A direct union of the ‘middle lines’ of the cardinal septum and the pseudocolumella suggests that the latter has a closer connection to, and is potentially derived from, the former. Two other young corallites illustrated by Poty (1975, pl. 2, figs 3, 4) depict a similar image, and therefore may be useful in assessing the original nature of the above-described corallite. A close examination of these excellent pictures reveals that the 'middle dark line' of the pseudocolumellae is directly connected to the cardinal septa, whereas the counter septa attaches to the sclerenchymal thickenings of the pseudocolumellae from the side. Thus, the axial septum is absent from those corallites, whereas derivation of the pseudocolumella from the cardinal septum can be suggested. The same is true for several other young corallites illustrated by Poty (1975, pl. 3, figs 1–3). In one of those corallites (Poty 1975, pl. 3, fig. 3, upper right), one long protoseptum is disconnected from the pseudocolumella, and the second protoseptum attaches to the pseudocolumella from the side. The pseudocolumella in that corallite can perhaps be described as moving towards total disconnection from the protosepta. These brief remarks may suggest the following: (1) The earliest growth stage of the *Dorlodotia* offset is aseptal. (2) Either the axial septum appears or the cardinal septum became elongated in the next step of an offset's growth. This variety is identical to the variety documented for *Colligophyllum dobroljubovae* below. The pseudocolumella was formed by the sclerenchymal thickening of either a middle part of an axial septum or the inner margin of the cardinal septum, although both protosepta may be elongated. (3) Poty (1975, 1981, 1993, 2007) and Denayer (2011) postulated that the pseudocolumella was connected in maturity to either protoseptum, with attachment to the counter septum being the more common variant. However, the state of existing documentation is inadequate to confirm their assessment at the present time. (4) The pseudocolumella may appear after a comparatively long period in acolumellate offset growth. It may also be reduced during the mature growth stage of some corallites. The question of pseudocolumella derivation in *Dorlodotia briarti* is discussed here at length due to its bearing on the position of *Dorlodotia* as a possible distant ancestor of Krynkaphyllidae fam. nov. (see Considerations). Indeed, Vassilyuk (1974, p. 7) already recognised the close morphological similarity and possible relationship of *Colligophyllum* gen. nov. (in her writing, *Lytvophyllum*) and *Dorlodotia* by stating: "The genus *Lytvophyllum* displays individual variability exposed in an extraordinarily clear way. It occupies the intermediate position in the morphological succession *Dorlodotia* → *Lytvophyllum* → *Darwasophyllum*." (translated here from Russian). I consider here the *Dorlodotia* → *Lytvophyllum* (i.e., *Colligophyllum*) relationship possible, but the study by Bamber *et al.* (2017) allowed the elimination of *Darwasophyllum* Pyzhyanov, 1964 from that lineage.

'*Dorlodotia*' *fomitschevi* Zhizhina in Vassilyuk and Zhizhina, 1978 is one of the species conditionally included by Denayer (2011) and Hecker (2012) in the synonymy of *Dorlodotia briarti*, a treatment not followed here. That Ukrainian species was introduced on the basis of two corallite fragments embedded in a small fragment of rock. In light of such restricted documentation, Zhizhina's (in Vassilyuk and Zhizhina 1978) suggestion of a colonial growth form for her specimen is unsupported, and there exists inadequate support for her generic identification. However, several morphological characters in the transverse and the longitudinal section of '*D.*' *fomitschevi* (Vassilyuk and Zhizhina 1978, pl. 1, fig. 1a–d) resemble *D. briarti* to such an extent that a relationship of those two taxa at generic level is feasible. The derivation of '*D.*' *fomitschevi* specimens from the $C_1{}^{v}b$ Zone, which corresponds to the lower Viséan part of the Chadian or Moliniacien in the western European nomenclature – i.e., contemporaneous with *D. briarti* – is consistent with that suggestion. There are conflicting characters between *D. briarti* and '*D.*' *fomitschevi*, which include: (i) the uncertain growth form and the morphology of the external wall; and (ii) the complex morphology of the pseudocolumella. Zhizhina (in Vassilyuk and Zhizhina 1978, p. 27) described the external wall as "thin and wavy". Thus, a septothecal occurrence is unlikely. However, those characters may vary in *D. briarti* as well (see above). In the case of the pseudocolumella, Zhizhina (in Vassilyuk and Zhizhina 1978, p. 27) wrote: "Stolbik [= pseudocolumella] thick with short swellings" (both citations translated here from Russian). The latter expression suggests the septal lamellae may be incorporated into the pseudocolumella, which would be consistent with a complex inner morphology. That recognition seems to be correct for the larger of two corallites illustrated, whereas the smooth shape of the pseudocolumella in the smaller (younger?) corallite may suggest a monoseptal origin. If that observation based on the published illustration is correct, a complex pseudocolumella morphology may appear only in the advanced ontogeny of '*D.*' *fomitschevi*. However, such a morphology may be either temporary as it is in *D. briarti* (Poty 1975, pl. 2, figs 3–5) or consistent. Only an inconsistent morphology of the pseudocolumella and the colonial growth form of '*D.*' *fomichevi* will allow it to be synonymized with *D. briarti*, whereas a complex morphology of the pseudocolumella will perhaps be adequate for its independent species position, if the colonial growth form is confirmed. These doubts are accepted as being adequate for distinguishing '*D.*' *fomitschevi* from

D. briarti and *D. euxinensis* Denayer, 2011 and for suggesting its possibly ancestral position to both subfamilies of the Family Krynkaphyllidae fam. nov. (see remarks to Subfamily Colligophyllinae subfam. nov. for further discussion).

The Family Petalaxidae is the next family which is potentially related to the corals described here. Fomichev (1953, p. 449) diagnosed that family as follows: "Massive colonial corals with columella plate-like (like in *Lithostrotion*); axial dissepiments may occur along columella in some 'forma' [taxa?] and sometimes a restricted number of radial plates [appear], making columella complex. Septa broken by big dissepiments. External wall complete. Tabulae incomplete, slightly downturned, meet columella at right angle, slightly elevated towards inner wall and columella in places". Beneath the diagnosis he added: "It is not clear to which major septum, cardinal or counter, the columella is united in the corals of this family. It is most probably derived from the axial septum in early growth stage." [both citations translated here from Russian]. Fomichev (1953) acknowledged *Stylaxis mccoyana* Milne Edwards and Haime, 1851 as the type species of *Petalaxis* Milne Edwards and Haime, 1852, but did not restudy the Moscovian (Myatchkovian) topotypes from the Moscow Basin and rather established the family on the basis of his study of the Donets Basin collection (see occurrences in Fomichev 1953, p. 456). Thus, the data established by Sutherland (1978) on the basis of topotypes should be accepted as supplementary to Fomichev's (1953) study. Hill (1981, pp. *F*404, *F*406) added fasciculate colonies to the diagnosis of this family, and included in the Petalaxidae the genera *Lytvophyllum* Dobroljubova in Soshkina *et al*., 1941 and *Paralithostrotion* Gorskiy, 1938. Her decision was followed by Kossovaya (1998) and Bamber and Fedorowski (1998), whereas Fedorowski *et al*. (2007) considered *Lytvophyllum dobroljubovae* Vassilyuk, 1960 as only probably fasciculate colonial.

Sando (1983) critically analysed all of the species bearing characters comparable to the genus *Petalaxis* known to him. He restricted the Family Petalaxidae to its cerioid colonial type genus, diagnosed the family, and divided all of the species analysed into five informal groups (Sando 1983, p. 25). That division was followed by Kossovaya (1998), but not by Bamber and Fedorowski (1998), who considered it unsupported by reliable data. In the context of this paper and the genus *Ceriodotia* Denayer, 2011, the following taxa require special attention: (i) Group 1 of Sando (1983), composed primarily of North American Viséan species, with one Viséan species described by Onoprienko (1976) from Chukotka that Denayer (2011) considered to be possibly related to *Ceriodotia.* (ii) *Lithostotionella monocyclica* de Groot, 1963 from the Santa Maria Limestone (Serpukhovian) in Spain, may belong to *Ceriodotia*. (iii) Some of the seven new species described by Kozyreva (1974) from the lower Bashkirian (*Petalaxis korkhovae* Kozyreva, 1974) and the lower middle Bashkirian (all other species) from the southern slope of the Voronezh Anteclize probably belong to the *Ceriodotia*-like group of species diagnosed by Denayer (2011) as lacking minor septa. *Petalaxis exilis* Kozyreva, 1974 and *P. mirus* Kozyreva, 1974 possibly did not develop minor septa. *Petalaxis korkhovae* possesses the rudiments of minor septa in one illustrated corallite, but several minor septa occur in another colony of the same species (Kozyreva 1974, pl. 1, fig. 7b, 7a, respectively). *Petalaxis exilis* and *P. mirus* may belong to *Ceriodotia*, but *P. korkhovae* may not, if the absence of minor septa is treated as a rigorous criterion. However, their appearance may suggest the need of a less rigid approach to that character than suggested by Denayer (2011), without contesting the introduction or validity of the genus *Ceridotia*.

I do not comment in detail on Denayer's (2011, fig. 14) reconstruction of the phylogenetic development within the *Dorlodotia–Ceridotia* lineage except for one statement. In the obvious absence of genetic data, only careful study of the protocorallites will allow for a reconstruction as detailed as the one cited. The astogeny will not help since all changes appearing during a colony growth are somatic. Genetic mutations have taken place either in larvae or earlier, i.e., in gamets. All specimens within a colony are clones, possessing an identical genotype. This may mean that all gamets released by a colony during breeding periods are genetically identical, but this may not be a case. However, I do not know of any paper dealing with the question of a genetic diversification of gamets released from a single colony of the Scleractinia and such a study cannot be expected on the Rugosa for the obvious reason. Thus large genetic mutations in diploids, i.e., larvae, are easier to accept. Such a genetic mutation should be reflected in a protocorallite skeleton, as mentioned above. I suspect, but cannot prove it in an adequate number of examples, that genetic mutations are to a large extent reflected during the early development of offsets. They may follow the main characters of protocorallites (e.g., Fedorowski *et al*. 2014). Unfortunately, a detailed blastogenetic study of either *Dorlodotia* or *Ceridotia* has not been made by Denayer (2011). The early post-larval growth stage of a colony is the only level, at which changes prior to reaching sexual maturity occurred and are recorded. Offsetting ability can perhaps be treated as indicative of maturity, but again it must be observed in the protocorallite. Reasons for a reduction or an increase in the size of corallites and the achievement of a cerioid growth form can vary. Thus, astogenetically advanced specimens cannot serve as the basis for such a reconstruction, as proposed by Denayer (2011). His remarks dealing with the possible relationships *vs.* homeomorphs of some massive colonies are indeed important. However, those remarks must be treated with some reservation until the blastogeny of both fasciculate and cerioid colonies are studied to an extent adequate for establishing the succession of major septa, the derivation of the pseudocolumella, the microstructure of septa, the microstructure of the external walls in fasciculate colonies, and the inter-corallite walls in the massive colonies (dividing walls *vs.* partitions).

Bamber and Fedorowski (1998, pp. 18–42, text-figs 16–23, table 4) offered a comprehensive discussion on the literature data, documented the diagnostic differences between the genera *Petalaxis* and *Cystolonsdaleia* Fomichev, 1953, established the probable synonymy of both genera, and made a list of species that either belonged to these genera or should be excluded from them in accordance with their understanding. They also studied in detail the morphology of the external wall and the axial structure, the microstructure of septa, and the blastogeny of both genera, all on the basis of a collection from Ellesmere Island, Arctic Canada. Finally, they compiled the age and geographical distribution of species attributed by them to both *Petalaxis* and *Cystolonsdaleia*. That comprehensive study suggests an extremely wide variability of the genus *Petalaxis* that, in turn, reflects on the generic variability within the Family Petalaxidae.

I am not concerned here either with the general ideas included in main papers dealing with the Family Petalaxidae, i.e., Fomichev (1953), de Groot (1963), Kozyreva (1974), Sutherland (1978), Hill (1981), Sando (1983), Bamber and Fedorowski (1998), Kossovaya (1998), Fedorowski (2004) and Fedorowski *et al*. (2007) or with their different opinions of the content of the Family Petalaxidae and other items discussed except for one question, i.e., an inclusion in that family of fasciculate colonial, protocolonial and solitary species. Those questions, except for that one, are beyond the scope and topic of the present paper. The comments here are only made to point out the possibility of a relationship of the families Petalaxidae and Krynkaphyllidae fam. nov. The relationship of the protosepta to the pseudocolumella, the inner morphology of the pseudocolumella, and the morphology of the tabularium in *Protokionophyllum* Vassilyuk in Aizenverg *et al*., 1983 and *Krynkaphyllum* gen. nov. are sufficient to distinguish these genera from the Family Petalaxidae at family level. The taxonomic position of *Colligophyllum*-like genera is more enigmatic. At least several representatives of those genera possess monoseptal pseudocolumellae, derived from and almost permanently united with the cardinal septa. In some taxa the connection of the pseudocolumella to a given protoseptum is disputable. The pseudocolumellae may display very weak axial structures. Both the simple, monoseptal and the slightly more complex axial structures resemble those found in *Petalaxis*. In addition, the morphology in longitudinal sections of the *Colligophyllum*-like taxa resembles *Petalaxis*. The solitary, gregarious, protocolonial and weakly fasciculate colonial growth form of the *Colligophyllum*-like corals and elongation of the counter septum in some corallites of *C. dobroljubovae* (see below in Text-figs 19G, H; 20C, H, K) are the main characters discussed in the remarks on the Subfamily Colligophyllinae subfam. nov. and in the considerations in the context of the Krynkaphyllidae fam. nov./Petalaxidae relationship. The reader is also referred to the discussion by Fedorowski *et al*. (2007, pp. 151, 153–158) devoted to the genus *Lytvophyllum* and other fasciculate (?) genera, some of which can be solitary and gregarious.

The status of the Family Koninckocariniidae evolved from the level of the subgenus *Koninckocarinia* Dobroljubova, 1937 of *Koninckophyllum*, to the Family Koninckocariniidae. De Groot (1963, p. 93) neglected its family status, but accepted the independent generic position of *Koninckocarinia*, and included it in the Family Lonsdaleiidae Chapman, 1893. Rodríguez (1985, p. 279) acknowledged the genus, but placed it within the Family Geyerophyllidae, whereas Cocke (1970, p. 42) synonymised it with the genus *Geyerophyllum* Heritsch, 1936 together with several other genera (see below). In contrast, Minato and Kato (1975b) and Hill (1981) accepted Dobroljubova's (in Soshkina *et al.* 1962) family designation despite the very incomplete data provided by the holotype, the only specimen representing the type species *Koninckocarinia flexuosa* Dobroljubova, 1937. That holotype corallite lacks the apical part; in addition, an axial septum and/or any kind of an axial structure is absent from the ontogenetically earliest part preserved (Dobroljubova 1937, pl. 11, figs 11–15). That important shortage is omitted from the discussion by the authors dealing with that genus (e.g., de Groot 1963; Minato and Kato 1975a, b;

Boll 1985; Rodríguez 1985). Minato and Kato (1975b, p. 23) wrote, "*Koninckocarinia* possesses only thin plate in its axial part of corallite through all growth stages". Such a misleading statement lacks support from the acolumellate early growth stage of the type species holotype. All doubts and misunderstandings mentioned will remain as such until complete topotypes are studied. The present knowledge of that taxon made both the independent generic and family status of *K. flexuosa* so dubious that a discussion of its relationship to the Family Krynkaphyllidae fam. nov. is without merit.

A critical analysis of the Family Geyerophyllidae is not the purpose of the present paper. However, the taxonomic status of its type genus must be considered in the context of the apparent similarity of the specimens here described to the geyerophyllids. The Family Geyerophyllidae seems to be nearly cosmopolitan in the Pennsylvanian and early Permian. However, its generic content differs greatly from author to author (e.g., Minato 1955; Cocke 1970; Minato and Kato 1975a; Hill 1981; Boll 1985; Rodríguez 1985; Wu and Zhao 1989; Rodríguez and Bamber 2012; Bamber *et al*. 2017). Such a differentiated approach perhaps results from the incompleteness of the holotype of *Geyerophyllum carnicum* Heritsch, 1936, the type species for the genus, which lacks the early growth stage and the calice (see Heritsch 1936, text-figs 36, 37, pl. 18, figs 18, 22). Furthermore, a longitudinal section of the holotype has not been prepared. That absence of data cannot be remedied. Remnants of the holotype are not known to exist and Heritsch's (1936) collecting localities – probably Gshelian strata in the Carnic Alps – disappeared during subsequent construction. These deficiencies make the status of the genus *Geyerophyllum* interpretative in such critically important details as early ontogeny and morphology in the longitudinal section. To this extent, it is enough to cite two extreme opinions. Cocke (1970, p. 42) acknowledged the genus *Geyerophyllum* and placed into its synonymy the genera *Carniaphyllum* Heritsch, 1936, *Carinthiaphyllum* Heritsch, 1936, *Lonsdaleoides* Heritsch, 1936, *Koninckocarinia*, *Amygdalophylloides*, and *Axolithophyllum* Fomichev, 1953. In contrast, Rodríguez (1985, p. 279), following Hill (1956) and Rowett and Kato (1968), synonymised *Geyerophyllum* with *Kionophyllum* Chi, 1931. Cocke (1970, p. 42) wrote: "However, because information on the type species, *K. dibunum*, is inadequate, the two genera are not placed in synonymy at this time." I agree with that comment and would further add that information on both genera is inadequate, as shown in this discussion.

The most important taxonomic doubts and misunderstandings of the taxa included in the Family Geyerophyllidae regard: (1) The colonial growth forms of *Carinthiaphyllum*, *Lonsdaleoides*, and *Darwasophyllum*. The solitary, gregarious growth form of *Carinthiaphyllum* was documented long ago (Fedorowski 1980, pl. 1, fig. 2a, b), and the colonial growth form of *Lonsdaleoides* was likewise contested (Fedorowski 2004). The colonial growth form of those genera was further questioned by Rodríguez and Bamber (2012) and Bamber *et al.* (2017), who also document a gregarious growth form of *Darwasophyllum*. Rodríguez and Bamber (2012, p. 358) concluded: "all geyerophyllid corals are solitary". According to them, only *Axolithophyllum* and *Lonsdaleoides* "show a minor tendency to form protocolonies". I agree with that conclusion so far as the taxa studied thoroughly are concerned. (2) The derivation of pseudocolumellae from cardinal septa has been established in most genera attributed to the Geyerophyllidae. However, the taxonomic value of differences in the inner morphology of pseudocolumellae should be documented as either constant and important, or varying randomly and consequently secondary in their taxonomic value. (3) A complex pseudocolumella, solid or loose internally, but constituted merely from a median lamella and septal lamellae should be clearly distinguished from an axial structure consisting of median lamella, loose septal lamellae, and axial tabellae. Both kinds are actually accepted for geyerophyllid taxa, what creates obvious doubts as to the reality of this arrangement. (4) The septal microstructure is unknown from most of the taxa treated by Minato and Kato (1975a) as members of the Family Geyerophyllidae. A diffuso-trabecular microstructure is suggested by these authors for some genera, whereas they attribute microstructures as distinct as fibro-normal and diffuso-trabecular to *Carinthiaphyllum*. Such distant microstructures can in no way be accepted within the same genus if the taxonomic rules well-established for the Scleractinia are expanded to the Rugosa.(5) The tabularium of some taxa may not contain clinotabulae or clinotabellae, as are generally attributed to the Family Geyerophyllidae. Some tabularia may be biform in their morphology (e.g., de Groot 1963, pl. 23, fig. 1d).

The listed doubts and the uncertain morphology of the type genus holotype make the status of the Family Geyerophyllidae dubious. Despite this curious situation, its independent taxonomic position is widely accepted. Assuming an occurrence in that family of clinotabulae or clinotabellae, and an absence of those structures in the Family Krynkaphyllidae fam. nov., the potential that the latter family is related to the Geyerophyllidae on a level lower than suborder is rejected. Whether the inconsistent arrangement of tabulae in *Colligophyllum* gen. nov. is adequate for suggesting that closer relationship, remains an open question.

None of the families discussed above bears characters similar enough to those of the Family Krynkaphyllidae fam. nov. to suggest their synonymy. The diagnostic characters of the genera *Protokionophyllum* and *Krynkaphyllum* gen. nov., in particular, are morphologically more distant from all of the remaining existing families than the diagnostic characters of the morphologically simpler, but more differentiated genus *Colligophyllum* gen. nov. Therefore, *Krynkaphyllum* gen. nov. was selected here as the genus most suitable for bestowing its name upon the family.

Subfamily Krynkaphyllinae subfam. nov.

CONTENT OF GENERA: *Protokionophyllum* Vassilyuk in Aizenverg *et al*., 1983; *Krynkaphyllum* gen. nov., ?*Amygdalophylloides* Dobroljubova and Kabakovich, 1948 of Yoshida and Okimura (1992).

Note. *Amygdalophylloides* of Yoshida and Okimura (1992) may be only homeomorphic to the remaining two genera (see Considerations).

DIAGNOSIS: Solitary, dissepimented Krynkaphyllidae; cardinal septum elongated and predominant; counter septum rarely reduced to length of remaining major septa, commonly elongated so as to meet pseudocolumella from aside; pseudocolumella simple or complex, derived from inner margin of cardinal septum; tabulae complete, elevated gently towards pseudocolumella.

REMARKS: Corals morphologically resembling or related to the Subfamily Krynkaphyllinae subfam. nov. are almost unknown from outside the Donets Basin and are rare in that basin as well. *Amygdalophylloides* Dobroljubova and Kabakovich, 1948 of Yoshida and Okimura (1992) is the only taxon outside that basin known to me as probably belonging to that subfamily. Among several species described by those authors from “Namurian A (Serpukhovian) to Namurian B (early early Bashkirian) age” of the Omi Limestone in Central Japan, *A. densus* and *A. denticulatus* introduced by Yoshida (in Yoshida and Okimura 1992) resemble the genus *Protokionophyllum* most closely. Both display the pseudocolumella solid and monoseptal, derived from and connected to the cardinal septum. Both lack the cardinal fossula. Also, the tabularia of several illustrated specimens are convex, not concave as they are in the Geyerophyllidae, and the clinotabulae are absent (Yoshida and Okimura 1992, figs 5:1C; 6:5; 7:6). The tabulae in other corallites illustrated by Yoshida and Okimura (1992) are horizontal and/or slightly down-sloping. Unfortunately, most of their longitudinal thin sections figured are eccentric and their illustrations poor, making the firm recognition of tabulae position uncertain. However, a variety of established characteristics, the lack of clinotabulae (requiring further confirmation), a close similarity in transverse sections to *Protokionophyllum*, and their similar or slightly older stratigraphic position suggest that they may be related to the Donets Basin corals. An open, accessible marine communication between Japan and Eastern Europe in the Viséan and Serpukhovian (Scotese 2001; Torsvik and Cocks 2016) supports that supposition. For more general discussion see Remarks to the family above and Considerations below.

Genus *Protokionophyllum* Vassilyuk in Aizenverg *et al.*, 1983

TYPE SPECIES: *Protokionophyllum facilis* Vassilyuk in Aizenverg *et al*., 1983, pl. 28, fig. 9, p. 20 (list of fauna) and p. 142 (figure captions). Right bank of the Kalmius River. Limestone D_7^3 or D_7^6. Lower Voznessenkian Horizon. Lower lower Bashkirian. By original designation.

SPECIES CONTENT: *Protokionophyllum facilis* Vassilyuk in Aizenverg *et al.*, 1983; *Protokionophyllum feninoense* sp. nov.; *Protokionophyllum* spp. 1, 2, 3; *Axolithophyllum* (?) sp. of Fomichev (1953).

DIAGNOSIS: Small, solitary dissepimented corals; arrangement of major septa in neanic growth stage and up to early maturity bilateral, in advanced mature growth stage radial; minor septa differentiated in length within particular corallites; pseudocolumella monoseptal, thick, derived from and connected directly to cardinal septum; in mature growth stage may be free from septa; counter septum touches pseudocolumella, but their middle lines not united; dissepiments interseptal and lonsdaleoid; microstructure of septa finely trabecular.

REMARKS: The genus *Protokionophyllum* with its type species *P. facilis* was introduced in a brief supplement to a comprehensive paper by Aizenverg *et al*. (1983) devoted to the stratigraphy and fauna of the upper Serpukhovian Substage in the Donets Basin as interpreted at that time. However, the paper deals with both Serpukhovian fossils in the present understanding and fossils derived from the Limestones D_5^8 up to D_7^8. Those Limestones form the lowest part of the Voznessenkian Horizon, now accepted as the lower Bashkirian (Poletayev *et al*. 2011; Gozhyk 2013; Nemyrovska 2017). Vassilyuk did not publish diagnoses or descriptions of any of the species illustrated in that paper. However, all new names introduced by her should be considered valid (see Fedorowski 2019a, p. 73 for discussion).

In addition to *Lytvophyllum* [= *Colligophyllum*] *dobroljubovae*, redescribed and renamed here, three other species included here in the Family Krynkaphyllidae fam. nov., were described by earlier authors from the Donets Basin: (1) *Axolithophyllum* (?) sp. of Fomichev (1953), represented by a single, incomplete specimen derived from Limestone F_1 on the left bank of the Kalmius River (Fomichev 1953, p. 427, pl. 29, fig. 6). Fomichev's (1953) description and illustration portrays that specimen as morphologically similar to *P. feninoense* sp. nov. and thus belonging to the genus *Protokionophyllum*. (2) '*Dorlodotia*' *fomichevi* Zhizhina in Vassilyuk and Zhizhina, 1978 from the C_1^vb Zone of the Sukhaya Volnovakha River; and (3) *Pseudodorlodotia subkakimii* Vassilyuk in Vassilyuk and Zhizhina, 1978 from the C_1^vf Zone of the left bank of the Kalmius River. Both two latter species are discussed in the remarks and in the Considerations as being important for the phylogeny of the Krynkaphyllidae fam. nov.

Most of the specimens here identified as *P. facilis* were derived from the type horizon (Limestone D_7^6) and the remaining ones from the same Group of Limestones (see Occurrence). Unfortunately, they supplement only minimally knowledge of the type species of the genus. A longitudinal section – i.e., one of the morphological characters, fundamental for the genus and thus for the family – was impossible to prepare from any of those fragmented corallites. Fortunately, that character was clearly established in *P. feninoense* sp. nov. That species occurs mostly in slightly younger strata (Limestone E_1^{verkh}), but may be present in Limestone D_7^6 as suggested by one poorly preserved specimen derived from that limestone. Besides, both species are morphologically similar to one another. Thus, documentation of the longitudinal section of *P. feninoense* sp. nov. is considered here as typical for the genus. This is to some extent proven by the oblique section of one hypotype of the type species (Text-fig. 6G) showing continuous tabulae elevated towards the pseudocolumella.

The generic name proposed by Vassilyuk (in Aizenverg *et al*. 1983) apparently suggests the Family Geyerophyllidae as the closest relatives of her new genus. Such a relationship is unsupported, as noted in the Remarks to Family Krynkaphyllidae fam. nov.

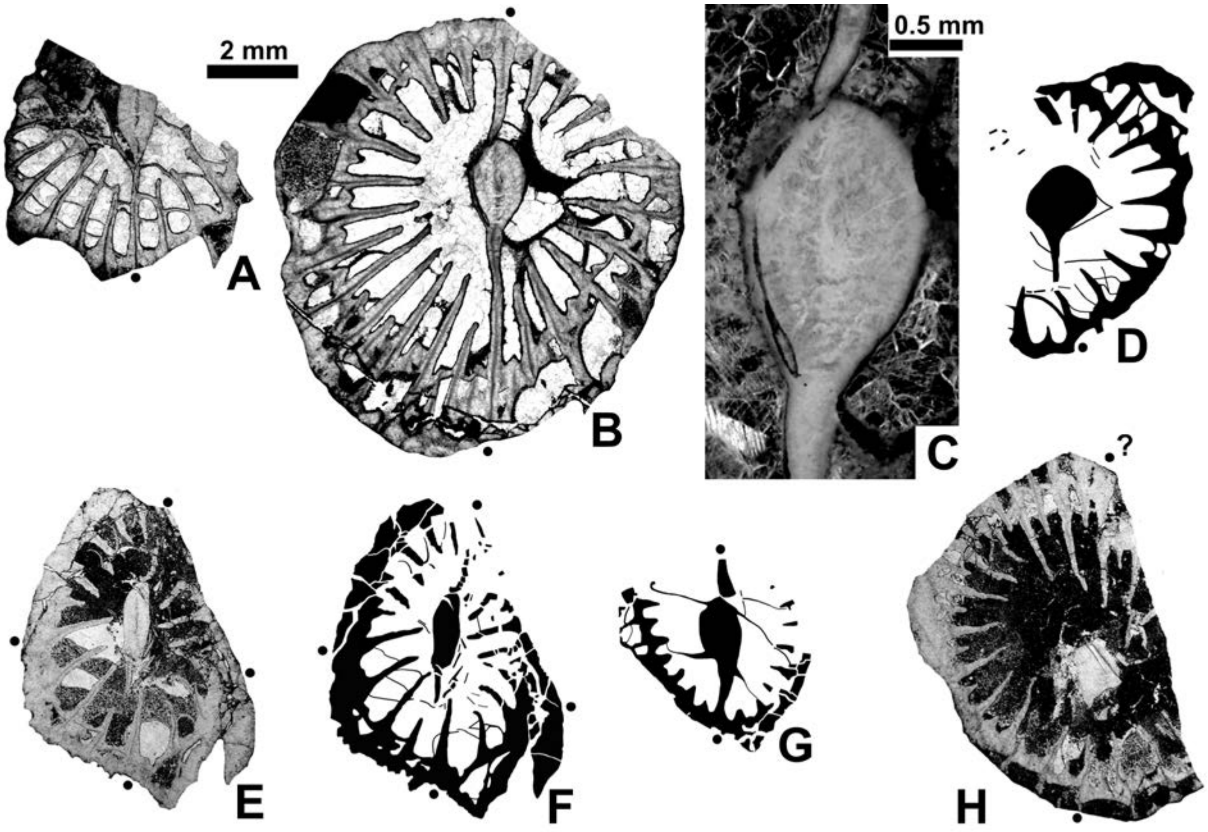
Protokionophyllum facilis Vassilyuk
in Aizenverg *et al*., 1983
(Text-fig. 6)

1983. *Protokionophyllum facilis* sp. nov.; Vassilyuk in Aizenverg *et al*., p. 21 (faunal list), p. 142 (figure captions), pl. 28, fig. 9.

MATERIAL: Holotype UAM-Tc.Don.1/346 (formerly 1405/12) restricted to two transverse thin sections with no corallite remnants preserved. Its macrostructure of possibly mature growth stage well preserved; microstructure of septa diagenetically altered. Five hypotypes UAM-Tc.Don.1/347–351 preserved as small fragments of different corallite growth stages, two of which are probably immature. All specimens diagenetically altered and corroded; some perhaps eroded. Some skeletal structures slightly to moderately crushed. Microstructure of septa diagenetically altered. Five thin sections and four peels available for study.

DIAGNOSIS: *Protokionophyllum* with n:d value approximately 24:10×9 mm; major septa continuous, 2/3–3/4 corallite radius long; in tabularium wedge-shaped. Minor septa commonly enter tabularium; their inner margins thickened; rare interrupted by small lonsdaleoid dissepiments. Monoseptal pseudocolumella connected to protosepta up to mature growth stage inclusively; dissepimentarium less than 1/3 corallite radius wide; dissepiments mostly interseptal.

DESCRIPTION OF HOLOTYPE: Major septa in ontogenetically most advanced growth stage of holotype (Text-fig. 6B) bilaterally arranged, slightly less than 3/4 corallite radius long, equally and slightly thickened in wedge shaped form, almost equal in length; only protosepta elongated and last major septa inserted slightly shortened. Cardinal septum united with monoseptal, lens-like pseudocolumella (Text-fig. 6C). Counter septum meets pseudocolumella, but their 'middle dark lines' not united. Minor septa differentiated in length. Most continuous, with peripheral parts joining major septa in formation of



Text-fig. 6. *Protokionophyllum facilis* Vassilyuk, 1983. Transverse thin sections. A–C – Specimen UAM-Tc.Don.1/346. Holotype. A – late neanic or early mature growth stage; B – mature growth stage; C – pseudocolumella (enlarged from B). D – Specimen UAM-Tc.Don.1/347. Hypotype. Mature growth stage. E, F – Specimen UAM-Tc.Don.1/351. Hypotype. Late neanic growth stage (F – drawing on E). G – Specimen UAM-Tc. Don.1/349. Hypotype. Late neanic growth stage. H – Specimen UAM-Tc.Don.1/350. Hypotype. Lower part of calice. For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bar between A and B corresponds to all images except C.

septotheca and inner, thickened parts penetrating tabularium. Rare minor septa restricted to dissepimentarium; some divided by lonsdaleoid dissepiments into inner parts attached to dissepiments and peripheral parts attached to septotheca. Unequal width and content of dissepimentarium result at least in part from slightly oblique section. Dissepimentarium widest adjacent to cardinal septum, consisting of irregular interseptal dissepiments and small lonsdaleoid dissepiments spanned between adjacent, continuous major septa. Only single row of interseptal dissepiments accompany counter septum. Some dissepiments felt in with sclerenchyme. Cardinal fossula absent. Immature part of holotype (Text-fig. 6A) resembles mature one in most characters, to the extent it is preserved. Dissepiments either absent or eroded and minor septa not seen in immature part.

One immature hypotype (Text-fig. 6E, F), with n:d value 18:7×5 mm, slightly pressed laterally as documented by broken septa and external wall, resembles immature growth stage of holotype. Second probably immature corallite (Text-fig. 6G) preserved in small slightly oblique fragment important as documenting strongly thickened pseudocolumella developed directly from cardinal septum, very short major septa, and sections of tabulae elevated towards pseudocolumella. Very thick pseudocolumella occurs in another probably mature or early mature corallite (Text-fig. 6D). Fragment of dissepimentarium of that corallite preserved resembles that found in holotype. Only the lower, incomplete part of calice preserved from fourth hypotype (Text-fig. 6H). Its thick pseudocolumella elongated towards cardinal septum but free from it. Most minor septa penetrate calice.

OCCURRENCE: Holotype UAM-Tc.Don.1/346: Right bank of Kalmius River (imprecise). Hypotypes UAM-Tc.Don.1/347–349: Kalmius and Berestovaya rivershed, UAM-Tc.Don.1/350, 351: Kalmius River Area, Voznesenka Village. All specimens from Limestone D_7^6. Lower Voznessenkian Horizon, *Homoceras–Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lower lower Bashkirian.

Protokionophyllum feninoense sp. nov.
(Text-figs 7–9)

HOLOTYPE: UAM-Tc.Don.1/352.

TYPE STRATUM: Limestone E_1^{verkh}, lower Feninian Horizon, upper lower Bashkirian.

TYPE LOCALITY: Kalmius River Area, Fenino Village.

ETYMOLOGY: Named after the type locality that yielded the holotype and some of the described paratypes.

DIAGNOSIS: *Protokionophyllum* with n:d value in lower part of calice 23:10 mm (holotype) to 25:10.5 (paratype); protosepta in premature growth stage connected to pseudocolumella, in maturity commonly elongated, with only cardinal septum connected to pseudocolumella directly; minor septa either restricted to septotheca or form ridges on tops of dissepiments; tabularium uniform; tabulae complete, spanning entire tabularium, elevated at low angle to reach pseudocolumella; dissepiments mostly interseptal, irregular; lonsdaleoid dissepiments sporadic.

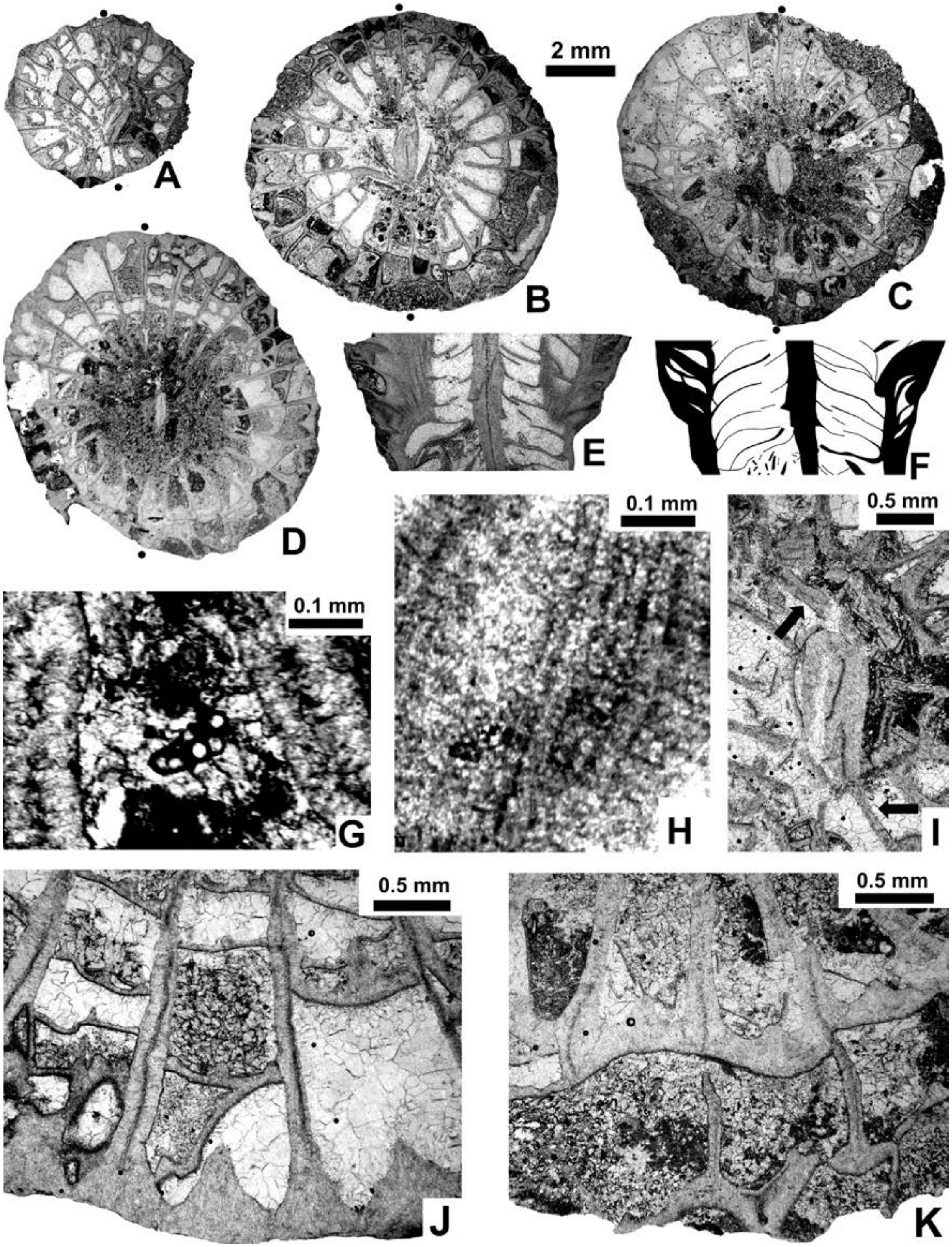
MATERIAL: Eight incomplete specimens. Holotype UAM-Tc.Don.1/352 and seven paratypes UAM-Tc. Don.1/353–359. Incomplete neanic growth stage preserved in one specimen, very early mature growth stage occurs in two specimens, and three corallites have major parts of calices preserved. Some skeleton fragments crushed, but main diagnostic characters recognisable in all specimens. Microstructure of most septa recrystallised. Remnants of trabeculae distinguishable in short parts of some septa. 15 thin sections and 26 peels available for study.

DESCRIPTION: Corallites conical. Calices approximately 8 mm deep as documented by remnants of corallites and transverse sections (Text-figs 7C, D; 8C, G). External wall composed of triangular bases of major and minor septa that form septotheca (Text-figs 7J; 8E). In incompletely preserved neanic growth stage of one corallite (Text-fig. 9D) with 3 mm diameter, major septa except for protosepta short and wedge shaped. Protosepta elongated, meet eccentrically, but their ‘middle dark lines’ do not unite. Cardinal septum much longer than counter septum, thickened at its inner margin. The connection of protosepta in thin section and their disconnection within 0.6 mm of corallite growth (Text-fig. 9D, E, respectively) suggests occurrence of axial septum very early in ontogeny. Only bases of major septa recognisable in external wall at that early growth stage (Text-fig. 9H). Minor septa not yet documented. Morphology described may be restricted to that corallite. Its mature growth stage (Text-fig. 9F, G) is broken in part and many of its septa in that growth stage are crushed. However, its main morphological feature resembles holotype and some paratypes closely.

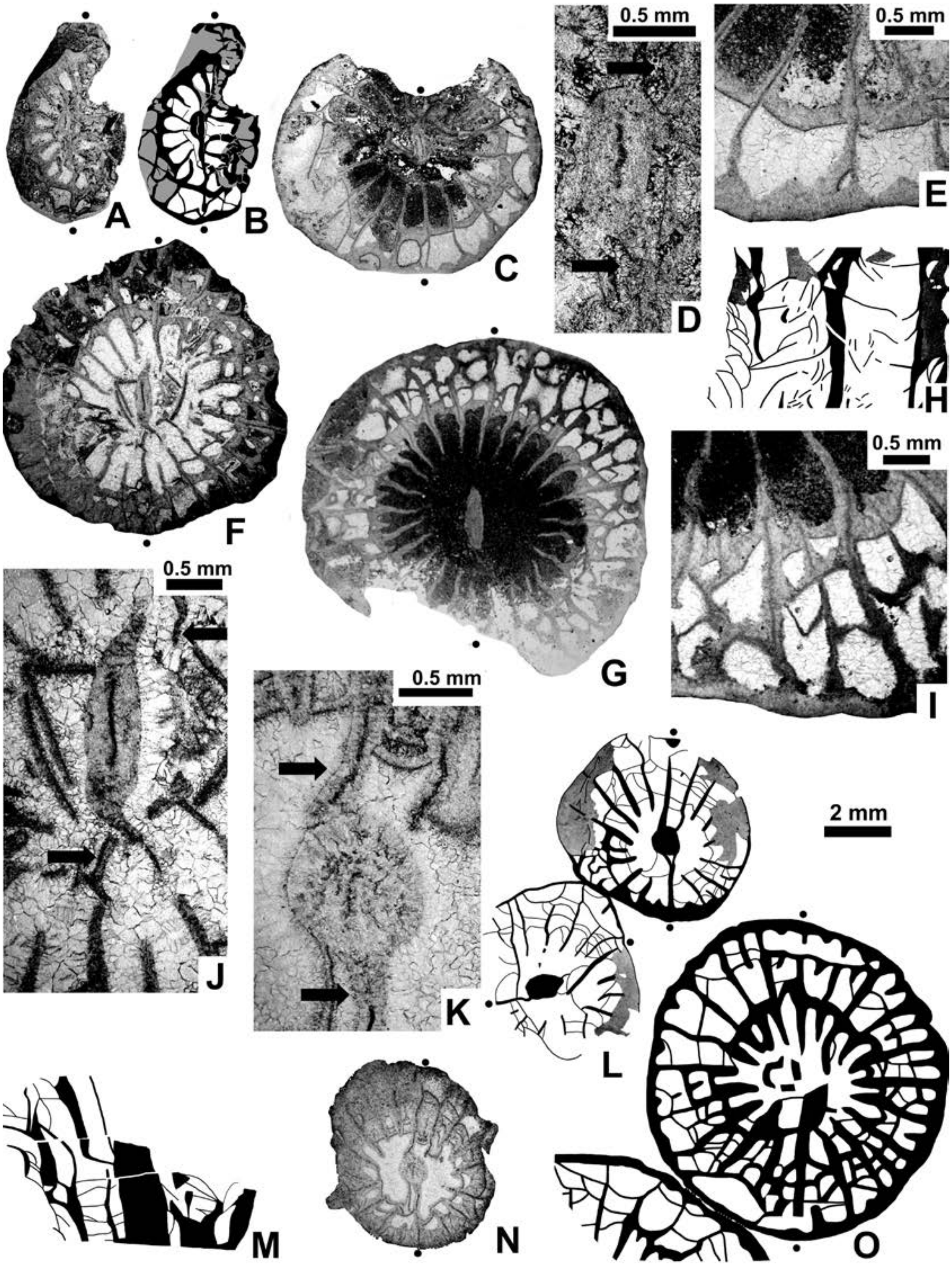
In very early mature growth stage of holotype and one paratype (Text-figs 7A; 8A, B respectively) with n:d values 21:5.5 mm (holotype) and approximately 16:6.0×3.8 mm (paratype), major septa approach, some reach pseudocolumella united with both protosepta (Text-figs 7I, arrows; 8A, B). Diagenetic alterations make that connection difficult to recognize. Cardinal fossula absent. Minor septa recognisable in septotheca. In comparable growth stage of another corallite (Text-fig. 8K, N), major septa 1/2 corallite radius long. Both protosepta meet very thick, circular, monoseptal pseudocolumella, but ‘middle dark lines’ of these three skeletal structures separated. Disconnection of ‘middle dark lines’ of pseudocolumella and cardinal septum may be diagenetic, but inner margin of counter septum is certainly disconnected (Text-fig. 8K, lower and upper, respectively).

In early to advanced mature growth stage, including calices (Text-figs 7B–D; 8C, F, G, O; 9B, F, G, I, J), n:d values differentiated. In holotype, 23:9.0 mm beneath calice and 23:10 mm in calice. In paratypes, 18:8.0×7.6 mm in calice of smallest corallite to 22:8.5 mm beneath calice and 25:10.5 in calice of largest corallite. Most major septa continuous, radially arranged, sharply ended, equal in length except for protosepta in most corallites. Disconnections of major septa (Text-figs 7K; 8O; 9J) resulted mostly from shallow rejuvenation (Text-figs 7K; 9J, upper) or from diagenetic alterations (Text-fig. 9B), but lonsdaleoid dissepiments may occur (Text-fig. 8C, G, O).

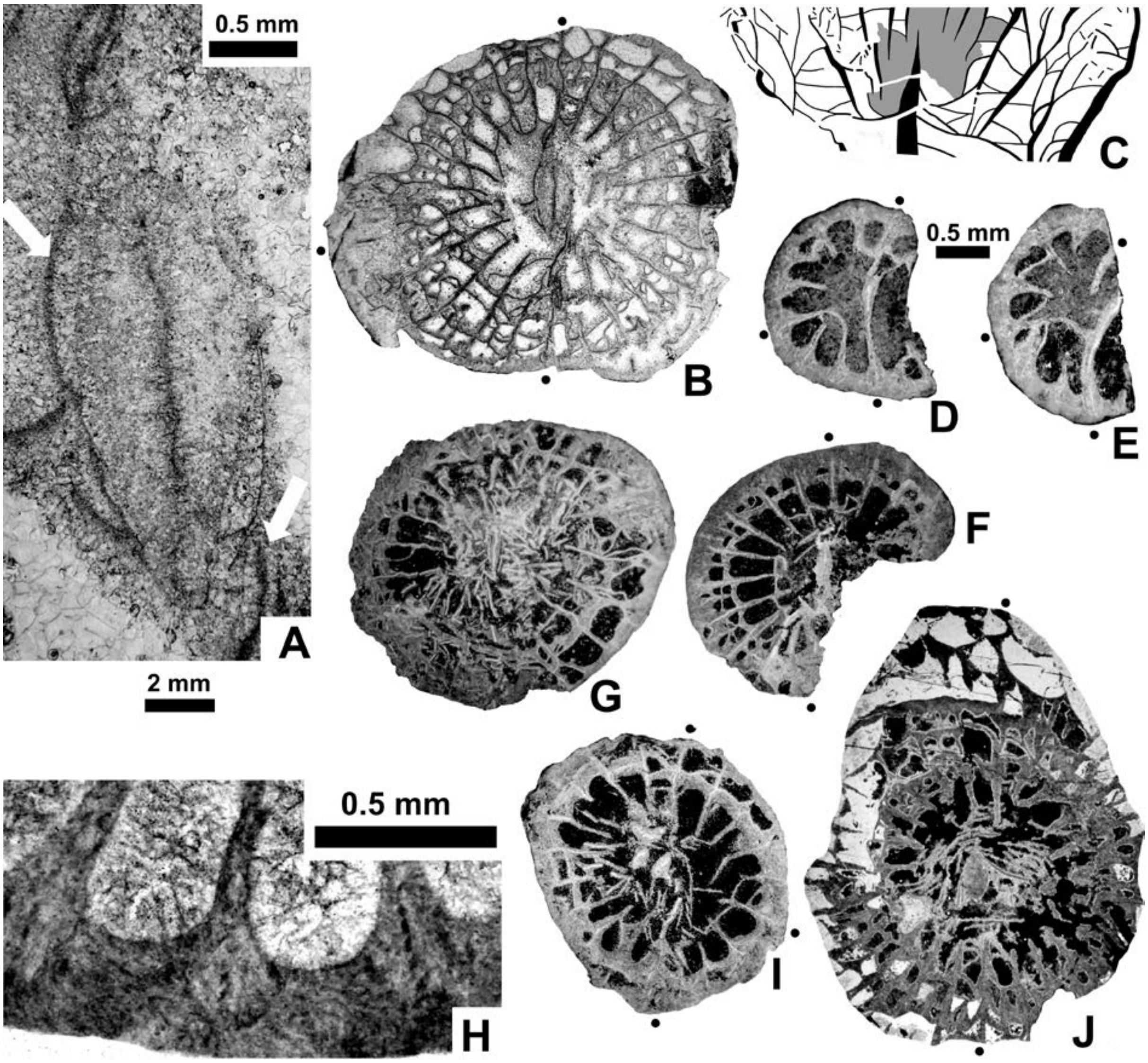
Protosepta length in mature growth stage and their relationship to pseudocolumella differ considerably. In calices, both protosepta disconnected from pseudocolumella and equal to remaining major septa in length and thickness with cardinal fossula absent (Text-figs 7C, D; 8C, G). In transverse sections made



Text-fig. 7. *Protokionophyllum feninoense* sp. nov. Transverse thin sections except when stated otherwise. Specimen UAM-Tc.Don.1/352. Holotype. A – late neanic or very early mature growth stage; B – mature growth stage immediately below calice floor; C, D – lower and middle part of calice; E, F – longitudinal section; E – slightly eccentric; F – centric (drawing on peel image); G – probable remnants of trabeculae in transverse section; H – probable remnants of trabeculae in longitudinal section; I – monoseptal pseudocolumella with cardinal septum attached and counter septum approaching (lower and upper arrows respectively; enlarged from A); J – septotheca and minor septa divided in short segments; K – shallow and local rejuvenation. For stratigraphic positions see text. Protosepta marked by black dots. Scale bar between B and C corresponds to images A−F.



Text-fig. 8. *Protokionophyllum feninoense* sp. nov. Transverse thin sections except when stated otherwise. A–E. Specimen UAM-Tc.Don.1/356. Paratype. A, B – early mature growth stage (B – drawing on A); C – mature growth stage, lower part of calice; D – enlarged from A to document relationship of pseudocolumella to protosepta (arrows); E – septotheca (enlarged from C). F–J – Specimen UAM-Tc.Don.1/353. Paratype. F – mature growth stage; G – middle part of calice; H – longitudinal section (drawing on peel image); I – peripheral part of corallite (enlarged from G); J – pseudocolumella connected to cardinal sepum; break of connection caused diagenetically; long counter septum disconnected from pseudocolumella (arrows; enlarged from F). K–O – Specimen UAM-Tc.Don.1/359. Paratype. K –pseudocolumella–protosepta relationship (enlarged from N; protosepta indicated by arrows); L – early mature growth stage of two corallites (upper corallite same as in N and O); M – longitudinal section; N – early mature growth stage; O – mature growth stage of upper corallite from L (M, L, O – drawings on peel images). For stratigraphic positions see text. Protosepta marked by black dots. Scale bar between I and O corresponds to all images except when marked separately.



Text-fig. 9. *Protokionophyllum feninoense* sp. nov. Transverse thin sections except when stated otherwise. A−C – Specimen UAM-Tc. Don.1/357. Paratype. A – monoseptal pseudocolumella and long protosepta (white arrows; enlarged from B); B – mature growth stage; C – oblique longitudinal section through calice in upper part (drawing on thin section image). D−H – Specimen UAM-Tc.Don.1/354. Paratype. D, E – neanic growth stage; F – early mature growth stage; G – mature growth stage; H – morphology of external wall (enlarged from D). I – Specimen UAM-Tc.Don.1/355. Paratype. Early mature growth stage. J – Specimen UAM-Tc.Don.1/358. Paratype. Mature growth stage with shallow rejuvenation (upper). For stratigraphic positions see text. Cardinal, counter and alar septa marked by black dots when recognisable. Scale bar between D and E corresponds to both. Scale bar between A and H corresponds to all images, except when marked separately.

below calice floor, protosepta differentiated in length. In holotype (Text-fig. 7B), protosepta broken, but probably elongated. In advanced mature growth stage of paratypes the following variants occur: (1) Both protosepta elongated to reach pseudocolumella directly (Text-fig. 9F; diagenetic disconnection not considered). (2) Cardinal septum elongated and thickened on its inner margin to form pseudocolumella; counter septum equal to adjacent major septa in length (Text-fig. 8O). Both protosepta unite with thick pseudocolumella in early mature growth stage of that corallite (Text-fig. 8L, upper), whereas only cardinal septum unites with thick pseudocolumella in its neighbor (Text-fig. 8L, lower). (3) Cardinal septum united with pseudocolumella, free inner margin of long counter septum terminated parallel to pseudocolumella (Text-fig. 8F, J, arrows). (4) Protosepta (arrows) so long as to meet pseudocolumella from aside; counter septum longer (Text-fig. 9A, B). Pseudocolumella/protosepta relationship in some corallites uncertain (Text-fig. 9F, G, I, J). Cardinal fossula absent from all specimens and growth stages observed.

Minor septa either restricted to their triangular bases in septotheca (Text-fig. 8E), or variously elongated up to entering tabularium with their slightly thickened inner margins. Rare minor septa continuous. Most broken into segments attached to dissepiments (Text-figs 7J; 8I). Dissepimentarium approximately 1/4 corallite radius wide. Dissepiments in transverse sections mostly irregular, large, in two to four rows. Inner wall thickened. In longitudinal sections (Text-figs 7E, F; 8H, M; 9C), dissepiments either hardly distinguishable due to strong sclerenchymal cover or differentiated in size, elongated, sloping down under approximately 45º. Tabulae complete, directed at low angle upwards, span entire tabularium, reaching thick pseudocolumella. Additional tabellae rare, occur in inner tabularium when present. Microstructure of septa diagenetically altered. Bodies resembling fine trabeculae recognisable in rare parts of septa (Text-fig. 7G, H).

REMARKS: *Protokionophyllum feninoense* sp. nov. demonstrates considerable variability in several diagnostic characters, resulting primarily from the poverty of the collection available for the study and a suspected absence of intermediate forms. Furthermore, the identification of specimens with partially crushed and/or incomplete skeletons (Text-figs 8C; 9G, F, I, J) are not incontrovertibly justified and proved. However, a description of these in open nomenclature, with remarks pointing to *P. feninoense* sp. nov. as the most closely related species, would only increase the length of this paper without substantially contributing to the taxonomy and subdivision of *Protokionophyllum*.

Protokionophyllum feninoense sp. nov. closely resembles *P. facilis* in its main diagnostic features, including n:d values. It differs in the radial arrangement of the major septa, in the minor septa being either underdeveloped or commonly divided into segments attached to dissepiments, in the differentiated nature of the pseudocolumella/protosepta relationship with counter septum in some corallites elongated so much as to extend behind corresponding margins of pseudocolumellae, and in the better development of the dissepimentarium.

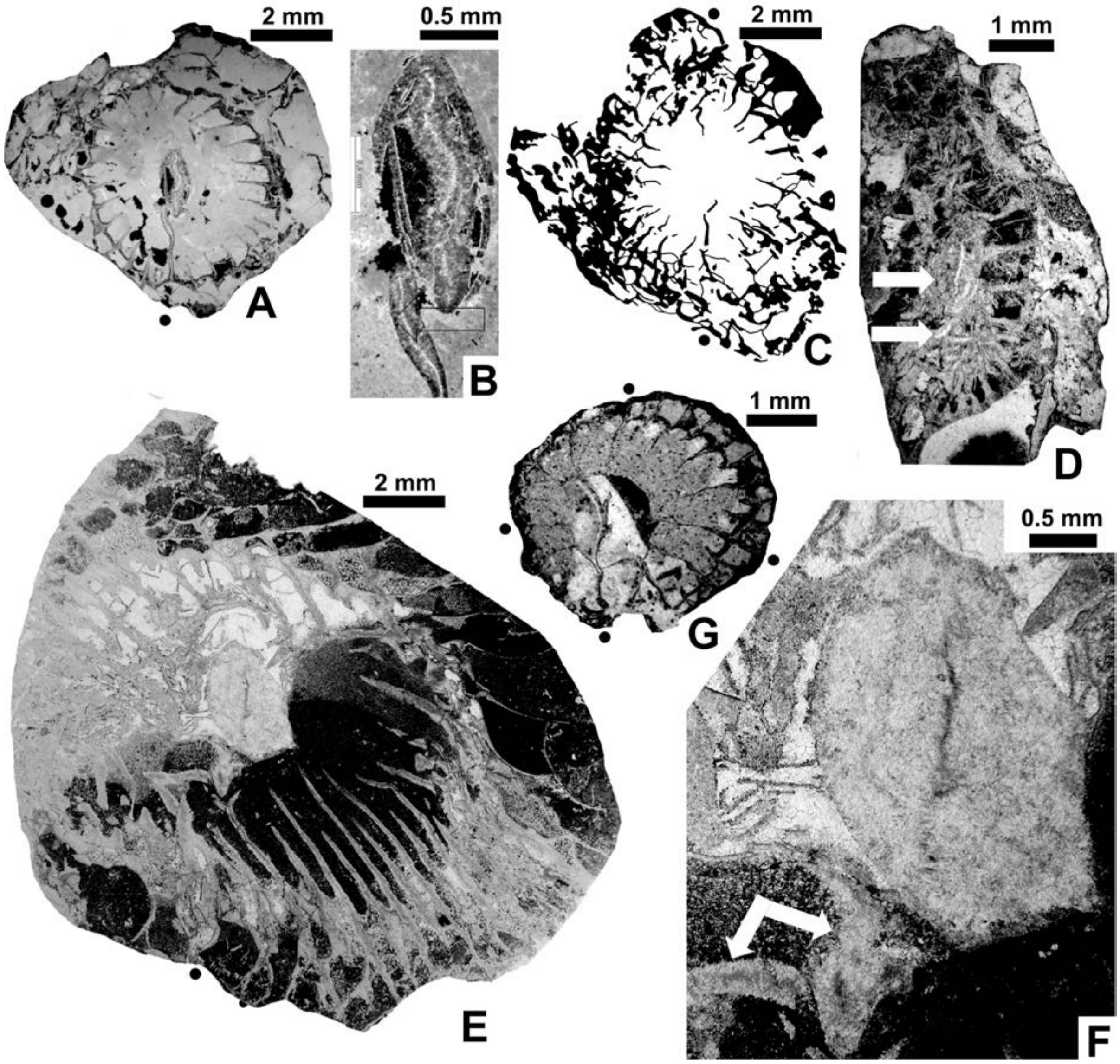
OCCURRENCE: Holotype UAM-Tc.Don.1/352 and paratypes UAM-Tc.Don.1/353–356, 359: Kalmius River Area, Fenino Village, Limestone E_1^{verkh}. Paratypes UAM-Tc.Don.1/357: Krynka River Area, Svistuny Village, Velyka Shyshivka Balka, Limestone E_1^{verkh}. All from lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus–Id. sulcatus sulcatus* conodont Biozone. Upper lower Bashkirian. Paratype UAM-Tc.Don.1/358: Kalmius River Area, Voznesenka Village, Limestone D_7^6. Lower Voznesenskian Horizon, *Homoceras–Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lower Bashkirian.

Protokionophyllum sp. 1
(Text-fig. 10)

REMARKS: Four fragmentary corallites, all derived from the D_7 subgroup of limestones (see Occurrence), differ from the holotype of *P. facilis* to an extent precluding their inclusion in that species, whereas their derivation from lowermost Bashkirian strata, which is notable for being almost barren of rugose corals, make them important for understanding the general characteristics of early Bashkirian rugose coral fauna. They differ from each other in several characters. Their brief description under a common open name avoids potentially unwarranted taxonomic splitting.

Specimen UAM-Tc.Don.1/360 (Text-fig. 10A, B). N:d value 27:12×10 mm (incomplete). Major septa thin, enter tabularium for approximately 1/4–1/3 corallite radius, equal in length except for long cardinal septum; their dissepimentarial segments almost totally reduced. Minor septa not seen in preserved corallite part. Pseudocolumella monoseptal, narrow, elongated, free from protosepta. Long cardinal septum meets its lateral surface (Text-fig. 10B). Dissepimentarium slightly more than 1/3 corallite radius wide; consists mostly of large, lonsdaleoid dissepiments.

Specimen UAM-Tc.Don.1/361 (Text-fig. 10C). Strongly corroded with skeletal elements broken in part. N:d value 25:12×10 mm (incomplete). Major septa thin, equal in length except for cardinal septum, enter tabularium for approximately 1/2 of corallite radius. Peripheral segments of some major septa interrupted by small lonsdaleoid dissepiments, other complete. Cardinal septum elongated, but not thickened and does not form pseudocolumella. Minor septa differentiated in length, some enter peripheral dissepimentarium that reaches up to 1/3 corallite radius. Dissepiments interseptal and lonsdaleoid.



Text-fig. 10. *Protokionophyllum* sp. 1. Transverse thin sections. A, B – Specimen UAM-Tc.Don.1/360. A – mature growth stage; B – pseudocolumella and long cardinal septum (enlarged from A). C – Specimen UAM-Tc.Don.1/361. Mature growth stage (drawing on thin section image). D–F – Specimen UAM-Tc.Don.1/362. D – early mature growth stage; pseudocolumella (upper arrow) united with cardinal septum (lower arrow); E – mature growth stage; F – broken cardinal septum (white arrows) meets monoseptal pseudocolumella. G – Specimen UAM-Tc. Don.1/363. Lower part of calice; mature (?) growth stage. For stratigraphic positions see text. Protosepta and alar septa marked by black dots when recognisable.

Specimen UAM-Tc.Don.1/362 (Text-fig. 10D–F). Compressed; its size and n:d value unknown. Measured diameter near calice floor 15.5×13.0 mm (Text-fig. 10E). Major septa wedge-shaped; thickest at dissepimentarium/tabularium border, thin in dissepimentarium; their total number unknown. Minor septa 3/4 length of major septa, penetrate calice deeply. Pseudocolumella monoseptal, thick, grain-shaped, perhaps connected to both protosepta in early mature growth stage, but only connection to cardinal septum documented (Text-fig. 10D, lower arrow). That connection remains up to calice floor (Text-fig. 10F, arrows). Width of dissepimentarium unknown. Dissepiments interseptal and lonsdaleoid in preserved part of corallite.

Specimen UAM-Tc.Don.1/363 (Text-fig. 10G).

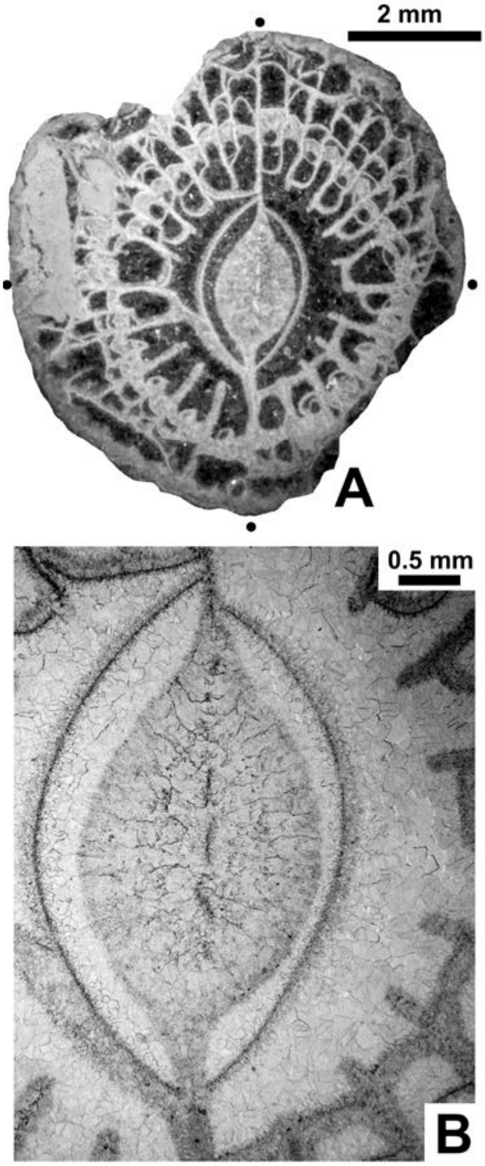
N:d value 16:4.0 mm. Major septa thin, continuous, enter tabularium for approximately 1/2 corallite radius, equal in length except for thin, wavy cardinal septum that extends up to corallite axis. Minor septa continuous, enter peripheral tabularium. Single row of regular, interseptal dissepiments.

OCCURRENCE: Specimen UAM-Tc.Don.1/360: Kalmius River Area, Voznesenka Village, Limestone D_7^3. Specimen UAM-Tc.Don.1/361: Kalmius River Area, Popova Balka, Limestone D_7^2. Specimen UAM-Tc.Don.1/362: Kalmius River Area, Voznesenka Village, Limestone D_7^6. Specimen UAM-Tc.Don.1/363: Kalmius/Berestovaya rivershed, Limestone D_7^6. All specimens from lower Voznesenkian Horizon, *Homoceras–Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lower Bashkirian.

Protokionophyllum sp. 2
(Text-fig. 11)

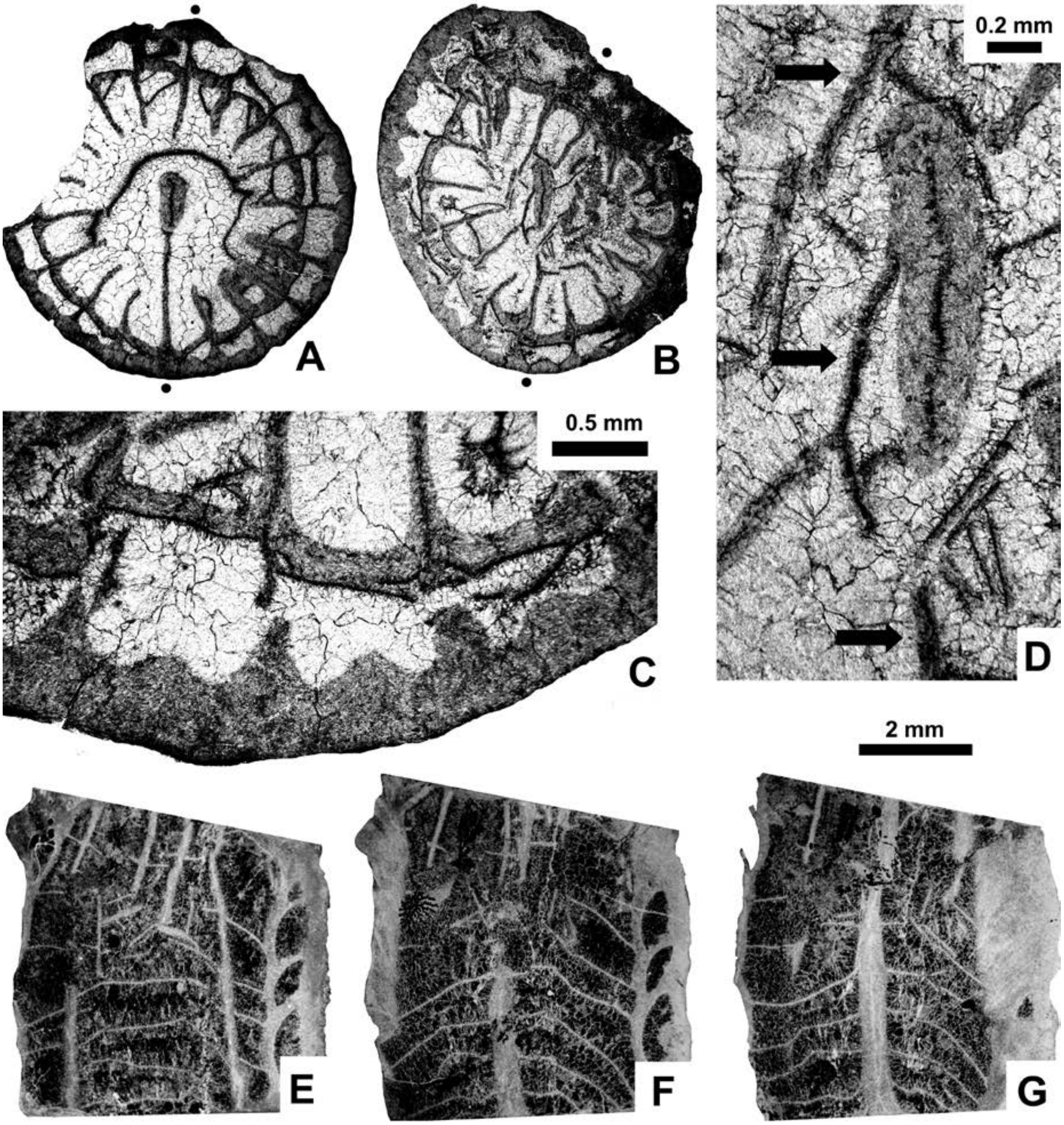
MATERIAL: One incomplete specimen, UAM-Tc.Don.1/364, with approximately 2.5 mm long fragment of skeleton preserved below calice. Calice incomplete, infilled with sediments. Microstructure of septa diagenetically altered. Morphology in transverse section well preserved. Longitudinal section not available. One transverse thin section and one peel available for study.

DESCRIPTION: Corallite with n:d value 22:11.5 mm. Major septa thin, except for thickened external wall where they thicken (Text-fig. 11A). Most continuous, reach 2/3 corallite radius. Some interrupted by lonsdaleoid dissepiments. Only last pair of major septa inserted short. Protosepta elongated and united directly with thick oval, monoseptal pseudocolumella (Text-fig. 11B). Minor septa enter tabularium; some deeply. Some minor septa continuous, most interrupted by lonsdaleoid dissepiments. Dissepimentarium interseptal in its inner part with minor septa continuous. Interseptal dissepiments regular, large slightly or distinctly convex peripheral wards, rare small pseudoherringbone. Lonsdaleoid dissepiments common, large – i.e., interrupting both major and minor septa – and small – interrupting only minor septa. Inner wall distinctly thickened. Bases of both septal cycles thickened up to the point that they meet each other laterally and form septotheca. Regular and limited tabulae circumaxial sections indicate their rather distant occurrence and elevation towards pseudocolumella. Peripheral tabularium biform, as suggested by sections of tabulae more numerous along one side of minor septa. Inner margins of several minor septa connected with adjacent major septa by distinct arches of tabulae sections (Text-fig. 11A, upper) indicate a rather distinct biformity in those septal loculi.



Text-fig. 11. *Protokionophyllum* sp. 2. Specimen UAM-Tc.Don.1/364. A – transverse section, mature growth stage; B – pseudocolumella (enlarged from A). For stratigraphic position see text. Protosepta and alar septa marked by black dots.

REMARKS: The discussed specimen differs from *P. facilis* in having the pseudocolumella united directly



Text-fig. 12. *Protokionophyllum* sp. 3. Specimen UAM-Tc.Don.1/365. A–D – Transverse thin sections. A – early mature growth stage; B – mature growth stage; C – septotheca; major septa broken diagenetically; D – monoseptal pseudocolumella; upper arrow indicates counter septum, two lower arrows indicate broken cardinal septum; E–G – longitudinal sections from corallite periphery to its axis (peels). For stratigraphic position see text. Protosepta marked by black dots. Scale bar above G corresponds to all images except C and D.

with both protosepta, in its lonsdaleoid dissepiments being much more numerous and commonly breaking both major and minor septa, and in the biform tabularium documented by sections of peripheral parts of tabulae. *Protokionophyllum* sp. 2 differs from *P. feninoense* sp. nov. in the union of the pseudocolumella with the protosepta, better developed minor septa that penetrate the biform tabularium deeper and large lonsdaleoid dissepiments.

OCCURRENCE: Krynka River Area, Svistuny Village, Velyka Shyshivka Balka, Limestone E_1^{verkh}.

Svita $C_2{}^{b}{}_{a}{}^{nizhn}$, Feninian Horizon, *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, *Idiognathodus sinuosus–Id. sulcatus sulcatus* conodont Biozone, *Reticuloceras–Bashkortoceras* (R_1) ammonite Biozone. Lower Bashkirian.

Protokionophyllum sp. 3
(Text-fig. 12)

MATERIAL: One incomplete specimen UAM-Tc. Don.1/365. Early growth stage and calice absent. Skeleton in mature growth stage crushed slightly. Three thin sections and seven peels available for study.

DESCRIPTION: In early mature growth stage (Text-fig. 12A), n:d value 18:6.3 mm. Major septa approximately 1/3 corallite radius long, equal in length, thin, in inner wall slightly widened, continuous. Only cardinal septum elongated to and directly united with monoseptal, narrow, and oval pseudocolumella. Minor septa restricted to their bases, widened so as to meet lateral bases of major septa to form septotheca (Text-fig. 12C). Dissepimentarium in one row of regular dissepiments. Advanced mature growth stage slightly damaged by diagenesis (Text-fig. 12B). Its morphology similar to early mature stage in most characters, only differing in relationship of protosepta to narrow, elongated pseudocolumella. Both protosepta elongated so as to extend behind cardinal and counter margins of pseudocolumella. Counter septum free ended (Text-fig. 12D, upper arrow). Cardinal septum broken; its innermost sector united with left side of pseudocolumella (Text-fig. 12D, middle and lower arrow). In longitudinal sections made from corallite periphery of tabularium to its axis (Text-fig. 12E–G respectively), tabulae complete, elevated gently towards pseudocolumella. Dissepiments with thickened walls, arranged in single vertical row.

REMARKS: The specimen described differs from all species of *Protokionophyllum* in its small diameter and number of septa, in a very differentiated in length of the counter septum, in the minor septa strongly underdeveloped, in the single row of regular dissepiments, and in the absence of lonsdaleoid dissepiments.

OCCURRENCE: Solona River bank, Novotroitske Village, Limestone F_1. Blagodatnian Horizon, upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella praegorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Upper middle Bashkirian.

Genus *Krynkaphyllum* gen. nov.

TYPE SPECIES: *Krynkaphyllum multiplexum* sp. nov.

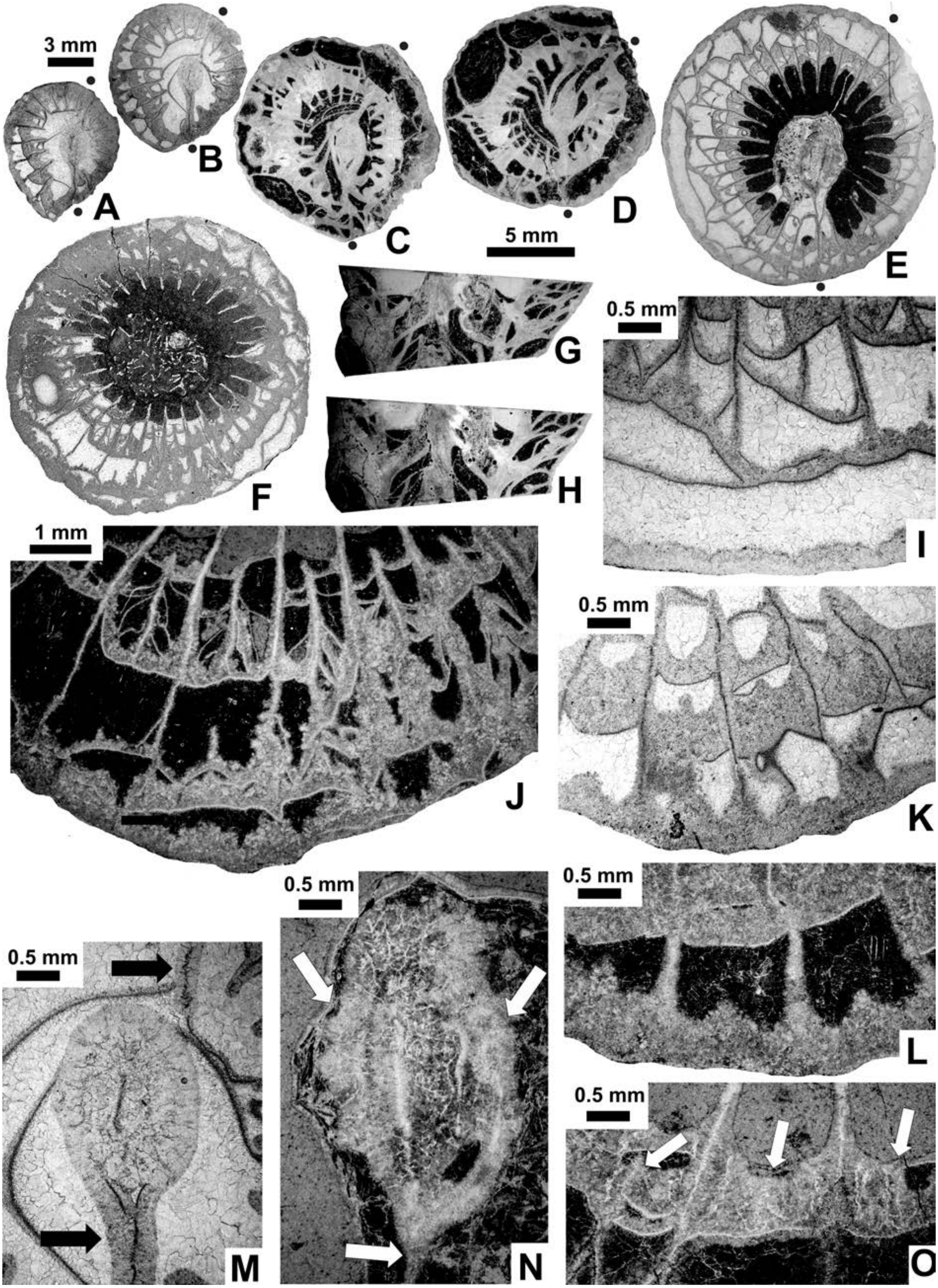
ETYMOLOGY: Named after the Krynka River in the Donets Basin.

SPECIES INCLUDED: *Krynkaphyllum multiplexum* sp. nov.; *Krynkaphyllum validum* sp. nov.

DIAGNOSIS: Solitary, dissepimented corals; cardinal septum united with median lamella in early ontogeny, may last permanently united; counter septum in maturity attaches to pseudocolumella or free; elongated in early growth stages; cardinal fossula absent; pseudocolumella in early growth stage monoseptal; in mature growth stage comprises median lamella and thick inner margin of tabula with short septal lamellae incorporated; tabularium normal; tabulae complete; dissepimentarium comprises interseptal and lonsdaleoid dissepiments; grapelike dissepiments may occur.

REMARKS: *Krynkaphyllum* gen. nov. resembles *Protokionophyllum* in several morphological characters mentioned in the family diagnosis. Its complex pseudocolumella constitutes the diagnostically most important difference. Variants in the pseudocolumella morphology and its relationship to the protosepta and the inner margins of tabulae, described in detail together with the species descriptions, may appear decisive not only for distinguishing on the generic level between *Protokionophyllum* and *Krynkaphyllum* gen. nov., but also on levels higher than generic when existing examples are considered. For instance, differences in pseudocolumella morphology was commonly accepted as adequate for distinguishing between the families Geyerophyllidae and Koninckocariniidae (see above). The distinction between *Krynkaphyllum* gen. nov. and *Colligophyllum* gen. nov. is discussed in the remarks under the latter.

Krynkaphyllum multiplexum sp. nov. is chosen as the type species because its holotype documents an almost complete ontogenetic progression and changes in the morphology of the pseudocolumella from monoseptal, derived from the cardinal septum early in ontogeny, to complex in the mature growth stage, including the calice. However, variation in pseudocolumella morphology over the course of corallite growth is best documented in the holotype of *K. validum* sp. nov., whereas variation in the morphology of the dissepimentarium is best demonstrated by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the paratype UAM-Tc.Don.1/373. All of those characters are important not only for the listed taxa, but also in a general approach to the study of the rugose corals and for selecting diagnostic characters at a genus level (see Considerations).

Krynkaphyllum multiplexum sp. nov.
(Text-figs 13–15)

e.p. 1960. *Lytvophyllum dobroljubovae* Vassilyuk, p. 103, pl. 26, figs 1c–h.

HOLOTYPE: Specimen UAM-Tc.Don.1/366.

TYPE LOCALITY: Krynka River Area, Svistuny Village. Velyka Shyshivka Balka.

TYPE STRATUM: Limestone E_1^{verkh}, Feninian Horizon, *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuosus*–*Id. sulcatus sulcatus* conodont Biozone, *Reticuloceras*–*Bashkortoceras* (R_1) ammonite Biozone. Upper lower Bashkirian.

ETYMOLOGY: *Latin multiplex* – manifold, multiple; after the variable and complex morphology of pseudocolumella.

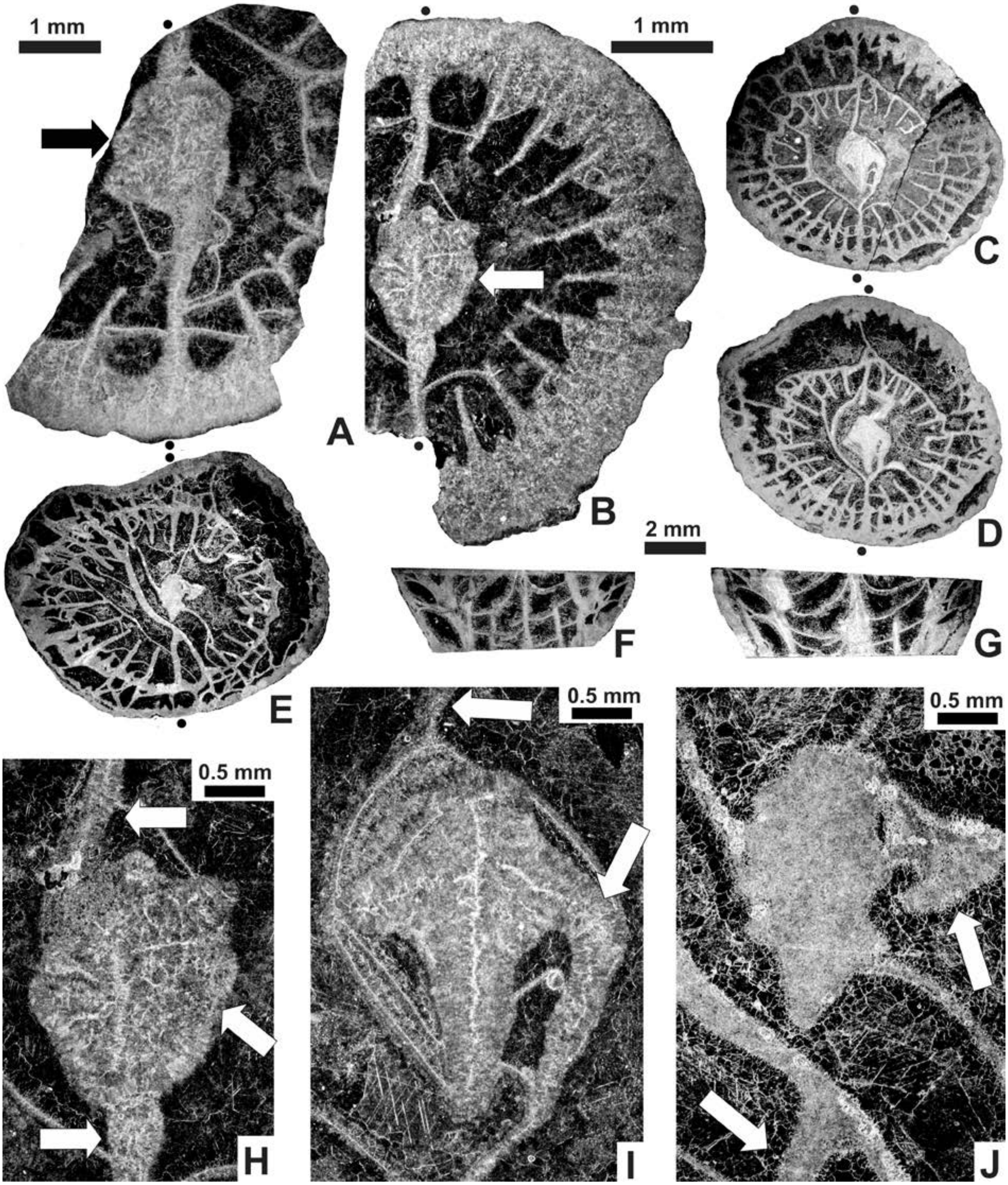
MATERIAL: Five corallites available for study here, and perhaps all four, or just two, paratypes of *Lytvophyllum dobroljubovae*, illustrated in Vassilyuk (1960, plate 26, figs 1c–1h; not available for restudy). Almost complete holotype, UAM-Tc.Don.1/366, with only the early neanic growth stage and upper part of calice missing; three corallites, UAM-Tc.Don.1/367–369, preserved in most parts of their skeletons; one corallite, UAM-Tc.Don.1/370, preserved in calice only. The latter identification is the most poorly documented. All four corallites temporarily accepted as paratypes (see remarks). 13 thin sections and 16 peels available for study.

DIAGNOSIS: *Krynkaphyllum* with maximum measured n:d value 25:17×15 mm (middle of holotype calice) and minimum n:d value 24:9.2×8.0 mm (middle of calice in paratype); major septa equal in length except for protosepta; cardinal septum dominates, united with median lamella in early growth stage; in mature growth stage may be elongated and separated from pseudocolumella; counter septum approaches pseudocolumella at least in early growth stage, may be equal to other major septa in advanced maturity; minor septa appear in corallite lumen late in ontogeny, commonly interrupted by lonsdaleoid dissepiments that may prevail in dissepimentarium; tabularium uniform; tabulae complete, elevated towards pseudocolumella.

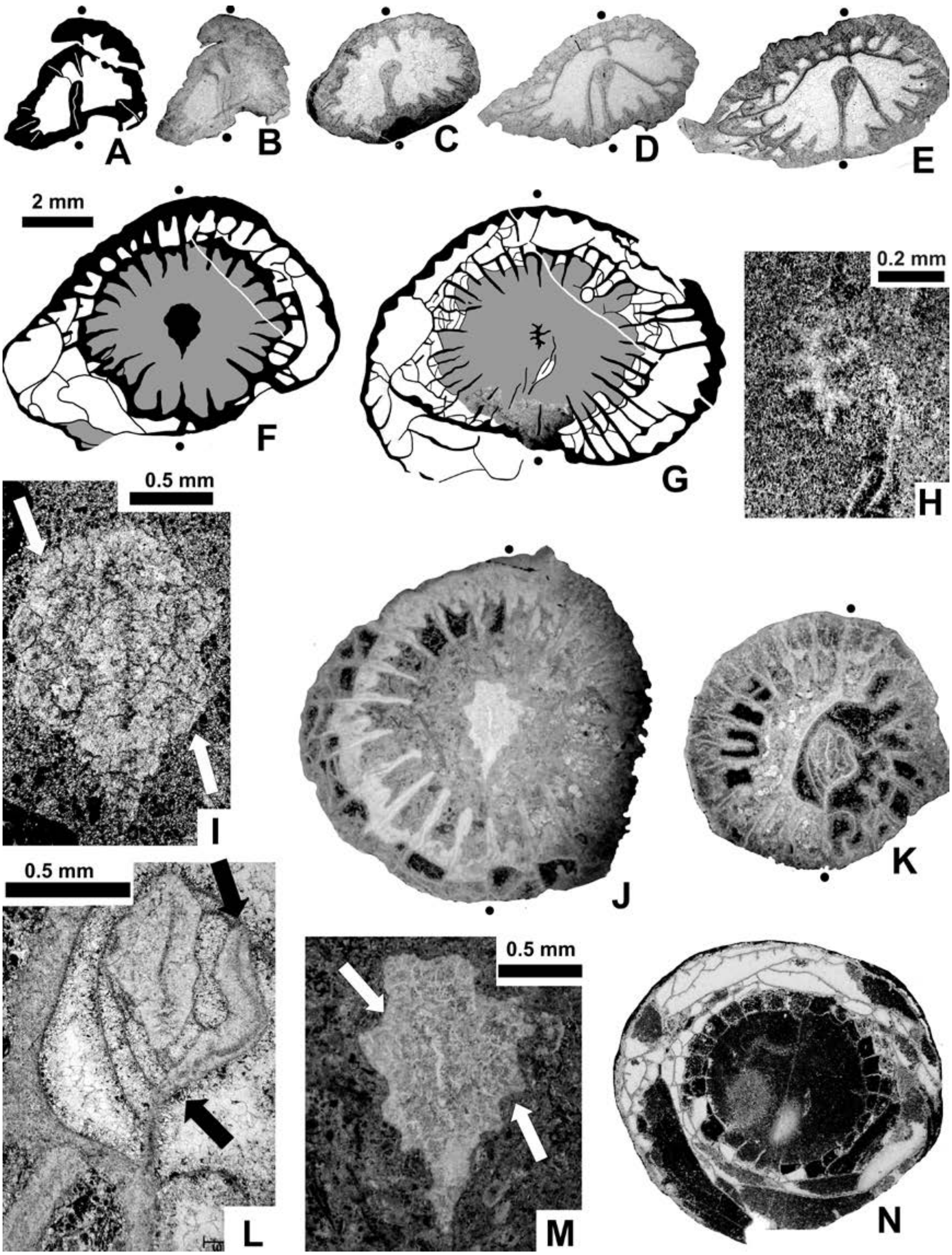
DESCRIPTION OF HOLOTYPE: Corallite conical in shape, asymmetric in inner morphology lasting up to calice floor. Earliest preserved ontogenetic growth stage (Text-fig. 13A, B), considered here as late neanic/early mature growth stage, with n:d vales 20:9.0×7.4 mm and 20:9.0 mm. All major septa continuous, thick short and less numerous on right corallite side than on its left side where dissepimentarium is present. On left corallite side, major septa up to 2/3 corallite radius long. In dissepimentarium major septa thin, thickened in inner wall and tabularium. Both protosepta elongated. Cardinal septum, much thicker and longer than counter septum, united with median lamella of pseudocolumella. Counter septum approaches pseudocolumella from side, but does not meet its surface in described growth stage (Text-fig. 13M, upper arrow). Break in union of 'middle dark lines' of cardinal septum and median lamella may be diagenetic; such a direct connection recognisable in mature columella despite alteration (Text-fig. 13N, lower arrow). Minor septa restricted to their thick bases in septotheca (Text-fig. 13L). Shortening of major septa adjacent to cardinal septum and elongation of tabularium next to that septum may suggest an occurrence of cardinal fossula at that growth stage and slightly upper in corallite growth (Text-fig. 13C), a character absent from more advanced mature growth of corallite (Text-fig. 13D).

In middle part of holotype growth (Text-fig. 13C, D), with n:d value 24:12 mm, arrangement of ma-

← Text-fig. 13. *Krynkaphyllum multiplexum* sp. nov. Specimen UAM-Tc.Don.1/366. Holotype. Transverse thin sections except when stated otherwise. A, B – late neanic/early mature growth stage (B – peel); C, D – middle part of mature corallite growth at distance of 1 mm (peels); E – lower part of calice; F – middle part of calice (peel); G, H – longitudinal sections; G – eccentric; H – centric; I–K – fragments of dissepimentaria; I – lower part of calice (enlarged from E); J – upper part of calice (enlarged from F); K – late neanic/early mature growth stage (enlarged from B); L – septotheca; minor septa absent from inner wall (enlarged from A); M – pseudocolumella and positions of protosepta (black arrows; enlarged from B); N – pseudocolumella surrounded by innermost parts of tabulae with septal lamellae incorporated (upper white arrows) and median lamella continuous into cardinal septum (lower white arrow; enlarged from E); O – separated inner segments of minor septa distinguished in inner wall (white arrows; enlarged from D). For stratigraphic position see text. Protosepta marked by black dots when recognisable. Scale bar between D and G corresponds to images C–H.



Text-fig. 14. *Krynkaphyllum multiplexum* sp. nov. Specimen UAM-Tc.Don.1/367. Possible paratype. A, B – transverse thin sections, immature growth stage; innermost tabulae with septal lamellae incorporated (arrows); C−E – transverse sections (peels), mature growth stage; F, G – longitudinal sections (peels); F – eccentric; G – centric; H−J – complex pseudocolumella/protosepta/tabulae relationship; H – protosepta (upper and lower arrows), innermost tabula with septal lamellae incorporated (middle arrow; enlarged from B); I – thickened, strongly elongated cardinal septum meets lateral surface of pseudocolumella (lower arrow), counter septum separated from pseudocolumella (upper arrow; enlarged from C); J – both protosepta separated from pseudocolumella; cardinal septum divided into two segments; inner segment approaches lateral surface of pseudocolumlla (upper arrow), peripheral segment slightly reduced in length (lower arrow); counter septum lacking from picture (enlarged from E). For stratigraphic position see text. Protosepta marked by black dots. Scale bar between F and G corresponds to images C−G.



Text-fig. 15. *Krynkaphyllum multiplexum* sp. nov. A–F, H–N. Transverse thin sections. A–I – Specimen UAM-Tc.Don.1/368. Possible paratype. A–E – immature growth stage (A – drawing on B); F, G – calice (F – drawing on thin section; G – drawing on peel); H – pseudocolumella in middle part of calice; free septal lamellae attached to median lamella (enlarged from G); I – lower part of calice; innermost parts of tabulae, with septal lamellae incorporated (arrows), closely fit pseudocolumella (enlarged from F). J–M – Specimen UAM-Tc.Don.1/369. Possible paratype. Mature growth stage. J – calice; K – 5 mm below calice; L –inner margin of cardinal septum strongly thickened (arrows), surrounding pseudocolumella free from both protosepta (enlarged from K); M – pseudocolumella; last tabula with septal lamellae incorporated, closely fits median lamella elongated towards cardinal septum (enlarged from J). N – Specimen UAM-Tc.Don.1/370. Possible paratype. Calice. For stratigraphic positions see text. Protosepta marked by black dots when recognisable. Scale bar between A and F corresponds to images A–G, J, K, N.

jor septa remains strongly asymmetric, with those of right side less numerous and thicker than those in opposite corallite side. Cardinal septum thick, united with median lamella of pseudocolumella. Counter septum not connected to median lamella, meets pseudocolumella slightly aside. Only very few minor septa are well developed and continuous (Text-fig. 13C, upper left). Most divided into bases within septotheca and short segments hidden within thick inner wall. Several minor septa either absent from that corallite part or diagenetically destroyed (Text-fig. 13C, D, I, K). Dissepimentarium constructed mainly from large lonsdaleoid dissepiments. Interseptal dissepiments either sporadic or combined with sclerenchyme to form thick inner wall.

N:d value in calice with pseudocolumella 25:15.0 mm, in calice above pseudocolumella 25:16.5×15.5 mm (Text-fig. 13E, F respectvely). Septotheca thicker in immature part of corallite, but present during its entire growth (Text-fig. 13L, K, I respectively). Major septa in upper part of calice equal in length and thickness (Text-fig. 13F). In lower part of calice (Text-fig. 13E) almost all major septa, including counter septum, thin and equal in length. Only cardinal septum elongated so as to meet median lamella of pseudocolumella. Minor septa (Text-fig. 13E, F, J) thin, expanded from thick inner wall from less than 1 mm to approximately 1.8 mm. In dissepimentarium, minor septa vary in thickness, thickest in inner wall and septotheca; many interrupted by lonsdaleoid dissepiments, rarely continuous. Some hardly recognisable inside of inner wall; much better exposed in upper than in lower calice sectors (Text-fig. 13F, J and 13E, I respectively). Pseudocolumella in calice bipartite. Median lamella thickened and united directly with long cardinal septum (Text-fig. 13N, lower arrow), surrounded on both sides by tabulae with short, thick septal lamellae incorporated (Text-fig. 13N, arrows). Dissepimentarium 1/3–1/2 corallite radius wide, with mainly lonsdaleoid dissepiments at periphery. These vary in size from small, interrupting only one minor septum, to large, interrupting several major and minor septa (Text-fig. 13E, F, I, J). Sporadic interseptal dissepiments at periphery. Inner dissepiments interseptal, larger and more regular in lower part of calice and beneath calice; in middle part of calice, several small dissepiments attached to minor septa obliquely (Text-fig. 13J).

Longitudinal section (Text-fig. 13G, H) slightly oblique, centric in upper part of Text-fig. 13H, made between transverse sections illustrated in Text-fig. 13D and 13E. Dissepiments differentiated in length, elongated, slope down at approximately 40º. Inner wall strongly thickened. Tabulae complete, differentiated in thickness, attached to thick pseudocolumella at approximately 45º. Inner margins of thick tabulae incorporated in pseudocolumella, increasing its thickness.

INTRASPECIFIC VARIABILITY: Maximum n:d values measured in specimens accepted as probable paratypes (see Remarks): UAM-Tc.Don.1/367 – 24:17×15 mm (beneath calice), UAM-Tc.Don.1/368 – 24:9×8 mm (just above calice floor), UAM-Tc.Don.1/369 – 21:9 mm (just above calice floor). Probable paratype UAM-Tc.Don.1/367 (Text-fig. 14A–J) resembles holotype closer than the remaining two specimens in its corallite size and number of septa. Its main differences from holotype concern length of protosepta and morphology of pseudocolumella. In earliest preserved growth stage (Text-fig. 14A), both protosepta either united with median lamella or only meet sclerenchymal sheets of pseudocolumella; diagenetic alteration prevents indisputable conclusion. During approximately 2 mm of further corallite growth, both protosepta lose that probable union with median lamella but remain attached to pseudocolumella (Text-fig. 14H, upper and lower arrows). Pseudocolumella in this growth stage resembles mature pseudocolumella of holotype by incorporating innermost part of tabula with three or four thick, short septal lamellae into its interior (Text-fig. 14A, B, arrows, H, middle arrow). In early part of mature growth stage (Text-fig. 14C, D, I), cardinal septum elongated so as to surround median lamella, reaching its counter septum side. Its thickened inner margin attaches median lamella (Text-fig. 14C, D, right, I, lower arrow). In most advanced growth stage studied, thick inner margin of cardinal septum, isolated from its slightly elongated peripheral part, obstinates next to lateral side of pseudocolumella (Text-fig. 14E, J, arrows). Counter septum approaches pseudocolumella during some period of corallite growth, but becomes isolated from it later (Text-fig. 14C and D, E, J, respectively). Mature pseudocolumella of this specimen differs from that in holotype by incorporating three or four septal lamellae directly (Text-fig. 14I, J), but not hidden within thickness of tabula as in holotype (Text-fig. 13N). In most advanced growth stage of this paratype (Text-fig. 14E, J), pseudocolumella free from both protosepta. Cardinal septum slightly thickened, divided into two segments (Text-fig. 14E, J, arrows). Counter septum equal to adjacent major septa. Minor septa absent from external wall in earliest growth stage studied, but secreted inside septotheca prior to secretion of dissepiments (Text-fig. 14A, B, respectively). Dissepimentarium in mature growth stage narrower and simpler than in the holotype. Also, dissepiments attached to minor septa obliquely, as demonstrated in the holotype, do not occur in this paratype. Huge lonsdaleoid-like dissepiments (Text-fig. 14D, E, upper left) document rejuvenation. Longitudinal section observed from peripheral to axial corallite part (Text-fig. 14F, G). Tabulae horizontal to down sloping in their peripheral and medial sectors, moderately to steeply up rising next to pseudocolumella.

Probable paratype UAM-Tc.Don.1/368 (Text-fig. 15A–I) differs considerably from holotype in its maximum n:d value (24:9×8.0 mm *vs.* 25:17×15 mm in the holotype). Its early growth stage (Text-fig. 15A–E) resembles holotype in that the cardinal septum dominates and is united with median lamella of thick pseudocolumella; counter septum shorter and thinner than cardinal septum, approaching but not meeting pseudocolumella; major septa short and thick. In probable paratype discussed, that morphology lasts much longer than in holotype, almost to the calice floor. Mature growth stage differs from holotype in absence of oblique dissepiments attaching minor septa, but resembles it in solid pseudocolumella, closely surrounded by innermost tabulae with septal lamellae incorporated in lower part of calice (Text-fig. 15F, I). In middle part of calice (Text-fig. 15G, H), pseudocolumella loses its stereoplasmic infilling exposing its complex nature with septal lamellae attached to median lamella as isolated bodies.

Probable paratype UAM-Tc.Don.1/369 (Text-fig. 15J–M) resembles probable paratype UAM-Tc.Don.1/368 in its n:d value (22:9.8 mm in calice and 20:7.2 just beneath calice), but considerably differs in that character from both holotype and paratype UAM-Tc.Don.1/367. Also, it differs from holotype and remaining corallites in a narrow dissepimentarium consisting mostly of interseptal dissepiments, with small lonsdaleoid dissepiments interrupting only some minor septa. Its pseudocolumella in calice resembles remaining corallites, consisting of thick median lamella and thick inner margin of a tabula incorporated on median lamella side together with short septal lamellae within tabula interior (Text-fig. 15M, arrows). Pseudocolumella/cardinal septum relationship in this corallite differs from holotype, but resembles probable paratype UAM-Tc.Don.1/367 in cardinal septum elongated so as to encircle pseudocolumella with its thick inner margin. However, in contrast to specimen UAM-Tc.Don.1/367, margin of cardinal septum remains free from pseudocolumella (Text-fig. 15L, upper arrow).

Specimen UAM-Tc.Don.1/370 (Text-fig. 15N) represented by calice only. Its incompleteness makes its identification problematic, based mainly on n:d value (25:11 mm) and character of its major septa and dissepimentarium.

REMARKS: Grouping corallites as different as those described above into one species may reflect an artificial construct. However, a lack of access to the solitary specimens identified by Vassilyuk (1960) as her new species *Lytvophyllum dobroljubovae* and the very restricted number of specimens studied here make this grouping more rational, at least for the time being, than splitting them into distinct, poorly documented species. Several shared characters support this approach and suggest a close relationship, if not a common species identity, of all of these specimens. The morphology of the pseudocolumella, and in particular the incorporation of thick inner tabulae margins comprising short, thick septal lamellae into it, is the most important common character. Two groups can be distinguished when only n:d values are considered, as follows: Group 1. The holotype and the paratype UAM-Tc.Don.1/367 of *K. multiplexum* sp. nov. and one specimen illustrated by Vassilyuk (1960, pl. 26, fig. 1e). Group 2. The specimens UAM-Tc.Don.1/368 and 369 of *K. multiplexum* sp. nov. and two or three corallites illustrated by Vassilyuk (1960, pl. 26, fig. 1b–d, f–h). A firm decision concerning her specimens cannot be taken on the basis of the illustrations. The wide diagnosis proposed here covers the characters of both groups. It is acknowledged that the rather broad content described is somewhat inconvenient for the type species of a genus, especially when establishing the relations of other species of the genus. However, this issue can be remedied and the diagnosis changed or emended when a more abundant, better preserved collection is studied.

OCCURRENCE: All specimens studied here and specimens illustrated by Vassilyuk (1960, pl. 26, fig. 1c–e), Krynka River Area, Svistuny Village, Velyka Shyshivka Balka, Limestone E_1^{verkh}. Specimen illustrated by Vassilyuk (1960, pl. 26, fig. 1f–h), Kalmius River Area, former “Chorna Skelya” (Black Rock), currently underwater at the Starobeshevo thermal power plant reservoir, Limestone E_2. All specimens from the lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus–Id. sulcatus sulcatus* conodont Biozone. Upper lower Bashkirian.

Krynkaphyllum validum sp. nov.
(Text-figs 16–18)

HOLOTYPE: Specimen UAM-Tc.Don.1/371.

TYPE LOCALITY: Krynka River Area, Svistuny Village. Velyka Shyshivka Balka.

TYPE STRATUM: Limestone E_1^{verkh}, Feninian Horizon, *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, *Idiognathodus sinuosus–Id. sulcatus sulcatus* conodont Biozone, *Reticuloceras–Bashkortoceras* (R_1) ammonite Biozone. Lower Bashkirian.

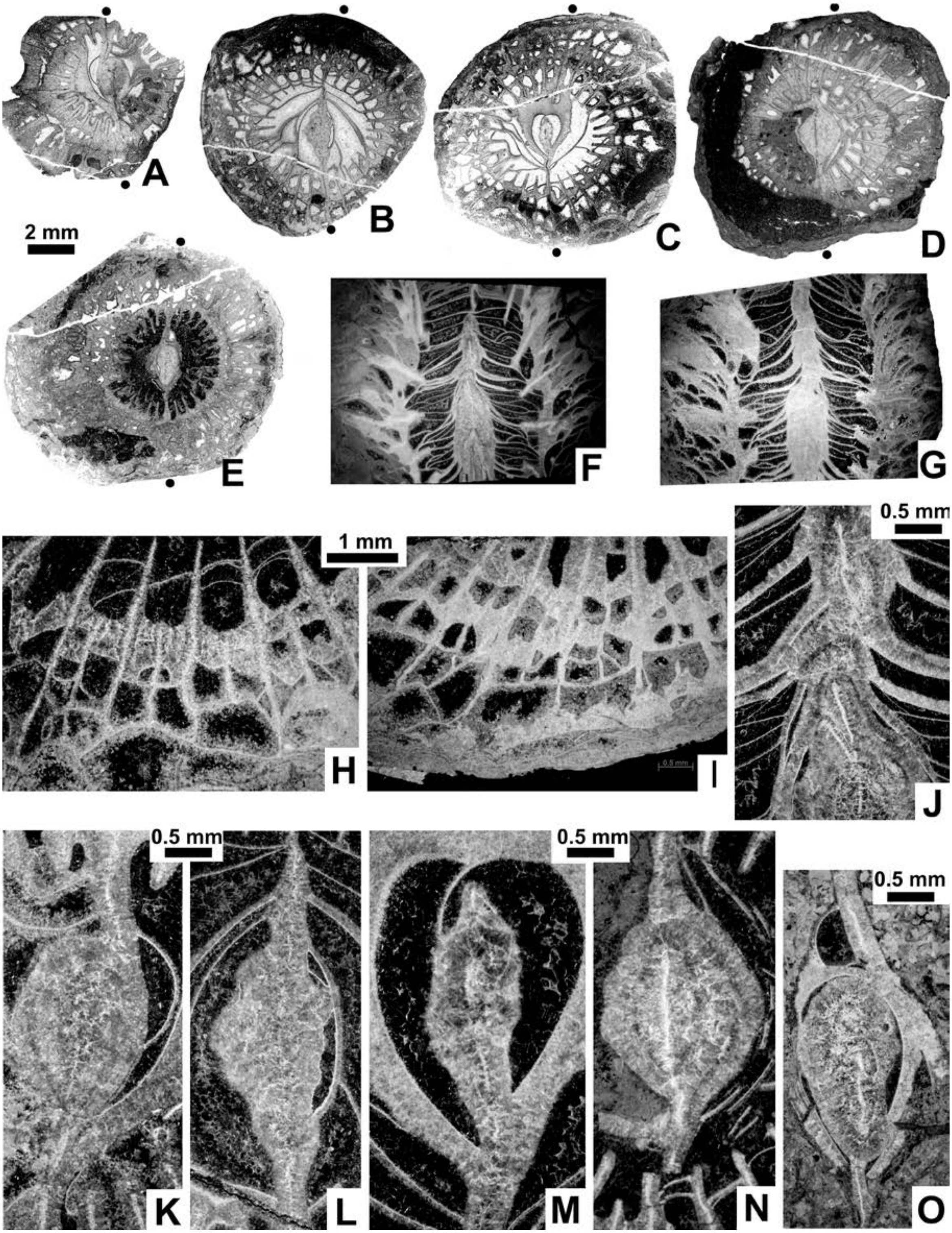
ETYMOLOGY: *Latin validus*, *a*, *um* – strong; after the strong and compact skeleton.

MATERIAL: Holotype UAM-Tc.Don.1/371 preserved as 5.7 cm long fragment, but neanic growth stage and calice missing. Three probable paratypes, UAM-Tc.Don.1/372–374, all incomplete, preserved in their mature growth stage only. Microstructure of septa and some parts of skeletons destroyed by diagenesis, but main characters of mature morphology reasonably preserved. 11 thin sections and 26 peels available for study.

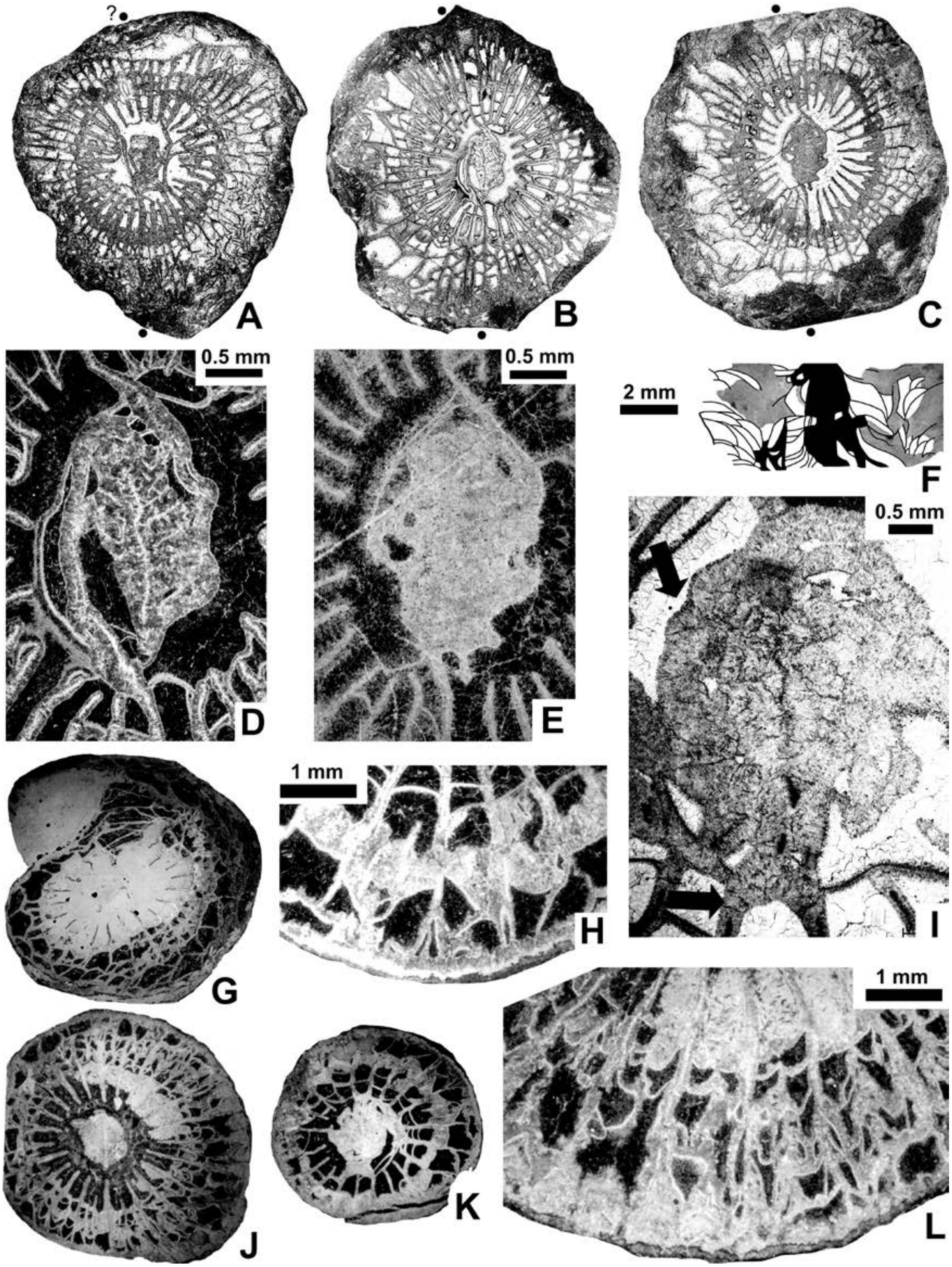
DIAGNOSIS: *Krynkaphyllum* with maximum measured n:d values of holotype 30:19×18 mm and paratype 32:20×19 mm; major septa 1/2–3/4 corallite radius long; minor septa either terminate within thick inner wall or penetrate peripheral tabularium; protosepta long, their inner margins may surround complex pseudocolumella; pseudocolumella comprises median lamella and inner margins of tabulae and/or tabellae with septal lamellae incorporated; tabularium normal; tabulae complete, sigmoidal in shape; dissepiments commonly interseptal; occurrence of lonsdaleoid dissepiments variable.

DESCRIPTION OF HOLOTYPE: Earliest preserved growth stage, with n:d value 26:13×12 mm (slightly incomplete) perhaps represents early mature growth stage (Text-fig. 16A). Major septa complete, 1/2–2/3 corallite radius long, thickened both in tabularium and dissepimentarium; more so in former. Minor septa either complete or broken by lonsdaleoid dissepiments into segments. Peripheral segments of major and minor septa jointly create septotheca. Inner segments of minor septa incorporated in thick inner wall. Changes in morphology of pseudocolumella described below. In more advanced mature growth stage and up to calice floor (Text-fig. 16B–E), major septa radially arranged, thickest in inner wall, slightly thicker in tabularium than in dissepimentarium, mostly complete, but series of flat lonsdaleoid dissepiments may locally occur (Text-fig. 16C, lower right). Minor septa restricted to dissepimentarium, either complete or broken by small lonsdaleoid dissepiments. Inner segments of most minor septa, only slightly thicker than their remaining parts, incorporated into inner wall (Text-fig. 16H, I). Dissepimentarium 1/3 corallite radius, or slightly greater locally. Dissepiments mostly interseptal and irregular. Lonsdaleoid dissepiments as mentioned above. Longitudinal sections slightly oblique (Text-fig. 16F, G, J). Dissepiments elongated, arranged in rows sloping down under less than 40º. Only innermost walls of inner row of dissepiments vertical. Tabulae complete, in most part of tabularium thin, almost horizontal to slightly elevated. Much more steeply elevated and thickened when approaching pseudocolumella. Sclerenchymal cones within pseudocolumella (Text-fig. 16J) correspond to thick innermost parts of tabulae or tabellae surrounding median lamella. Tabellae elevated steeper than underlying tabulae.

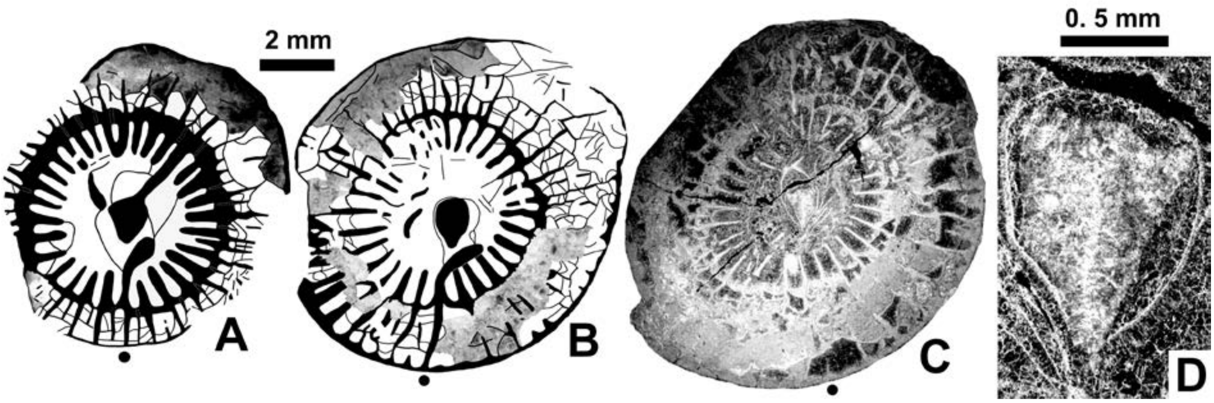
Pseudocolumella morphology and relationships require special attention for both its variety and taxonomic value. In general, pseudocolumella probably monoseptal, composed of median lamella and inner margins of tabulae and/or tabellae with or without short, thick septal lamellae incorporated within their thickness. In ontogenetically youngest part of corallite available for study, pseudocolumella comprises median lamella surrounded by thick inner margins of tabula (Text-fig. 16K). Uncertain occurrence of septal lamellae within that tabula fragment. Both protosepta attached to pseudocolumella. Cardinal septum straight, counter septum slightly aside. Middle lines of both protosepta curved when approaching pseudocolumella, but almost certainly connected to middle line of median lamella. Direct connection of middle line of median lamella to both protosepta – i.e., occurrence of axial septum – demonstrated in next transverse section (Text-fig. 16L) and in one transverse thin section taken from a higher corallite part (Text-fig. 16N). Presence of septal lamellae within the body of innermost part of tabula clearly demonstrated in both these transverse sections (Text-fig. 16L, N), but absent in transverse section made in lower part of calice (Text-fig. 16O). Thick, oval median lamella dominates in that part of pseudocolumella. Inner margins of tabulae only touch median lamella, separating its middle dark line from both protosepta. Cardinal septum attached to pseudocolumella directly, counter



Text-fig. 16. *Krynkaphyllum validum* sp. nov. Specimen UAM-Tc.Don.1/371. Holotype. Transverse thin sections except when stated otherwise. A – early mature growth stage; B–D – mature growth stage beneath calice; E – mature growth stage, lower part of calice; F – slightly oblique, eccentric longitudinal thin section (peel); G – slightly oblique, centric longitudinal section (peel); H, I – mature dissepimentaria; J – inner morphology of pseudocolumella in longitudinal section (enlarged from G); K–O – inner morphology of pseudocolumella in transverse sections (enlarged from A–E, respectively). For stratigraphic position see text. Protosepta marked by black dots. Scale bar between A and E corresponds to images A–G.



Text-fig. 17. *Krynkaphyllum validum* sp. nov. Paratypes. Transverse sections except when stated otherwise. A–F – Specimen UAM-Tc. Don.1/372. A–C – subsequent sections of mature growth stage (A, C – peels, B – thin section); D, E – protosepta/pseudocolumella relationship (enlarged from B and C, respectively); F – longitudinal section (drawing on peel image). G–L – Specimen UAM-Tc.Don.1/373. G – rejuvenation in calice (peel); H – morphology of dissepimentarium in early mature growth stage (enlarged from K); I – pseudocolumella (enlarged from K); J – mature growth stage immediately beneath calice (thin section); K – early mature growth stage (thin section); L – dissepimentarium in mature growth stage (enlarged from J). For stratigraphic positions see text. Protosepta marked by black dots when recognisable. Scale bar between E and F corresponds to all images except when marked separately.



Text-fig. 18. *Krynkaphyllum validum* sp. nov. Specimen UAM-Tc.Don.1/374. Paratype. Transverse sections. A–C – early to late mature growth stage (A, B – drawings on peel images, C – thin section); D – pseudocolumella (enlarged from C). For stratigraphic position see text. Cardinal septum marked by black dots. Scale bar between A and B corresponds to images A–C.

septum on aside. Connection to median lamella of counter septum much less rigid than that of cardinal septum, and role of inner margins of tabulae in that connection well demonstrated in Text-fig. 16M. This transverse thin section, made immediately below thick tabula, documents direct, constant connection of median lamella to cardinal septum and its derivation from that septum. It also shows a complete isolation of median lamella from counter septum, and amplexoid character of that septum.

INTRASPECIFIC VARIABILITY: Specimen UAM-Tc.Don.1/372 (Text-fig. 17A–F) resembles the holotype in n:d value, with only slightly larger dimensions (32:20×19 mm), and in similar width of dissepimentarium. It differs in having longer major and minor septa by comparison to corallite radius, and in much more numerous lonsdaleoid dissepiments in some sectors of corallite growth (Text-fig. 17C). However, morphology of pseudocolumella and its relationship to protosepta differ so much from those characters in holotype that co-specific position of those two specimens may be contested. Median lamella restricted to 'middle dark line', i.e., primary septum. Septal lamellae attached to median lamella and contiguous laterally, forming complex pseudocolumella. Peripheral margins of septal lamellae either hidden within frame of pseudocolumella or, in the case of some, stick out of it (Text-fig. 17D, E respectively). Protosepta extremely long. Each surrounds pseudocolumella and either attaches to its opposite end or to its middle part (Text-fig. 17D, E, respectively). Short fragment of poorly preserved longitudinal section (Text-fig. 17F) is not unequivocal in terms of corallite morphology exposed in that section. Arrangement and shape of dissepiments, and arrangement of tabulae, closely resembles holotype. Also, axial parts of some tabulae may be incorporated in pseudocolumella, but this cannot be considered proven.

Specimen UAM-Tc.Don.1/373 (Text-fig. 17G–L) differs from all specimens of *K. validum* sp. nov. in its small dimensions, with maximum n:d value 24:18.0×15.2 mm. Its early mature growth stage (Text-fig. 17K) resembles holotype in morphology of minor septa and dissepimentarium (Text-fig. 17H). Also, at least one, thick inner margin of tabula with inner margins of thick septal lamellae incorporated attaches to median lamella (Text-fig. 17I, upper arrow). Cardinal septum probably joins median lamella directly, while diagenetic alterations and thick stereoplasmic deposits prevent firm recognition of counter septum. It perhaps only touches pseudocolumella surface. Mature growth stage (Text-fig. 17J) differs from holotype by having pseudocolumella free from protosepta that equal other major septa in length and thickness. Its dissepimentarium, very complex in this growth stage (Text-fig. 17J, L), contains numerous grape-like dissepiments (see Fedorowski 2017 for explanation), but lonsdaleoid dissepiments sporadic and break only minor septa. Morphology of dissepimentarium changes drastically in rejuvenating skeleton (Text-fig. 17G), comprising mostly lonsdaleoid dissepiments at periphery and some irregular interseptal dissepiments in inner dissepimentarium.

Early mature skeleton of specimen UAM-Tc.Don.1/374 differs from its ontogenetically more advanced growth in a way suggesting pathology in the former stage (Text-fig. 18A–D). Advanced mature morphology (Text-fig. 18C) resembles holotype in dimensions and n:d value (30:19×17 mm), in length and morphology of minor septa, commonly divided by lonsdaleoid dissepiments into peripheral and inner sectors, and in morphology and width of dissepimentarium, consisting of interseptal and lonsdaleoid dissepiments. Also, length and thickness of its major septa in this growth stage resemble major septa in holotype. Its pseudocolumella consists of thick median lamella and two or three thick septal lamellae, incorporated either directly or together with inner margins of tabulae (Text-fig. 18D). Advanced diagenetic alteration prevents recognition of that detail. Cardinal septum possibly joins pseudocolumella within its thin inner margin. Counter septum potentially equals remaining major septa in length and thickness. Longitudinal section not made. Shape and directions of tabulae sections closely resemble those in transverse sections of specimens with longitudinal sections studied. Thus, a similar specimen morphology compared to other specimens of this species seems very probable. Peculiar shape of cardinal septum in mature growth stage preceding the growth stage described above suggests its pathologic character. Also, neither elongated major septa (left broken) in ontogenetically earliest growth stage studied (Text-fig. 18A) can be accepted as counter septum. That ephemeral elongation and thickening disappears within approximately 1.5 mm of corallite growth (Text-fig. 18B). Thus counter septum perhaps equal to remaining major septa during entire corallite growth studied. Strong thickening of major septa in tabularium in this early growth stage constitutes an additional difference of this specimen from the remainder of specimens attributed here to *K. validum* sp. nov.

REMARKS: Specimens identified here as paratypes may either represent various extremes of a very variable species or belong to different species, closely related to both the holotype and each other. The first option is accepted here, since only a study of a large collection can address this issue. The variability in the morphology of the pseudocolumella and its relationship to the protosepta and inner margins of tabulae, described and illustrated in detail in the holotype, is the most important character of the species.

OCCURRENCE: All specimens as the holotype.

Subfamily Colligophyllinae subfam. nov.

TYPE GENUS: *Colligophyllum* gen. nov.

DIAGNOSIS: Solitary and gregarious, pseudocolonial and probably fasciculate colonial Krynkaphyllidae; cardinal septum strongly dominated in length since very early growth stage; counter septum elongated in immature growth, equal to other major septa in maturity; pseudocolumella monoseptal, free from cardinal septum rarely and only in advanced maturity; fragments of axial column may occur; minor septa underdeveloped; tabularium normal; tabulae vary in arrangement from horizontal or very slightly down slopping to strongly elevated within same corallite; lonsdaleoid dissepiments commonly dominate over interseptal.

CONTENT OF GENERA: *Colligophyllum* gen. nov.; ?*Dorlodotia* Salée, 1920; ?*Lytvophyllum* Dobroljubova in Soshkina *et al*., 1941; ?*Pseudodorlodotia* Minato, 1955; ?*Pseudolytvophyllum* Yu and Wang in Yu *et al*., 1983; ?*Luia* Yu, 1985; ?*Prolytvophyllum* Wu and Zhao, 1989; *Paralytvophyllum* Wu and Zhao, 1989.

Note. 1. The inclusion of *Dorlodotia* in this subfamily is conditional, as commented elsewhere in this paper. 2. The Chinese genera and the Japanese *Pseudodorlodotia* require more comprehensive investigations to firmly establish both their independent taxonomic positions and relationship to *Colligophyllum* gen. nov. (see Considerations).

REMARKS: The recognition of corals related or homeomorphic to the new genus *Colligophyllum* may have begun with the introduction by McCoy (1849) of *Cyathophyllum pseudovermiculare*. The identification of this species as *Dorlodotia* seems to be largely accepted (e.g., Poty 1981; Ogar 2010; Denayer and Poty 2011; Hecker 2012). Denayer and Poty (2011) not only accepted that species as *Dorlodotia*, but also suggested that it possesses an ancestral position to the Chinese species with an underdeveloped or absent pseudocolumella. Indeed, Xu and Poty (1997) placed such species in *Dorlodotia*. McCoy (1849) did not illustrate his species. The best illustration known to me is that by Garwood (1912, pl. 49, fig. 2a–d) who named that species *Thysanophyllum pseudovermiculare* (McCoy) and illustrated a part of the colony with the offsetting corallite, two fragments of a colony in transverse section, and in longitudinal section. He also drew attention to the elongation of one major septum. In fact, two major septa may be elongated as shown by one corallite (Garwood 1912, pl. 49, fig. 2c, middle corallite). Also, the external wall is almost certainly of a septothecal kind. The tabulae in the illustrated corallites (Garwood 1912, pl. 39, fig. 2d) are horizontal or slightly sagging, but that feature may have resulted from an inadequately elongated septum in the longitudinally sectioned specimens. In light of these characters, the specimen illustrated by Garwood (1912, 1916) can be treated as related to *Dorlodotia*, but not necessarily as belonging to that genus. The studies of Smith (1915, pl. 17, figs 29, 30) who applied the generic name *Thysanophyllum* for *C. pseudovermiculare*, and Vaughan (1915, p. 39, pl. 5, fig. 3) who named his specimen *Endophyllum* cf. *pseudovermiculare* McCoy, do not substantially contribute to the knowledge of that species.

A restricted number of early descriptions of *Colligophyllum*-like corals other than *Dorlodotia* and '*Cyathophyllum*' *pseudovermiculare* are cited here to illustrate the variety in their distribution. All of them were included in the genus *Thysanophyllum* Thomson and Nicholson, 1876 and all require detailed restudy prior to their reliable consideration in the modern paradigm of Rugosa knowledge. Yabe and Hayasaka (1920) introduced *Th. longiseptatum* from the Carboniferous of Hunan Province, China. Soon after, two new species from the Carboniferous deposits of the eastern slope of the Southern Urals, *Th. simplex* Perna, 1923 and *Th. successor* Perna, 1923 were published in a *post mortem* paper. *Thysanophyllum tschernovi* Soshkina, 1925, discussed elsewhere in this paper, ends this short list of the earliest described *Colligophyllum*-like corals in eastern Europe and Asia, all of which were considered to represent the fasciculate colonial *Thysanophyllum*. However, the type species for that genus, *Th. orientale* Thomson, 1880, as selected by Gregory (1917), is a cerioid colonial taxon. That completely different colonial growth form consequently excludes the weakly fasciculate colonies from *Thysanophyllum*. Moreover, the habit of most *Thysanophyllum* species, while described as fasciculate colonial, is left undocumented.

Only *Th. tschernovi* of those four species listed above received a consideration by subsequent authors. Dobroljubova (in Soshkina *et al.* 1941) designated that species as the type of her new genus *Lytvophyllum* and selected the Permian (Artinskian) specimen as its lectotype. That specimen, represented by a single corallite, was derived from the Lytva River site in the Southern Urals (Soshkina 1925, pl. 3, fig. 1a–v; Dobroljubova in Soshkina *et al.* 1941, pl. 22, fig. 1a–c). The remaining loose corallites included by Soshkina (1925, pl. 3, figs. 17–21) in *Thysanophyllum tschernovi* were accepted by Dobroljubova (in Soshkina *et al.* 1941, pl. 22, figs 2–5) as fasciculate colonial paralectotypes of that species. All paralectotypes, represented by incomplete corallites, were derived from the Middle Carboniferous deposits of the Sim River Bank, Southern Urals, Ufa Region.

Two items pertaining to the original investigations of *Lytvophyllum tschernovi* should be noted. 1) The longitudinal section of the lectotype is shown reversed in both papers (Soshkina 1925, pl. 3, fig. 16b; Dobroljubova in Soshkina *et al.* 1941, pl. 22, fig. 1c), causing some misunderstandings with regard to the shape and arrangement of the tabulae. In the illustrated longitudinal section, the tabulae are slightly wavy and either horizontal or elevated towards the median lamella, but not concave. 2) The cardinal, but not the counter, septum is elongated. This mistake was already corrected by Fedorowski *et al.* (2007, p. 158) in their comprehensive overview of the *Lytvophyllum*-like taxa known to them. They re-described and re-illustrated the lectotype (Fedorowski *et al.* 2007, pp. 158, 159, text-fig. 23), and expressed several doubts with regards to both the morphology and the growth form of many taxa either similar to or attributed to *Lytvophyllum*. Most of the conclusions of Fedorowski *et al.* (2007, pp. 153–158) about *Lytvophyllum*-like taxa are followed here, with the notable exception of Kossovaya (2009) concerning *Lytvophyllum antiquum* Gorskiy, 1978 established by that author for both the paralectotypes of *L. tschernovi* and some of his own specimens. Unfortunately, the specimen that Gorskiy (1978) selected as the holotype does not bear the characters of either *Lytvophyllum* or the corals distinguished here as *Colligophyllum* gen. nov. Thus, Fedorowski *et al.* (2007) suggested the necessity of introducing a new species name for some of Gorskiy's (1978) specimens other than the holotype and the "paralectotypes" of *L. tschernovi*. Following that suggestion, Kossovaya (2009) included all those specimens into her new species ?*Pseudolytvophyllum askynensis* and established its stratigraphic position as the lowermost Akavasian, i.e., lowermost Manuilovian (lower middle Bashkirian) in the Ukrainian chronostratigraphic scheme. The growth form of that species may be very differentiated as discussed with the Considerations.

One more question concerning the *Lytvophyllum* (= *Colligophyllum* gen. nov.) relationship should be discussed in these remarks. The morphology of the lectotype of *L. tschernovi* (Soshkina 1925, pl. 3, fig. 16; Dobroljubova in Soshkina *et al.* 1941, pl. 22, fig. 1a, b; Fedorowski *et al.* 2007, fig. 23) is similar to the morphology of the holotype of *C. dobroljubovae* (see below in Text-figs 19 and 20; Vassilyuk 1960, pl. 26, fig. 1a, b) to such an extent that a close relationship could be conceivable. However, placing both those taxa in a single genus, despite a more than 30 Ma interlude between their occurrences, is controversial. On the other hand, the solitary and gregarious growth form of *L. tschernovi*, if proven, and similarity in the immature morphology of *L. tschernovi* and *Colligophyllum dobroljubovae* if/when established, may put in doubt the correctness of introducing a new genus for the latter species. However, an introduction of a new well-defined genus for '*Lytvophyllum*' *dobroljubovae* seems safer than its continued placement in *Lytvophyllum*, with numerous 'ifs' considered in discussion.

Fedorowski *et al*. (2007, pp. 152, 153) compiled a long list of the suspected synonyms of *Lytvophyllum*. Most of those citations are either questionable or concern parts of a species cited and are omitted as such from this analysis. In addition to the best known species considered in the present paper, the following important species were omitted by Fedorowski *et al*. (2007):

Pseudodorlodotia subkakimii Vassilyuk in Vassilyuk and Zhizhina, 1978 (their pl. 1, fig. 2a–g) requires special attention for two reasons: its occurrence in the Donets Basin and derivation from the C_1^{v}f Zone, which roughly corresponds to the Asbian or lower Warnantien (lower upper Viséan) in the western European nomenclature. As such, the occurrence of Vassilyuk's (in Vassilyuk and Zhizhina 1978) specimen is bounded between *Dorlodotia briarti* and '*Dorlodotia*' *fomitschevi* and the upper Viséan Uralian and Chinese *Colligophyllum*-like species (see Considerations). The specimen consists of more than a dozen, size-differentiated corallites. It is described as fasciculate colonial and laterally offsetting (Vassilyuk in Vassilyuk and Zhizhina 1978, p. 29). However, there is no evidence for such a statement in either two subsequent transverse sections or in two eccentric longitudinal sections (Vassilyuk and Zhizhina 1978, pl. 1, fig. 2a–g). Most immature corallites occur at some distance from the mature ones, and one of them only touches a mature corallite along its external wall. Thus, the holotype and only specimen representing *P. subkakimii* is temporarily treated here as likely solitary and gregarious, with some corallites eligible to produce lost structures. Derivation of "the weak, indistinct 'stolbik' [pseudocolumella], curved at its margin" from the counter septum, as suggested by Vassilyuk (in Vassilyuk and Zhizhina 1978, p. 29), is questionable. The pseudocolumella is connected to the cardinal septum in at least three of the mature corallites illustrated, whereas in the remaining corallites the connection of a pseudocolumella to a clearly established protoseptum is impossible to point out. Two more statements by Vassilyuk (in Vassilyuk and Zhizhina 1978, p. 29) are important: "Peripheral surface strongly ribbed, resulting in the festoon-like character of the external wall" and "Tabulae rare, elevated towards the 'stolbik' [pseudocolumella]" (all citations translated here from Russian). Short, but distinct projections of the external wall, corresponding to both septal cycles, suggest the occurrence of at least an incomplete septotheca: i.e., septal bases in either direct lateral contact, or supplemented by a sclerenchyme in between. The characters mentioned, occurrence of large lonsdaleoid dissepiments, lack of a cardinal fossula, and underdevelopment of the minor septa constitute a set of characters which make *Pseudodorlodotia subkakimii* a species that closely resembles *Colligophyllum* gen. nov., and allows for its inclusion within the Subfamily Colligophyllinae subfam. nov., irrespective of its growth habit.

Thysanophyllum ex. gr. *pseudovermiculare* McCoy of Kozyreva (1978) from the southern slope of the Voronezh Anticline is discussed here as the stratigraphically oldest species in the region that resembles the Subfamily Colligophyllinae subfam. nov. It was derived from the local horizon ve$_1$, corresponding inclusively to the Limestones E$_1$ to E$_7$: i.e., the Feninian Horizon in the Donets Basin and the Kinderscoutian in the western European nomenclature. Its resemblance to *Colligophyllum dobroljubovae* and ?*P. askynensis* is primarily due to the domination of the lonsdaleoid dissepiments, the underdeveloped minor septa, and one elongated major septum (perhaps cardinal) in immature corallites. It differs from these two species in the horizontal arrangement of flat, complete tabulae. That character may have resulted from the lack of an elongated major septum in the corallite sectioned. The arrangement of tabulae in a specimen with an elongated major (cardinal?) septum is unknown. In addition, its growth form is uncertain, and the morphology of the external wall is not mentioned by Kozyreva (1978) and cannot be recognised from her poor illustrations. Detailed study of *Th.* ex. gr. *pseudovermiculare* may document its placement within the Subfamily Colligophyllinae subfam. nov. as a morphologically simplified lineage of species starting with '*Cyathophyllum*' *pseudovermiculare* McCoy, 1849. Such a lineage has been already suggested by Xu and Poty (1997).

Two new species of Kozyreva (1976), *Pseudodorlodotia suigeneris* and *P. aisenvergi,* from the southern slope of the Voronezh Anticline display characters that suggest their relationship to *Colligophyllum* gen. nov. *Pseudodorlodotia suigeneris* was derived from the local horizons ve$_{3,4}$, considered by Kozyreva (1984, p. 103) as lower Bashkirian. Those horizons are equivalents to the Limestones G$_1$ to H$_3$, i.e., the Zuyevian Horizon of the Donets Basin, which is at present considered lower middle Bashkirian and lower Langsettian in the western European nomenclature. *Pseudodorlodotia aizenvergi* was derived from the local horizon ve$_5$, placed by Kozyreva (1984, p. 103) in the upper Bashkirian. It corresponds to the Limestones H$_4$ to I$_1$, i.e., the Makeivkian Horizon of the Donets Basin, representing the upper middle Bashkirian and the upper Langsettian. Both species are described as colonial, but a probable offset is illustrated only in one corallite of *P. suigeneris* (Kozyreva 1976, fig. 2zh, lower left). A single illustration of an offset is insufficient to document a colonial growth form. The offset illustrated may well be a lost structure and the corallite protocolonial. Also, the reasonably clear illustration of one corallite of the holotype of *P. aisenvergi* (Kozyreva 1984, pl. 2, fig. 9a) documents an elongation of the cardinal septum, but not the counter septum, as described (Kozyreva 1976, p. 125). Although inadequately documented and with questionable generic identification, both species may belong to the Subfamily Colligophyllinae subfam. nov.; if this is the case, *P. aisenvergi* would be the stratigraphically youngest Carboniferous taxon of that subfamily in the Donetsk–Voronezh part of the Eastern European Province known so far.

Fedorowski *et al.* (2007) already considered several Chinese genera to be potentially related to *Lytvophyllum*, i.e., *Colligophyllum* gen. nov., and placed in doubt the interpreted colonial growth forms of *Luia* Yu, 1985, *Prolytvophyllum* Wu and Zhao, 1989, *Paralytvophyllum* Wu and Zhao, 1989, *Pseudodorlodotia* Minato, 1955, *Pseudodorlodotia* and *Pseudolytvophyllum* both of Fan *et al.* (2003). That opinion is followed here and the genera listed are here included in the Subfamily Colligophyllinae subfam. nov., with reservations pointed out in the note to the generic content of the subfamily. Several Chinese species included in the genus *Thysanophyllum* and considered fasciculate colonial should be added to that list. Only a few selected species are mentioned at the beginning of these remarks and here as an example: *Th. longiseptatum* Yabe and Hayasaka, 1920; *Th. circulocysticum* Chu, 1928; *Th. asiaticum* Yu, 1937; *Th. magnum* Xu in Jia *et al.*, 1977; *Th. irregulare* Wang in Wang *et al.*, 1978; and *Th. pseudovermiculare* M'Coy of Wu and Zhao, 1989. The description, documentation, and illustration of all of these species are completely inadequate for firm identification. Xu and Poty (1997) did not clarify the situation, since only transverse sections of *Th. circulocysticum* and *Th. magnum* were illustrated as documentation for the transfer of those species into the genus *Dorlodotia*. This transfer led Xu and Poty (1997) to rename the *Thysanophyllum* Zone introduced by Yu (1931) as the *Dorlodotia* Zone. In addition, Xu and Poty (1997, table 1) correlated the Chinese *Thysanophyllum*, i.e., *Dorlodotia*, Zone with European stratigraphy and restricted it to the upper part of the Moliniacien, instead of encompassing the entire lower Viséan as Yu (1931) had suggested. Their new stratigraphic concept, further developed by Poty *et al.* (2006) has led to a better understanding of the relationship of the European *Dorlodotia* and *Colligophyllum*-like corals and the far Asiatic taxa. It is not the task of this paper to discuss Chinese coral zonation, but I would like to point out that *Th. magnum* may not belong to *Dorlodotia* since both illustrations of that species (Jia *et al.* 1977, pl. 77, fig. 1; Xu and Poty 1997, pl. 2, fig. 2) show many immature corallites, either free or attached to mature ones. Also, a single offsetting corallite is shown in the second paper cited. That single occurrence, confronted to the entire content of corallites within the transverse section of the specimen discussed, cannot forejudge its growth form. *Thysanophyllum magnum* may be solitary and gregarious with some corallites aligible to produce 'lost structures' of Fedorowski (1978). The offsetting corallite may well be one of those. With all facts and uncertainties mentioned, the position of *Th. magnum* within *Dorlodotia*, suggested by Xu and Poty (1997), is here considered as unsupported.

The upper Carboniferous Chinese genus *Paralytvophyllum* Wu and Zhao, 1989, requires special attention. Illustrations of separate corallites of its type species *Koninckophyllum shuichengense* Yoh, 1961 do not confirm its growth form (Wu and Zhao 1989, pl. 44, fig. 5a–g). However, *P. majus* Wu and Zhao, 1989 (see their pl. 43, figs 4, 7; pl. 44, figs 1, 4; pl. 47, fig. 6; text-figs 75, 76) is a solitary, gregarious species, as documented by young corallites that are either free or attached to mature corallites but separated by continuous external walls. The arrangement of tabulae in the longitudinal section (Wu and Zhao 1989, text-fig. 75, right) resembles that in *Colligophyllum* gen. nov. and in genera included in the Krynkaphyllidae fam. nov. The middle part of the longitudinal section of both *P. majus* and *P. shuichengense* of Wu and Zhao (1989, text-fig. 74a, b) differ from all the genera discussed in these remarks through the occurrence of an incomplete axial column. Wu and Zhao (1989, p. 201) commented on that genus in the English summary as follows: "According to the development of the column and the appearance in the stratigraphic coral sequence, the *Paralytvophyllum* may evolved from *Lytvophyllum*." I agree with that comment except for the putative ancestral genus: *Colligophyllum* gen. nov. or a similar genus, rather than *Lytvophyllum*, gave rise to *Paralytvophyllum*. Consequently, the upper Carboniferous Chinese genus *Paralytvophyllum* is here included in the Subfamily Colligophyllinae subfam. nov.

Colligophyllum gen. nov.

TYPE SPECIES: *Lytvophyllum dobroljubovae* Vassilyuk, 1960, p. 103, pl. 26, figs 1a, b only (designated herein).

ETYMOLOGY: *Latin colligo, -legi, -lectum* – to come together, to accumulate; after the formation of the colony-like gregaria.

SPECIES ASSIGNED: *Lytvophyllum dobroljubovae* Vassilyuk, 1960; ?*Pseudodorlodotia sinensis* Fan, 2003.

DIAGNOSIS: Solitary, gregarious rugose corals; earliest growth stage either zaphrentoid followed by short septal or short septal from beginning; cardinal septum dominating in both instances; in maturity inner margin of cardinal septum either straight or curved; free median lamella sporadic; rare, short septal lamellae may attach median lamella; cardinal fossula absent; tabularium normal; tabulae from horizontal to steeply elevated within specimen; lonsdaleoid dissepiments always present, may dominate; septotheca formed by wide bases of major and minor septa may be incomplete.

REMARKS: As for the Colligophyllinae subfam. nov.

Colligophyllum dobroljubovae (Vassilyuk, 1960)
(Text-figs 19–22)

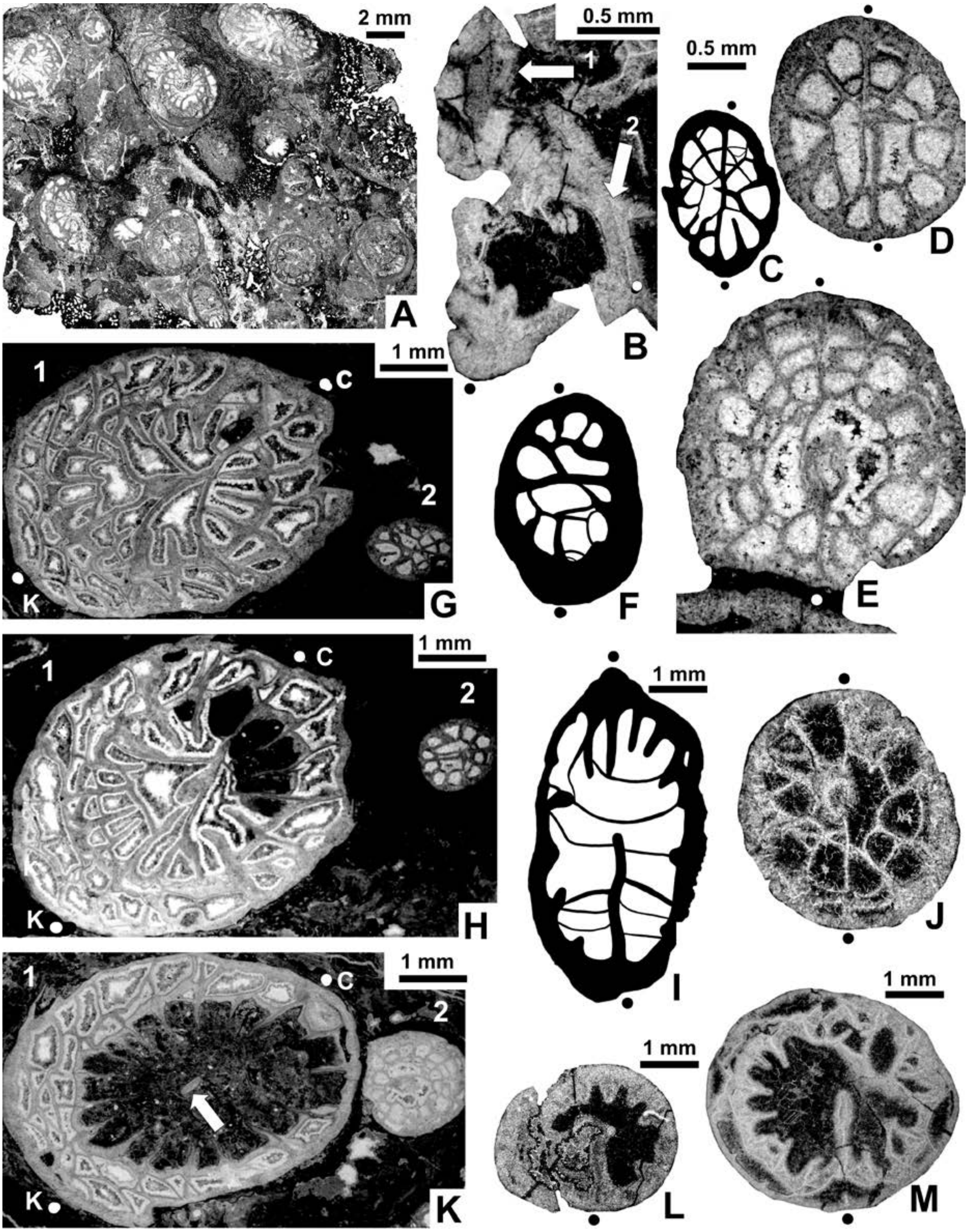
e.p. 1960. *Lytvophyllum dobroljubovae* Vassilyuk, p. 103, pl. 26, fig. 1a, b only.

?1971. *Lytvophyllum dobroljubovae* Vassilyuk; Kachanov, p. 69, pl. 2, figs 1–3.

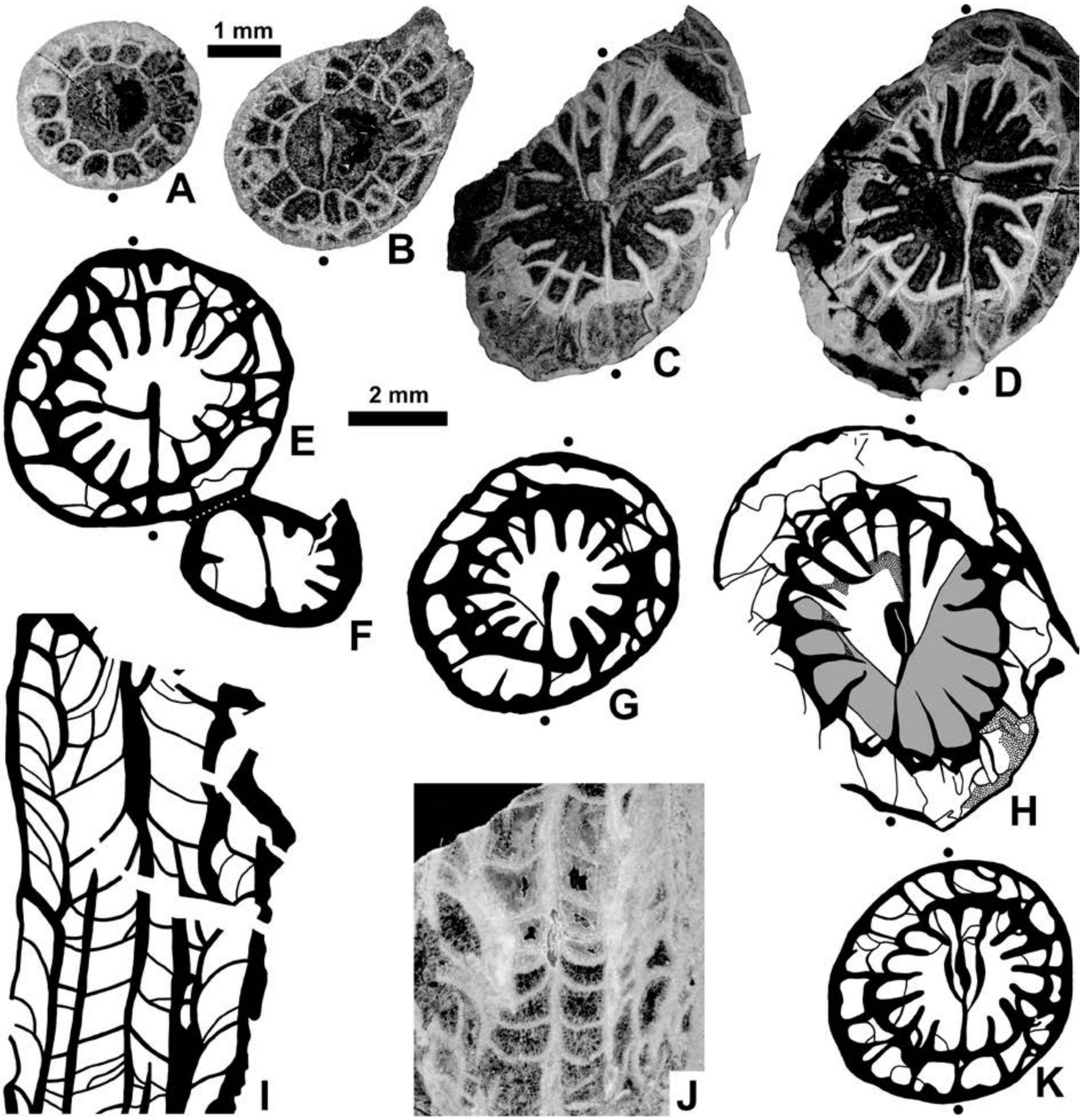
DIAGNOSIS: *Colligophyllum* with n:d value 15–17:4.7–7.3 mm, most commonly 16–17:5–6 mm.

MATERIAL: Two specimens from unknown parts of gregaria. Type specimen, former number No. 1405/12, now housed in the Institute of Geology Museum, Adam Mickiewicz University in Poznań, Poland under the new number UAM-Tc.Don.1/375. One paratype, UAM-Tc.Don.1/376. Type specimen consists of 24 incomplete corallites, most of which are immature (Text-fig. 19A). None of the immature specimens present in eight successive transverse thin sections and one peel taken from an approximately 12 mm thick slab of the type specimen achieved characters of fully mature corallite. Most are ephemeral skeletons present in one to three thin sections only. Two very young corallites preserved as short, broken skeletons attached to broken mature corallite (Text-fig. 19B, arrows). Longest, incomplete mature corallite, extending from bottom to top of fragment of type gregarium investigated, 5.8 cm long and 7.2 mm in maximum width. Lack of calice and immature growth stages suggest its total length longer; best-preserved part illustrated in Text-fig. 20I. Paratype specimen contains 22 corallites, most preserved in late neanic/early mature to mature growth stage (Text-fig. 21A). Corallites preserved in earliest growth stages not traced in five thin sections taken from approximately 8 mm thick slab of that specimen. All corallites in both specimens diagenetically altered. Microstructure of septa recrystallised completely. Several corallites crushed to various extent by compaction, some flattened. 13 thin sections and nine peels available for study.

DESCRIPTION: Corallites in type specimen loosely arranged. Only some immature corallites attached temporarily to mature ones (Text-figs 19B, G, H, K; 20E, F). Youngest corallite (Text-fig. 19B, corallite 1) with n:d value 0:1.4×0.6 mm, representing brephic, aseptal growth stage, preserved as thick external wall, broken by compaction into five fragments. In larger specimen (n:d value 4(?):2.4×1.4 mm) attached next to previous (Text-fig. 19B, corallite 2), two short, thick major septa recognised and marked by black and white dots; possible occurrence of two other major septa damaged by compaction. Continuous border dividing mature corallite from that young corallite (Text-fig. 19B, lower arrow) excludes parent/offset relationship. Most neanic corallites within holotype gregarium (Text-figs 19F, I, L; 20F) short septal. Their cardinal septa either hardly distinguishable from other major septa by longer length or clearly elongated; counter septa hardly recognisable; major septa short and thick. One corallite (Text-fig. 19C–E and G, H, K, corallite 2) investigated from neanic to late neanic/early mature growth stage. Its early neanic growth stage (n:d value 11:1.5×1.1 mm) zaphrentoid with axial septum clearly developed and most major septa attached either to it or to each other (Text-fig. 19C, G, corallite 2). Arrangement of major septa changes to radial within 0.8 mm of corallite growth (n:d value 11:2.0×1.8 mm).

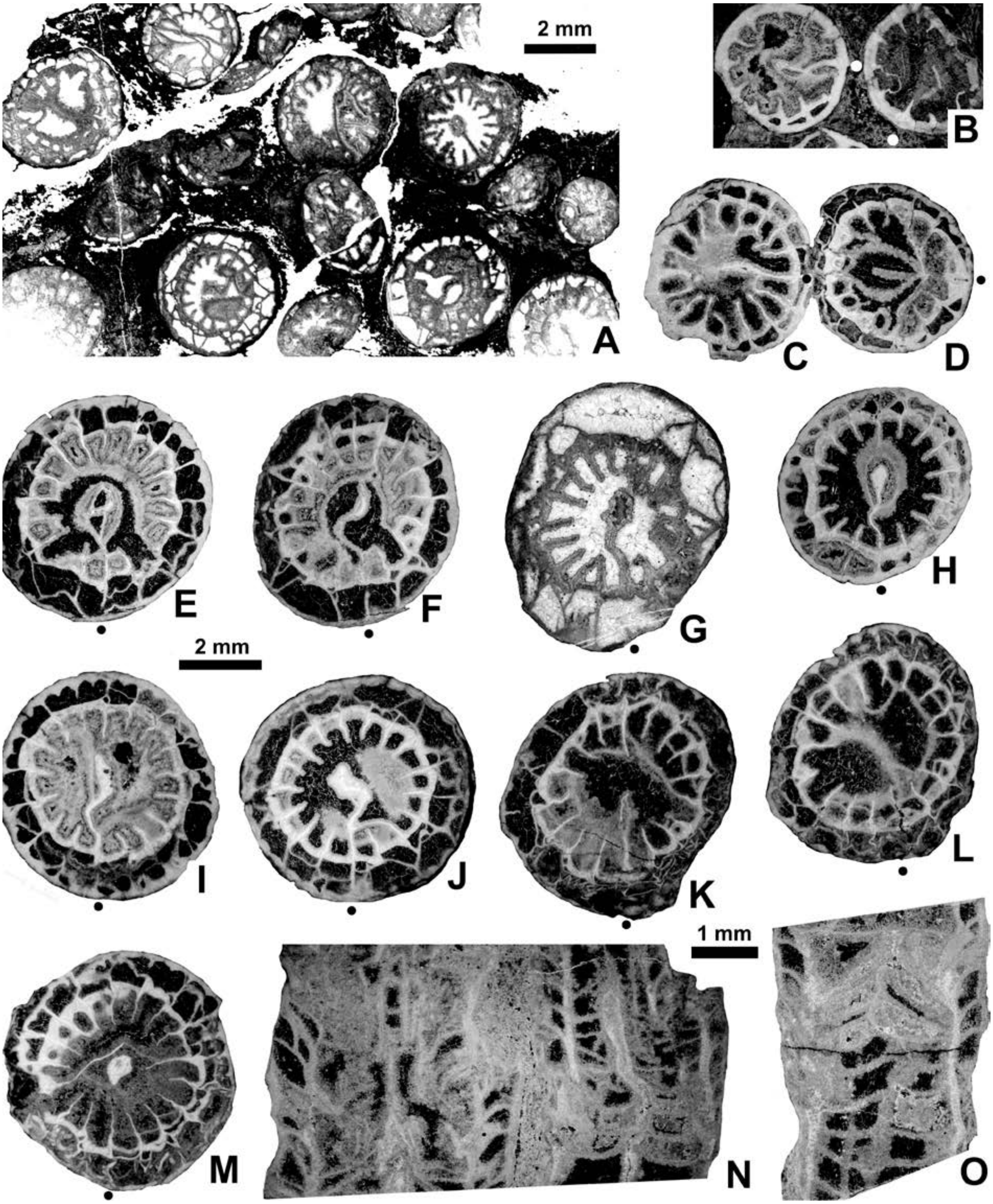


Text-fig. 19. *Colligophyllum dobroljubovae* (Vassilyuk, 1960). Transverse thin sections except when stated otherwise. Type specimen UAM-Tc. Don.1/375 (= 1405/12; Vassilyuk 1960, p. 103). A – gregarium; B – two poorly preserved corallites in brephic (corallite 1) and early neanic (corallite 2) growth stage; C–E – successive sections from neanic to early mature growth stage of one corallite (enlarged from 18G, H, K, corallite 2); F, I, J, L, M – four immature corallites; G, H, K – successive transverse sections of two corallites from mature growth stage to calice with free pseudocolumella (arrows) in corallite 1; corallite 2 as described above. For stratigraphic position see text. Cardinal and counter septa marked by black or white dots when recognisable. Scale bar between B and D corresponds to images C–F, J.



Text-fig. 20. *Colligophyllum dobroljubovae* (Vassilyuk, 1960). Type specimen UAM-Tc.Don.1/375 (= 1405/12; Vassilyuk 1960, p. 103). A, B – two successive transverse sections of small corallite; C, D, H – successive transverse thin sections (C, D) and drawing on peel image of mature growth stage and lowermost part of calice (H); E, G, K – transverse sections, mature growth stage (drawing on peel images); F – transverse section, neanic growth stage (drawing on peel image); I, J – longitudinal sections (I – drawing on peel image, J – peel). For stratigraphic positions see text. Cardinal septum marked by black dots when recognisable. Scale bar between E and G corresponds to all images except A, B.

Most major septa reduced in length to 1/2 corallite radius. Cardinal septum intersects corallite axis, almost meeting counter septum (Text-fig. 19D, H, corallite 2). Corallite ends growth with n:d value 16:2.5 mm. Major septa radially arranged, 1/2–2/3 corallite radius long. Only cardinal septum extends to corallite axis with its curved, thickened inner margin. Minor septa not traced. One row of interseptal dissepiments occurring in this growth stage allows classification as late neanic/early mature (Text-fig. 19E, K, corallite 2). Although present in only one corallite, this morphotype forms one extremum in the premature coral

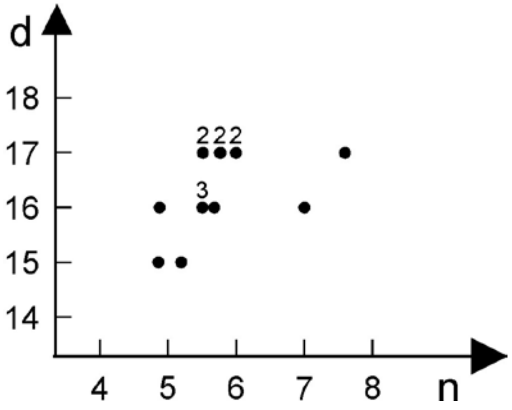


Text-fig. 21. *Colligophyllum dobroljubovae* (Vassilyuk, 1960). Transverse thin sections except when stated otherwise. Paratype UAM-Tc. Don.1/376 (not illustrated by Vassilyuk 1960). A – gregarium; B – two immature specimens growing next one another; C, D, H – early mature growth stage of three corallites; E−G – three successive sections of one specimen from a 2.2 mm thick slab; mature growth stage; I, J – two sections at distance of 1 mm of corallite with cardinal septum strong and curved; K, L – two sections at distance of 1 mm of corallite with cardinal septum thin and slightly elongated or equal to other major septa; M – corallite with thick, free pseudocolumella; N, O – longitudinal sections of mature (N) and immature (O) specimens (peels). For stratigraphic position see text. Cardinal septum marked by black or white dots when recognisable. Scale bar between I and J corresponds to all images except A, N, O.

morphology. Corallite illustrated in Text-fig. 19L, M (n:d values 12:2.9 mm and 17:3.9 mm) represents extremum of second, short septal and most common morphotype. Fragmentary corallite seen only in one thin section (Text-fig. 19J) with n:d value 12:2.0×1.7 mm shows characters intermediate between two morphotypes described above. Reason for morphological differentiation in early growth stages as large as described cannot be explained. Youngest growth stage studied of one small corallite in type gregarium, with n:d value 14:2.3 mm (Text-fig. 20A), resembles corals with aulos or columnotheca. Rudiment of skeleton in its axial part and presence in slightly more advanced growth stage (Text-fig. 20B) of medial lamella, extending towards protosepta with its thin margins, suggests diagenetic alteration of that small specimen (its maximum n:d value 16:3.7×2.7 mm). Nevertheless, its taxonomic position is doubtful (see Remarks).

In paratype gregarium (Text-fig. 21A) immature corallites rare and most flattened. Best preserved ones (Text-fig. 21B), with n:d values 12:2.9 mm and 12(?):2.7 mm, short septal with only cardinal septum elongated. Thick bases of major septa incorporated within external corallite walls. Sectors of external wall between them fibro-lamellar. Thus, bases of minor septa absent from this growth stage. In one young corallite (Text-fig. 21B, left), first interseptal dissepiments appeared. None of those corallites matured. Immature growth stages of mature corallites not traced. In early mature growth stage of paratype gregarium with n:d values 15:3.5 and 17:4.0 mm (Text-fig. 21C, D), major septa radially arranged, from less than 1/2 to 2/3 corallite radius long; in dissepimentarium thin, in tabularium slightly thickened, equal in length except for straight cardinal septum extending to corallite axis. Swellings of external wall between thick bases of major septa document occurrence of very short minor septa, restricted to septotheca. Cardinal fossula absent. One row of interseptal dissepiments. Inner wall thickened. Inner margin of cardinal septum may be thickened in only slightly larger corallite (Text-fig. 21H) with n:d value 16:4.5 mm. First lonsdaleoid dissepiments present in growth stage represented by that corallite.

Mature growth stage of corallites in both gregaria (Text-figs 19G, H, K, corallite 1; 20C–E, G, H, K; 21E–G, I–M) differ in both n:d value (Text-fig. 22) and several morphological characters. Most (11) mature corallites measured contained between 5–6 mm and 15–17 major septa; these data are considered typical for the species. Extreme corallites contained between 4–5 mm and 15–16 major septa or 7–8 mm and 16–17 major septa (2 corallites in each frame). Characters in common for all mature corallites: major septa radially arranged, approximately 2/3 corallite radius long, in tabularium thickened, in dissepimentarium thin; minor septa either not traced (perhaps due to diagenetic alterations) or restricted to external wall where their thick bases supplement major septa in forming septotheca; cardinal fossula absent. Differentiated characters: cardinal septum continuous and elongated to corallite axis; its inner margin either straight and equal in thickness with its remaining part (Text-figs 20E, G; 21K), or curved and thickened to various extent (Text-fig. 21E–J), with median lamella not separated. However, three corallites investigated in their uppermost stages of growth document formation of monoseptal pseudocolumella free from major septa (Text-fig. 21M). Three successive sections of one corallite from holotype gregarium document temporary elongate counter septum through formation of thickening at inner margin of cardinal septum to free pseudocolumella in calice (Text-fig. 19G, H, K, arrow, respectively). Such a process, confirmed to some extent by another corallite of the holotype gregarium (Text-fig. 20C, D, H), may be typical for the species. Only single corallite traced in paratype gregarium that reached ontogenetic level with pseudocolumella free and cardinal septum equal to other major septa (Text-fig. 21M); that process cannot be faithfully confirmed. Equality of cardinal septum to remaining major septa present in one corallite studied (Text-fig. 21K, L) forms extreme variant of that septum. Counter septum equal to adjacent major septa in length and thickness in great majority of specimens studied in neanic and mature growth stage. However, in three corallites of mature gregarium it meets median lamella (Text-figs 19G, H, corallite 1; 20C, H, K).



Text-fig. 22. *Colligophyllum dobroljubovae* (Vassilyuk, 1960). N:d value where n = number of septa and d = corallite diameter. Numbers above black dots correspond to number of corallites with given value.

Minor septa invariably restricted to septotheca. Their absence from several corallites apparently diagenetic. Dissepiments interseptal and lonsdaleoid, in single row; in rare septal loculi 2–3 rows.

In longitudinal sections (Text-figs 20I, J; 21N, O), single row of long dissepiments; their inner, vertical parts thickened. Tabularium normal. Tabulae complete, commonly sagging in their middle part. i.e., slightly downturned at periphery and elevated in their inner part to meet median lamella or inner margin of cardinal septum. Some tabulae horizontal, exceptionally down sloping within the same section. Variability in arrangement of tabulae and waviness of inner margin of cardinal septum accentuated stronger in paratype corallites than in holotype (Text-figs 21N, O and 20I, J respectively).

REMARKS: The observed morphologic variability, especially that of the early immature growth stage, extends beyond the frames of intraspecific variation commonly acceptable for rugose corals. However, the close similarity in several of the characters listed above supports the monospecific character of the gregaria with the exception of one corallite in the holotype gregarium (Text-fig. 20A, B). The arrangement of tabulae sections in that corallite closely resembles a columnotheca typical for species belonging to the genus *Kumpanophyllum* Fomichev, 1953 (see Fedorowski 2019b). A tabularium similar to that one is absent from all corallites assigned to *Colligophyllum* gen. nov. Thus, that dubious corallite may either i) belong to the *C. dobroljubovae* gregarium and forms an extreme intraspecific variant of that species; ii) may belong to the genus *Kumpanophyllum* growing together with the gregarium; or iii) could have been attached to the gregarium *post mortem*. A small fragment of skeleton, restricted to two random transverse thin sections, precludes a reasonable selection of one of these possible options.

The incertitude of the growth form of most species included by various authors in *Lytvophyllum* and other taxa resembling *Colligophyllum* gen. nov. makes a comprehensive discussion unsupported and direct comparisons of species impossible. However, the close morphological similarity of several of these to *C. dobroljubovae* and to each other makes a close relationship very probable. In particular, *Lytvophyllum dobroljubovae* of Kachanov (1971), ?*Pseudolytvophyllum askynensis* Kossovaya, 2009, ?*Lytvophyllum minor* Wu and Zhao, 1974, and ?*Pseudodorlodotia sinensis* Fan in Fan *et al*., 2003 are among those species that could conceivably belong to this grouping. However, I prefer to avoid directly comparing *C. dobroljubovae* to the Chinese species at the species level until the latter are better known. Additionally, I do not have direct access to the remaining specimens listed. Dr. Ye. I. Kachanov has passed away and his collection is currently unavailable to me. A peculiarity of ?*Pseudolytvophyllum askynensis* is discussed in Considerations.

OCCURRENCE: Amvrosievskiy Kupol, Artemovki Village, Panska Gora, Limestone E_2. Lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus–Id. sulcatus sulcatus* conodont Biozone. Upper lower Bashkirian.

CONSIDERATIONS

The large observed variability both in particular parts of individual skeletons and at an intraspecific scale, the repetition of characters known from phylogenetically distant taxa, and the considerable rugose coral turnover during the Serpukhovian and early Bashkirian make the taxa described in this paper suitable – and quite insightful – for some specific and general considerations. However, the restricted number of specimens available for the study, their often poor preservation, and the incomplete literature data leads to rather weak support for some of the suggestions that follow.

A question regarding the taxonomic value of growth forms ought to be examined prior to discussing the suspected relationships and origins of the corals described in this paper. In most Rugosa, morphologically diagnostic characters and growth form are consistent. Rugose coral taxa displaying close morphological similarity combined with disproportionate variety in their growth form are extremely rare (e.g., Fedorowski 1978; Webb 1987; Oliver and Sorauf 2002). From the examples cited, only the specimens described by Fedorowski (1978) were all derived from a single bed in the same Leonardian (Permian) locality in the Glass Mountains, SW Texas. Their preservation suggested an *in situ* position and growth under similar extrinsic conditions, thus eliminating environmental controls as a factor driving that variability. The corals identified as *Caninostrotion variabilis* Easton, 1943 analysed by Webb (1987) occur in the same stratigraphic level (Pitkin Formation, upper Mississippian), but across a rather wide area in Oklahoma and Arkansas. *Heliophyllum halli* Milne-Edwards and Haime, 1850, analysed by Oliver and Sorauf (2002), displays both wide geographic and stratigraphic distributions. The taxa cited were recently discussed in the context of speciation (Fedorowski and Ohar 2019, pp. 613–615), but that discussion can readily be transferred to the taxonomic value of coloniality. An increased rate of speciation and instability in growth form observed during elevated faunal turnover periods is the most important conclusion of that discussion in the context of the present paper. Most of the corals described and/or discussed here occurred in the late Viséan, Serpukhovian, and early Bashkirian – that is, in the most dramatic turnover period of the Carboniferous history of the Rugosa (Fedorowski 1981). Thus, that conclusion may be true for them as well.

Taking those examples in mind and considering the data available so far, the following preliminary conclusions is suggested for both subfamilies of the Krynkaphyllidae fam. nov.:

1) The totally inorganic nature of the exoskeleton eliminates the potential for palaeogenetic studies. Besides, finding of DNA in exoskeletons of organisms extinct more than 250 my must be accepted as impossible. Without access to genetic data, the real value of growth forms in the biological sense, and thus the relationship (i.e., species or genus) of specimens in those growth forms, cannot be established firmly. This, in turn, means that a subjective approach to the taxonomic value of any particular feature is *de facto* necessary. As a firm believer in genetic controls on growth forms, and tending towards a 'splitting' mentality with regards to taxonomy, I consider a great majority of truly colonial, protocolonial, and solitary species, including gregarious taxa, to be distinct genera, that can be related to each other at the subfamily level. However, growth habit may not be a decisive taxonomic criterion for corals occurring in a major turnover period of rugosan evolution, as pointed out above. During an interval of increased speciation, individual local lineages may either keep the full genetic potential of offsetting inherited from their suspected ancestors, such as *Dorlodotia* (fasciculate colonial habit), or may have that potential increased (cerioid colonies such as *Ceridotia*), reduced in part (protocolonial habit), or eliminated completely (solitary habit).

Despite the doubts expressed by Fedorowski and Ohar (2019), the solution postulated by Webb (1987) for *Caninostrotion variabilis* Easton, 1943 may be the best approach to treat the corals described here and the corals from outside the Donets Basin discussed elsewhere in this paper. The implication is that *Colligophyllum* gen. nov. and morphologically similar genera should be, and are treated here, as being related to each other irrespective of growth form. In particular lineages, that relationship may vary from the specific to subfamily level.

Unpublished data on ?*Pseudolytvophyllum askynensis* Kossovaya, 2009 may serve as an example of growth form instability within a species. On my request, Dr O.L. Kossovaya from the A.P. Karpinsky Russian Geological Research Institute (VSEGEI), St. Petersburg, Russian Federation, checked her collection of that species from the Askyn River section and found one offsetting corallite (e-mail, October 29, 2019). My request to Professor V.V. Ohar, Kyiv University, Ukraine, to check his collection from the same section resulted in the identification of both weak fasciculate colonies and protocolonies located next to each other within the same sample (e-mail, December 20, 2019). Both of those recognitions require detailed studies on larger collections that may document not only the protocolonial and colonial forms of that species, but also solitary specimens that together form gregaria.

2) The evolutionary roots of the Krynkaphyllidae fam. nov. can only be postulated. *Dorlodotia* and its type species *D. briarti*, revised by Poty (1975), is one of the two taxa known to me that could be provisionally considered ancestral for the corals described here when their main diagnostic features and stratigraphic positions are considered. *Dorlodotia briarti* ranges from the lower Viséan (Moliniacien) to the middle Viséan (Livian) in Western Europe and Turkey. '*Cyathophyllum*' *pseudovermiculare* McCoy, 1849 is a somewhat less feasible ancestral taxon, although it cannot be discounted *a priori*.

'*Dorlodotia*' *fomitschevi* from the lower Livian (Zone C_1^vb) of the Donets Basin is the second species considered as a potential progenitor. Denayer (2011) included it, albeit questionably, in synonymy with *D. briarti*. While his synonymy is not accepted here, '*D.*' *fomitschevi* displays some characters shared with *D. briarti*, and may be placed among the earliest ancestors of the Krynkaphyllidae fam. nov. known so far. It legitimizes the possibility that the genus *Dorlodotia* migrated eastwards, and likewise its suspected ancestry for the Donets Basin taxa described here.

Both *D. briarti* and '*D.*' *fomitschevi* bear a closer resemblance to the Krynkaphyllinae subfam. nov. than to the Colligophyllinae subfam. nov. Nevertheless, the main morphological characters of *D. briarti*, in both the immature and mature growth stages, are repeated in both subfamilies.

3) Assuming that the ancestral position of *D. briarti* for the Krynkaphyllidae fam. nov. is correct, *Dorlodotia* should be removed from either the Family

Lithostrotionidae (see Hill 1981) or the Subfamily Lonsdaleiinae of the Family Axophyllidae (see Poty 1981), and placed either in the Krynkaphyllidae fam. nov., as conditionally suggested here, or left outside of any established family as suggested by Denayer (2011). The latter suggestion would require the introduction of a new family for both that genus and *Ceridotia*, since no family other than three listed above is a feasible taxonomic possibility. The taxonomic position of *Dorlodotia* may be dependent on the putative ancestor. I do not address this question in the absence of the firm data required for such a discussion. Neither Poty (2007), who suggested *Dorlodotia* was derived from a caninoid species, nor Denayer and Poty (2011), who point to *Corphalia* Poty, 1981 as a descendent of a caninoid species and an ancestor of *Dorlodotia,* have offered satisfactory support for their suggestions. Moreover, it was earlier suggested that *Corphalia* evolved from *Dorlodotia* (Poty 1993, pp. 148, 149).

4) The eastern Asiatic taxa, which are most numerous and differentiated in China, are not included in the succession below. Despite this, several of these taxa are similar to and conditionally included in the Subfamily Colligophyllinae subfam. nov. The same is true for the Japanese *Amygdalophylloides* of Yoshida (in Yoshida and Okimura 1992) in the case of the Subfamily Krynkaphyllinae subfam. nov. The rationale of a restriction to European taxa in the succession is mainly due to: i) gaps in the knowledge of the Asiatic taxa; and ii) the coarse nature of their reported stratigraphic occurrences, which is generally too vague to make firm comparisons to the occurrences and succession of the European taxa.

5) It must be clearly noted that the available data are inadequate to call the successions established below phylogenetic. They reflect the succession in time of particular species, irrespective of their growth habit and other characters that may eventually influence their final positions within phylogenetic lineages. With that caveat noted, the morphology and stratigraphic occurrences of species discussed with remarks to the Krynkaphyllidae fam. nov. and remarks to both subfamilies of that family can be used to establish the following stratigraphic successions of the European taxa. Both successions start with the lower Viséan *D. briarti* and ‘*D.*’ *fomitschevi* as the oldest European species known.

The Subfamily Krynkaphyllinae subfam. nov. line: → *Protokionophyllum facilis* (lowermost Bashkirian) → *Protokionophyllum* sp. 2. Both species of *Krynkaphyllum* gen. nov. released phylogenetic offsprings contemporaneous with *Protokionophyllum* sp. 2 (late early Bashkirian) → *Protokionophyllum* sp. 3 and *Axolithophyllum* (?) sp. Fomichev, 1953 (late middle Bashkirian).

The Subfamily Colligophyllinae subfam. nov. line: → *Pseudodorlodotia subkakimii* (early late Viséan) → ‘*Lytvophyllum*’ *dobroljubovae* Vassiljuk of Kachanov (1971) (late Viséan) → *Colligophyllum dobroljubovae* and ?*Pseudodorlodotia askynesis* (late early Bashkirian) → *Pseudodorlodotia suigeneris* (lower middle Bashkirian) → *P. aisenvergi* (late middle Bashkirian).

6) The differential and somewhat inconsistent treatment of the European and eastern Asiatic taxa in this analysis – that is, their conditional inclusion in the generic and subfamily listings, on the one hand, and their exclusion from the stratigraphic successions established above, on the other hand – is due to the following reasons: i) morphological similarities suggest the possibility of a taxonomic relationship; ii) there was relatively easy communication between both areas, as documented by compilations of late Viséan to Bashkirian paleaogeography (Scotese 2001; Torsvik and Cocks 2016); iii) both morphologic and stratigraphic gaps are present in the data available for robust comparison. Those gaps, which include both uncertain growth habits and some important morphological characters, superimposed on the generally imprecise correlation of coral bearing strata, may result in guessing and speculation unrooted in any firm documentation regarding the taxonomy and succession of the Krynkaphyllidae, which would be ultimately misleading.

7) *Pseudodorlodotia subkakimii* is the second species in the stratigraphic succession, following *D. briarti* and ‘*D.*’ *fomitschevi*. Therefore, its close morphological similarity to *Colligophyllum* gen. nov. is important as an indicator for an early splitting of the taxa grouped within the Krynkaphyllidae fam. nov. into two parallel successions. That early splitting, and certain characters of the Subfamily Colligophyllinae subfam. nov. shared with the Petalaxidae can be interpreted in two ways: i) as opening to discussion of the position of the Subfamily Colligophyllinae subfam. nov. within the Family Krynkaphyllidae fam. nov. vis-à-vis the Family Petalaxidae; or ii) as suggesting the homeomorphic nature of the Subfamily Colligophyllinae subfam. nov. relative to the Family Petalaxidae. The study by Denayer (2011) enables the theoretical possibility of combining both these possibilities. However, I have inadequate data to examine this in detail. Thus, the Subfamily Colligophyllinae subfam. nov. is included here within the Family Krynkaphyllidae fam. nov., as noted.

8) The inconsistent position of tabulae, characteristic of *Colligophyllum dobroljubovae* and most of the taxa that resembling *C. dobroljubovae* to an extent allowing for their conditional inclusion in the Subfamily Colligophyllinae subfam. nov. may suggest a relationship of that subfamily with the Family Geyerophyllidae. Vassilyuk (1974) had already preempted this possibility by placing *Lytvophyllum* (= *Colligophyllum*) as a taxon intermediate between *Dorlodotia* and *Darvasophyllum*. In the context of the discussion on the Geyerophyllidae (see remarks to the Krynkaphyllidae fam. nov.) and doubts concerning that family, this relationship is considered here as theoretically possible, but the present data are inadequate for comprehensive discussion and suggestion.

9) The stratigraphic range and relationship of *Colligophyllum* gen. nov., and its type species *Colligophyllum dobroljubovae*, to the genus *Lytvophyllum s.s.*, represented solely by the lectotype of its Artinskian type species *L. tschernovi* (Soshkina, 1925) remains enigmatic. A lengthy interlude between the known occurrences of those species (approximately 30 Ma) may be even potentially elongated, if the upper Viséan *Pseudodorlodotia sinensis* Fan in Fan *et al*., 2003 and *Lytvophyllum soshkinae* Kachanov, 1971 are considered. In the framework of Rugosa development, a 30 Ma interval may be conceivably too long for a single genus to continually develop. While this argument is strengthened by a gap in the occurrence of any *Colligophyllum*-like taxa above the Bashkirian strata, the homeomorphy of the type specimens of both species is suggestive of such a long interval of generic development. Yet again, this is a question that remains unsolved in the absence of pertinent studies.

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