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Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 8. The Family Kumpanophyllidae Fomichev, 1953

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ABSTRACT:

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The Family Kumpanophyllidae Fomichev, 1953, synonymised by Hill (1981) with the Family Aulophyllidae Dybowski, 1873, is emended and accepted as valid. The new concept of this family, based on both new collections and discussion on literature data, confirms the solitary growth form of its type genus *Kumpanophyllum* Fomichev, 1953. However, several fasciculate colonial taxa, so far assigned to various families, may belong to this family as well. The emended genus *Kumpanophyllum* forms a widely distributed taxon, present in Eastern and Western Europe and in Asia. Its Serpukhovian and Bashkirian occurrences in China *vs* Bashkirian occurrences in the Donets Basin and in Spain, may suggest its far-Asiatic origin, but none of the existing taxa can be suggested as ancestral for that genus. Thus, the suborder position of the Kumpanophyllidae remains unknown. Four new species: *K. columellatum*, *K. decessum*, *K. levis*, and *K. praecox*, three *Kumpanophyllum* species left in open nomenclature and one offsetting specimen, questionably assigned to the genus, are described.

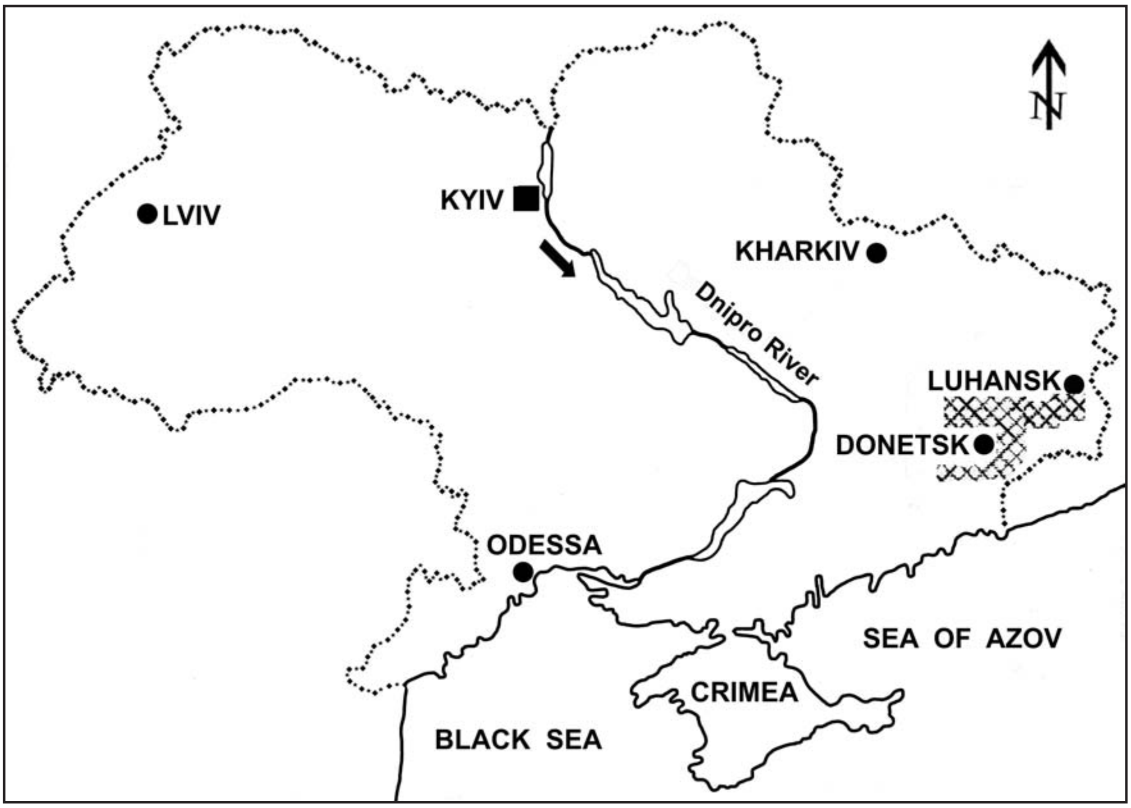
Key words: Rugosa (Anthozoa); Carboniferous (early Pennsylvanian); Taxonomy; Palaeogeography.

INTRODUCTION

The present paper, devoted mainly to the redefined Family Kumpanophyllidae Fomichev, 1953, represents the eighth part of the series of papers dedicated by the present author to the Bashkirian rugose corals from the Donets Basin, Ukraine (Text-fig. 1). Thus, information concerning all general topics connected to that fauna can be found in the earlier published papers of the series, starting with that by Fedorowski (2009a). Fomichev (1953) established the Family Kumpanophyllidae on the basis of an extremely restricted number of poorly preserved specimens. The type species of the type genus *Kumpanophyllum kokinense* Fomichev, 1953 comprises only four incomplete corallites, all illustrated (Fomichev 1953, pl. 15, figs 5–8). Such an incomplete documentation resulted in the family and genus being abandoned. The collection investigated herein, consisting of reasonably well preserved and comparatively numerous specimens (60 studied), allows for a new approach to the Family Kumpanophyllidae and the reconsideration of its taxonomic validity. The review of literature data (see remarks on the family) suggests its wide geographic distribution. It probably appeared during the Serpukhovian, but its ancestry remains uncertain (see Considerations).

Fenino village which gave its name to the Feninian Horizon was formerly located in the area presently occupied by the water reservoir of the Starobiesheve Power Plant (Fedorowski and Ogar 2013, p. 299, text-fig. 4) and is consequently omitted from the maps (Text-figs 2–4) showing the positions of the indexed limestones and the names of the main collecting sites.

Following Hudson (1936) and Fedorowski (1997), only the cardinal and the counter major septa are



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

considered as the protosepta that are derived from the axial protoseptum. As in my earlier papers, the term 'primary septa' used herein refers to the innermost parts of septa, created within septal pockets prior to the secretion of the sclerenchymal sheets. Such primary septa are described in the present paper under the microstructure of septa.

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

Repetitions of the family name in diagnoses of genera and the genus name in the diagnoses of species means the occurrence in the genus or species in question of all the main diagnostic characters of a taxonomically higher level taxon. Such an approach allows the reduction of diagnoses to the characters typical solely for the genus or species being diagnosed.

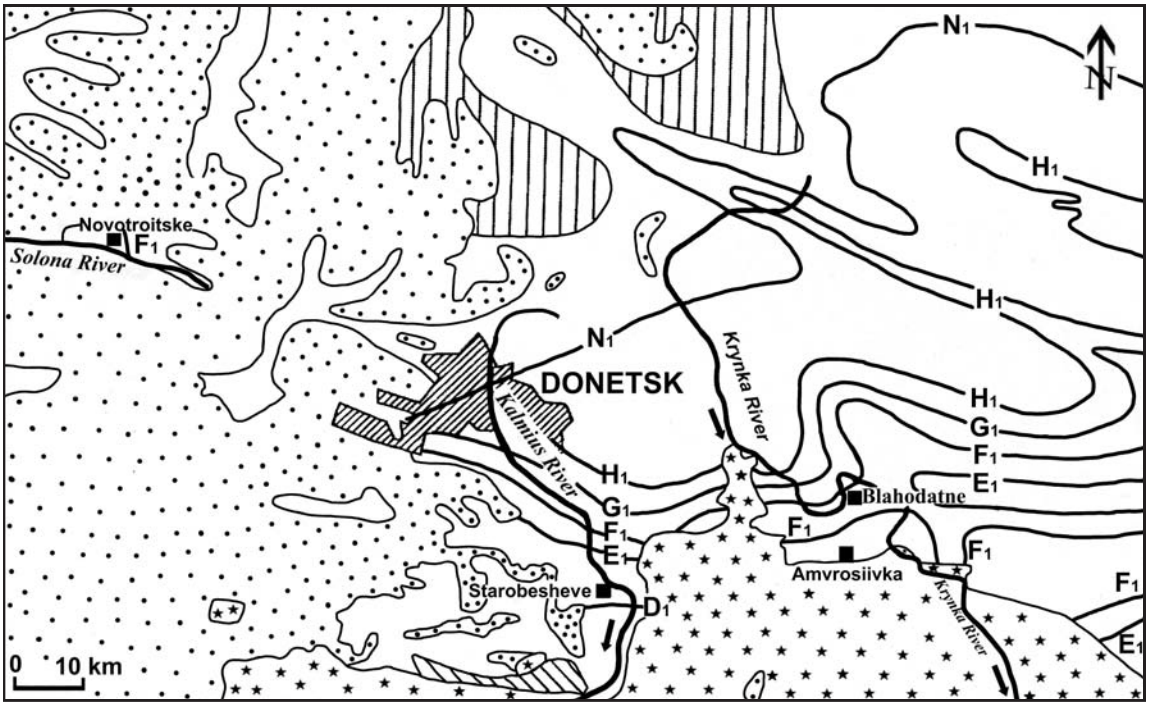
Corals described in the present paper are housed in the collections of the Institute of Geology, Adam Mickiewicz University (Poznań, Poland) and bear the acronym UAM-Tc/Don.1.

GEOLOGICAL SETTING

This paper forms the eighth part of the series of papers devoted to the early Bashkirian rugose corals from the Donets Basin (Text-figs 2–4). Thus, the reader is kindly directed to the first paper of the series Fedorowski (2009a) for an overview of the history of the Bashkirian Stage and its faunal content. Poletaev *et al.* (2011) provided detailed descriptions and logs of the Mississippian, Pennsylvanian and lower Permian (Cisuralian) stratotypes of the local subhorizons and horizons established in the Donets Basin. The comprehensive compendium edited by Gozhyk (2013) supplements the data summarised by Poletaev *et al.* (2011).

MATERIAL AND METHODS

All corals investigated in this paper were collected by Dr N.P. Vassilyuk, Professor Emeritus of the Donetsk Polytechnic, during many years of her field investigations. Also, a few thin sections were



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

made by her. The total collection described here (60 specimens) is adequate for a reasonable documentation. Several corallites are almost complete, including calices and early growth stages preserved. Unfortunately, recrystallisation, dolomitisation and calcitic veins make details of the morphology of some of them difficult to demonstrate on images. Thus, drawings upon the images of several specimens appeared necessary for a firm documentation. Traditional methods of thin sectioning, peeling and polishing have been applied in order to make the material available for the detailed study.

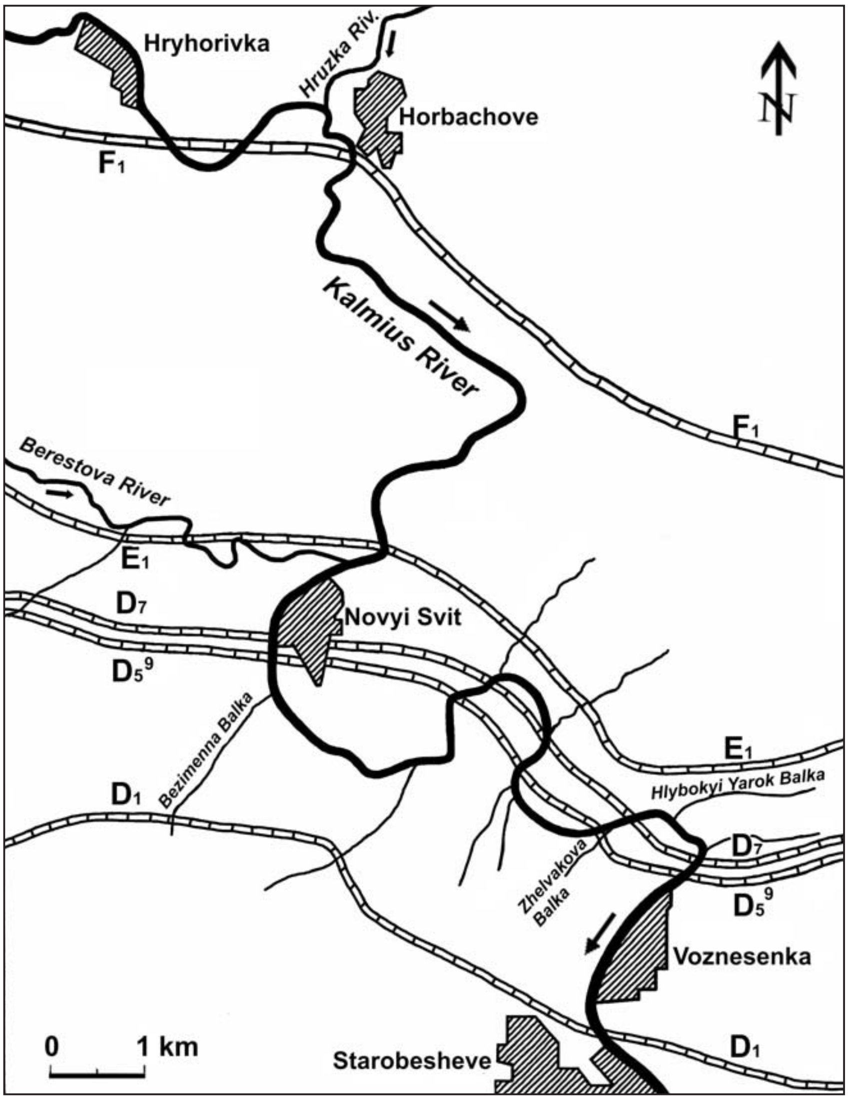
SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder *incertae sedis*
Family Kumpanophyllidae Fomichev, 1953

EMENDED DIAGNOSIS: Solitary to weakly fasciculate (?); major septa amplexoid, equal in length; protosepta not shortened, may reach pseudocolumella; axial septum present early in ontogeny; pseudocolumella monoseptal or complex, derived from axial septum; in maturity mostly free; in advanced maturity may be reduced or disrupted when complex; biformity of tabularium advanced to various extent; axial tabellae form columnotheca; dissepimentarium appears late in ontogeny; dissepiments mostly interseptal; lonsdaleoid dissepiments may occur at periphery; microstructure of septa finely trabecular; calices shallow.

GENERA ASSIGNED: *Kumpanophyllum* Fomichev, 1953; ?*Paradiphyphyllum* Wu and Lin in Lin *et al.*, 1984; ?*Pseudosemenoffia* Yu, 1985; ?*Paranemistium* Yu, 1985; ?*Kapuphyllum* Yu and Wang, 1987, ?*Diphyphylloides* Wu and Zhao, 1989. The reasons for questionable inclusions of particular genera are discussed in the remarks below.

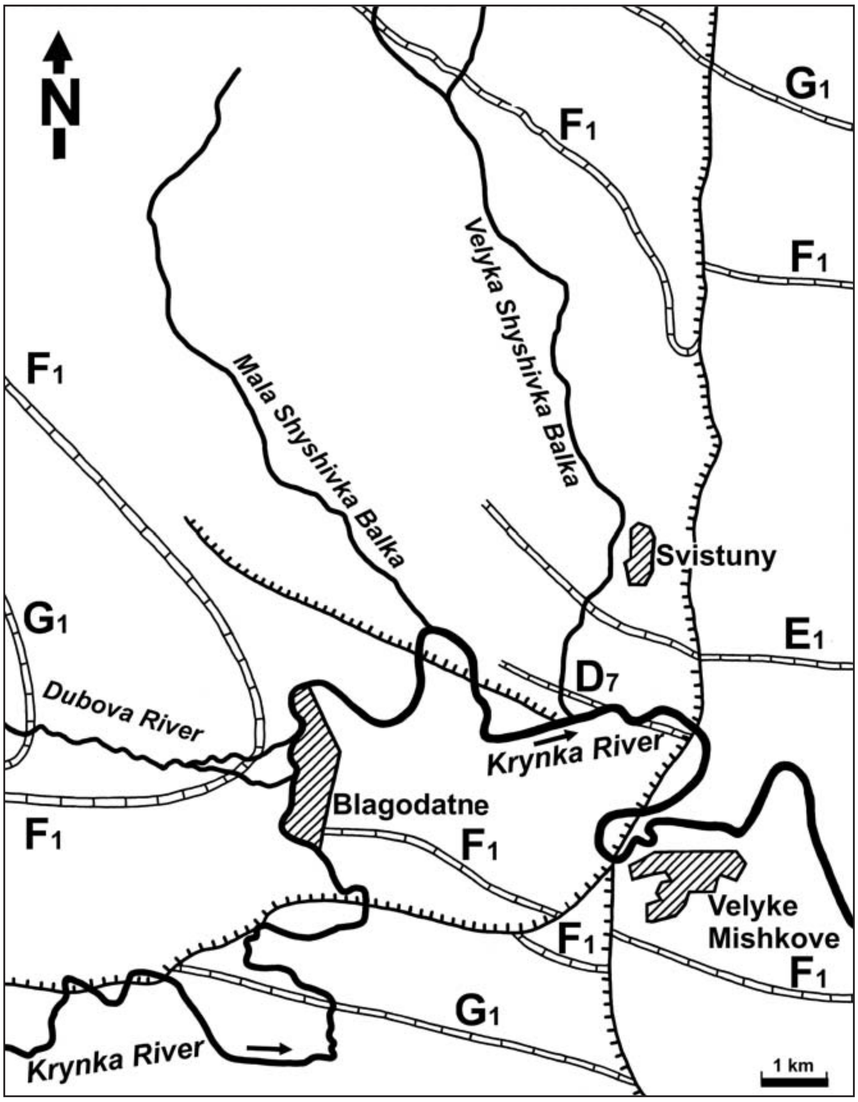
REMARKS: Fomichev (1953) established the Family Kumpanophyllidae on the basis of very incomplete and poorly preserved corallites. Only four specimens, each represented by one transverse thin section, illustrate *K. kokinense*, the type species of the genus (Fomichev 1953, pl. 15, figs 5–8). All these specimens were derived from Limestone H_2. The second species included in that genus, *K. derevetschkense* Fomichev, 1953, was derived from Limestone I_2. One



Text-fig. 3. Outcrops of Limestones D to F in the Kalmius River area (after Fedorowski 2009a, with geographic names in Russian replaced by Ukrainian)

transverse thin section of the mature growth stage and one from the calice illustrate its holotype and one transverse thin section of the immature growth stage illustrates the paratype (Fomichev 1953, pl. 15, fig. 9a, b and 9v respectively). Longitudinal sections were not made for either of the two species. Such a poorly documented genus representing a new family was totally ignored by subsequent authors. Only Hill (1981, pp. *F*353, *F*355, *F*358) questionably included the family in the synonymy with the Family Aulophyllidae Dybowski, 1873 and the Subfamily Amygdalophyllinae Grabau in Chi, 1935, and characterised it as an insufficiently known taxon. Details provided by the new collection studied herein, limited data available from Fomichev's (1953) descriptions and illustrations, supplemented by my brief restudy in 1968 of his specimens, allow for a new approach to the Family Kumpanophyllidae. An overview of the existing literature data, superimposed on the study mentioned, suggests a wide geographical distribution of the potential members of that family and their stratigraphic range from at least the Serpukhovian to the late Bashkirian.

The most important details established by Fomichev (1953) for the type species of the genus and translated here from Russian are: "A solid, thick



Text-fig. 4. Outcrops of Limestones D to G in the Krynka River area (after Fedorowski 2009a, with geographic names in Russian replaced by Ukrainian)

pseudocolumella [*stolbik*], connected to counter septum, appears in those corals early in the ontogeny. The median lamella and, sometimes, radial dark lines are seen within the pseudocolumella” (p. 256). This means that a complex, amygdalophyllid pseudocolumella has been recognised. “The cardinal fossula absent from all growth stages” (p. 256) and “the cardinal fossula and the cardinal septum unrecognisable” (pp. 257, 258). “Inner margins of long straight major septa commonly rest on concentric lines surrounding the pseudocolumella and corresponding to sections of tabulae.” (p. 258). The latter statement is of special value due to lack of the longitudinal section. Comparison with the transverse and longitudinal sections of the specimens studied here allows one to consider those sections of tabulae as a proof for the occurrence of the columnotheca.

The original documentation of *K. derevetschkense* is limited making a firm solution impossible. Its oval pseudocolumella is probably monoseptal and connected to the counter septum. A slight differentiation in length and free ends of several major septa in the holotype may have resulted from the obliqueness of the section (Fomichev 1953, pl. 15, fig. 9a). Its cardinal septum was described by Fomichev (1953, p. 259) as “slightly shorter than other major septa”, but the illustration (Fomichev 1953, pl. 15, fig. 9a) contradicts that statement. Neither shortening of the cardinal septum nor the cardinal fossula is traced in the illustrations of that specimen. The "very rare connections (or traces of sections of tabulae) seen here and there between the major septa" (Fomichev 1953, p. 259) are interpreted here as remnants of transverse sections of the columnotheca forming tabellae. All the characters listed are barely recognisable and can either be contested, or accepted as poor proof for the common generic status of both species discussed. The latter option is applied provisionally herein.

The overview of literature allows one to indicate numerous taxa comparable to or bearing characters diagnostic for the Kumpanophyllidae. Two characters, i.e., the development of both a columnotheca and a dissepimentarium are selected here as most important for the introductory discussion. This means that both solitary and fasciculate colonial taxa are taken in mind although the relationship of the colonial taxa to the Family Lithostrotionidae d'Orbigny, 1852 cannot be excluded (see Considerations). Also, the first description of a species selected as the type for a given genus is always cited here as reference. The subsequent descriptions of a type species or species included by subsequent authors in a given genus are mentioned only when agreeing with the type in their diagnostic characters and if offering supplementary data, important for a more complete description of a type species or of a genus. The generic name *Diphyphyllum* Lonsdale, 1845 can be mentioned as an example of that approach. Species with and without a columnotheca that offset axially, peripherally or laterally were included in that genus by various authors making it a taxonomic 'waste basket' rather than a true genus. Thus, only species resembling *Diphyphyllum concinnum* Lonsdale, 1845, i.e., the type species for that genus, are considered here as true members of the genus *Diphyphyllum*. The holotype of that species has been considered lost until the revision by Rosen and Wise (1980). Thus, Smith (1928, p. 114) selected *Diphyphyllum gracile* McCoy, 1851 as the type for his *Diphyphyllum β*. Fortunately, the morphology of McCoy's (1851) species follows the main criteria of the holotype of *D. concinnum*, making Smith's (1928) selection acceptable. Further important contributions are: Hill (1938–1941), Dobroljubova (1958), Vassilyuk (1960), Semenoff-Tian-Chansky (1974) and Khoa (1977). The specimens described and illustrated in the papers listed document the occurrence of a continuous columnotheca, the axial increase and the absence of the axial septum in early growth stages of offsets. All those characters are important for the discussion on the derivation and relationships of the Kumpanophyllidae (see Considerations).

The following taxa, both solitary and fasciculate colonial, are briefly discussed below in the context of their relationship or morphological similarity to the Kumpanophyllidae: *Cyathophyllum echinatum* Thomson, 1880, revised by Hill (1938–1941); *Campophyllum carinatum* Carruthers, 1909; *Nemistium* Smith, 1928 and *Nemistium* spp. of Rodríguez (1984), Igo and Igo (2004) and Denayer (2014); *Koninckophyllum* spp. of Vassilyuk (1960), Armstrong (1962) and Rowett and Sutherland (1964) non Thomson and Nicholson (1876); *Lithostrotion ineptum* Gorskiy, 1978; *Semenoffia* Poty, 1981 and species included in that genus by Yu and Wang (1987); *Lithostrotion* (*Siphonodendron*) *nipponalpinum* Igo and Adachi, 1981, renamed as *Koninckophyllum*? by Igo and Adachi (2000); *Pseudosemenoffia* Yu, 1985 and in Yu in Fan *et al.* (2003); *Paranemistium* Yu, 1985; *Kapuphyllum* Yu and Wang, 1987 and in Yu in Fan *et al*. (2003); and *Diphyphylloides* Wu and Zhao, 1989.

Aulina Smith, 1917 and genera developing a true aulos of Smith (1928) and Fedorowski (2009b), such as *Solenodendron* Sando, 1976 and *Hillaulina* Yu in Yu *et al*., 1983 are omitted from the discussion. Doubts concerning *Aulokoninckophyllum* Sando, 1976, and some species included in that genus by Poty (1981), are discussed separately (Fedorowski *et al*., submitted) making a further discussion unnecessary. None of the species included by Sando (1976) in *Aulokoninckophyllum* bears characters comparable to the Kumpanophyllidae.

The genus *Kumpanophyllum* comprises solitary species. Thus, such species are mentioned first and are discussed in accordance with the sequence of dates of their introduction. Also, the original generic designation of those species are followed.

Koninckophyllum elpasoensis Armstrong, 1962 (pl. 2, figs 29–37) from the Helms Formation (Chesterian) of the Franklin Mountains in SW Texas, USA is described and illustrated in an adequate manner for accepting its solitary growth form and diagnostic features. Lack of designation of the holotype and ambiguous figure captions (Armstrong 1962, p. 75) are the main disadvantages. The differentiated size and morphology of individual transverse thin sections illustrated by him represent probably three or four different specimens. Nevertheless, the occurrence of the columnotheca and the pseudocolumella present at various ontogenetic growth stages correspond to the Donets Basin species of *Kumpanophyllum*, *K. decessum* sp. nov. in particular. Thus, *Koninckophyllum* *elpasoensis* is here transferred to *Kumpanophyllum* as a separate species.

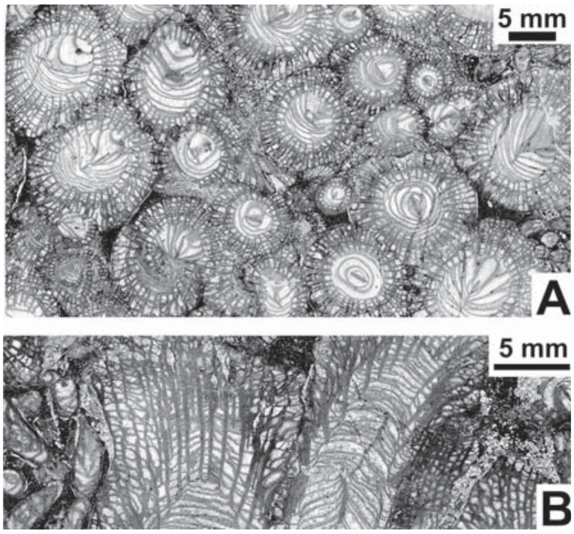
Nemistium liebanense Rodríguez, 1984 has been originally described as colonial. However, Professor Sergio Rodríguez (letter from 20th December 2017) concluded his answer to my question as follows: "the specimens are not colonial, but gregarious." Close morphological similarity of the Spanish specimens to some of the Donets Basin specimens is discussed below with remarks to *Kumpanophyllum praecox* sp. nov. and *K. columellatum* sp. nov. Both *N. liebanense* and *Nemistium* sp. of Rodríguez (1984) are here transferred to *Kumpanophyllum*.

Pseudosemenoffia from the "uppermost part of L. Carboniferous", south Shaanxi Province, China (Yu 1985, p. 92) has been introduced as a subgenus of *Semenoffia*. It has been claimed to be solitary and is characterised as follows: "Aulos developed. Cardinal fossula prominent and columella developed in early stages, but they losed [sic] in late stages." (Yu 1985, p. 92, English summary). However, a fragmentary illustration of a single specimen representing the type species *Semenoffia* (*Pseudosemenoffia*) *typica* Yu, 1985, precludes an undisputable confirmation of the characters described. For instance, the occurrence of the "prominent cardinal fossula" apparently present in the ontogenetically younger of the two transverse sections illustrated, is not documented by either dipping into the dissepimentarium or by an increased number of sections of tabulae in septal loculi next to the cardinal septum. The shortening of the cardinal septum seen in this growth stage is apparent as well. My restudy of that thin section allows the consideration that the shortening is diagenetically caused. The cardinal septum in the ontogenetically advanced growth stage is equal in length to the adjacent major septa and the cardinal fossula is absent (Yu 1985, pl. 2, figs 1a, 1c, respectively). All characters of that species follow the diagnosis of *Kumpanophyllum*. The lack of adequate confirmation of the solitary growth form of *Pseudosemenoffia* is the only reason precluding its firm synonymy with *Kumpanophyllum* and results in its inclusion with a question mark in the list of genera of the Family Kumpanophyllidae.

Kapuphyllum, based on *K. typicum* Yu and Wang, 1987, is restricted to that species represented by two incomplete specimens, illustrated by one transverse and one longitudinal section each. Those incomplete specimens, derived from the "Lower Carboniferous, Guizhou, China" (Yu and Wang 1987, p. 86), demonstrate all the features of the mature growth stage of *Kumpanophyllum* (compare Yu and Wang 1987, pl. 2, figs 6–8), confirmed by my own re-examination of the thin sections. Just as in *Pseudosemenoffia*, *Kapuphyllum* will be synonymised with *Kumpanophyllum* if/when its solitary growth form is proven. My attempt to recollect more material and to make that species better known has failed despite having an opportunity to visit the type locality of that genus. Corals collected from that section, abundant *Dibunophyllum bipartitum* McCoy, 1849 and "*Siphonodendron*" of Fedorowski (2008) among the other taxa, have confirmed the late Mississippian (either late Viséan or Serpukhovian) age of that section.

Semenoffia Yu and Wang, 1987 non Poty, 1981 is the next taxon bearing a close similarity to *Kumpanophyllum*. The solitary growth form was claimed (Yu and Wang 1987, pp. 78, 87) for two new species of those authors included by them in *Semenoffia*. One of those species, i.e., *S. kapuensis* was derived from the lower Carboniferous and the second one (*S. weiningensis*) from the *Profusulinella* Biozone (Yu and Wang 1987, pl. figs 4a, b; 5a, b). Both species are illustrated by one transverse and one longitudinal thin section each of the incomplete specimen. Both possess the columnotheca, but lack a pseudocolumella in the mature growth stage whereas their early growth stages are missing. The morphology in the transverse sections resembles both the morphology of *Kapuphyllum* and the acolumellate parts of growth of *K. decessum* sp. nov. Thus, both species of the Chinese *Semenoffia* may represent an advanced growth stage of *Kapuphyllum*. Also, both may belong to *Kumpanophyllum* as suggested here with restrictions concerning their solitary growth form and an occurrence of a pseudocolumella early in the ontogeny. Both are described as being collected from the Kapu section near Dushan City, i.e., the same as that mentioned above for *Kapuphyllum*. However, neither representatives of those species have been found nor the coral bearing deposits of the *Profusulinella* Biozone has been traced during the field investigation. The Chinese *Semenoffia* is not related to that described by Poty (1981) from Europe when the main characteristics of both are compared.

Semenoffia viseensis Poty, 1981 from the upper Warnantien (upper Viséan) of Belgium, the type species of that genus, is based on three incomplete specimens, all illustrated. Its early morphology and the microstructure of septa remain unknown. Both the description and the illustrations deal only with a fairly advanced growth stage (Poty 1981, p. 69, pl. 34, figs 1–3). Also, the phrase "…un aulos formé par l'incurvation ou la bifurcation des bords internes des septes majeurs…" does not find its indisputable documentation in the illustrations published. Inner



Text-fig. 5. *Koninckophyllum*? *nipponalpinum* (Igo and Adachi, 1981). Specimen UAM-Tc.Don.1/305. A – transverse sections of aggregated corallites, B – longitudinal section and some branches of *Syringopora* sp. (left). Central Japan, Fukui Area, Hida Massif, uppermost Viséan–?Serpukhovian (after Igo and Adachi 2000, p. 55)

margins of septa are free ended in most of the thin sections illustrated and an aulos *sensu stricto*, if present, is perhaps incomplete. However, even an incomplete aulos accompanied by the occurrence of the cardinal fossula with the cardinal septum shortened, as demonstrated by Poty (1981), makes that genus valid and eliminate it from the Kumpanophyllidae. Also, its relationship to the Chinese species bearing that name, is rejected here.

The uppermost Viséan–?Serpukhovian *Lithostrotion* (*Siphonodendron*) *nipponalpinum*, transferred by Igo and Adachi (2000, p. 53) questionably to *Koninckophyllum* Thomson and Nicholson, 1876, was originally considered colonial. However, Prof. H. Igo (letter from 21st August 2000) expressed his doubts concerning a colonial growth form of that species. All samples collected by himself and Dr. S. Adachi represent accumulations of solitary corallites. Indeed, offsetting corallites are absent from both the specimens illustrated by Igo and Adachi (1981, 2000) and from the topotype specimen, kindly offered by Prof. H. Igo for re-study (Text-fig. 5). Mature and young corallites rest next to each other within the rock and most of them are pressed into each other. The columnotheca is well developed in all corallites studied. The monoseptal pseudocolumella occurs in most corallites, although it commonly is incomplete. With all those data the Japanese species is treated here as being solitary, closely related to *Kumpanophyllum* and belonging to the Kumpanophyllidae. However, a new generic name is recommended here to be introduced by Japanese colleagues.

Protocolonial and fasciculate colonial corals have been mentioned above as potential members of the Kumpanophyllidae. *Pseudozaphrentoides nitellus* Moore and Jeffords, 1945 could serve as an example of such corals if the type specimens from the Hale Formation of SW Texas are co-specific with those of the Wapanucka Formation of Oklahoma, as suggested by Rowett and Sutherland (1964). Both collections in question were derived from lower Pennsylvanian strata, but the specimens from Texas are exclusively solitary. They expose all characters diagnostic for the Kumpanophyllidae except for the presence of the pseudocolumella (Moore and Jeffords 1945, text-figs 144–146, 153, 154). Rowett and Sutherland (1964, p. 66) commented that absence as follows: “However, the authors illustrated and described only adult stages and apparently did not examine early growth stages”. I agree with that comment. Nevertheless, the occurrence of the pseudocolumella early in the ontogeny of Moore and Jeffords’ (1945) specimens remains unknown. That disadvantage makes its inclusion in the Kumpanophyllidae tentative.

The doubts mentioned above are expanded when the Oklahoma specimens assigned by Rowett and Sutherland (1964, pp. 63–66, pl. 9, figs 1–5) to *Pseudozaphrentoides nitellus* are analysed. The transfer by those authors of *P. nitellus* to *Koninckophyllum* is not accepted here. Neither the type species nor other species truly belonging to the genus *Koninckophyllum* develop a columnotheca. Besides, specimens assigned by Rowett and Sutherland (1964) to *Koninckophyllum nitellus* not only differ from those from Texas in their morphology, but also vary in their growth form. Thus, an additional study is required in order to make their taxonomy acceptable. Rowett and Sutherland (1964, p. 63, pl. 9, figs 1–5) included in that species both the solitary corallites and the offsetting specimens. Judging from the description, some of those offsets (not illustrated) may be categorised as multiple rejuvenations, some may represent the ‘lost structures’ of Fedorowski (1978). One corallite illustrated by Rowett and Sutherland (1964, pl. 9, fig. 5) produced three generations of corallites and should be categorised as weakly colonial. However, the first created offset looks like a rejuvenation, whereas the two upper ones may have resulted from either peripheral or axial offsetting. All those doubts should be clarified in order to establish a true generic position of *K. nitellus* of Rowett and Sutherland (1964). However, the main characters of specimens assigned to that species allow its consideration as a member of the Kumpanophyllidae.

Three probably solitary taxa, represented by one to three incomplete corallites each, bear characters suggesting either their relationship to the Kumpanophyllidae or homeomorphy. *Aulina amarensis* Semenoff-Tian-Chansky, 1974 from the upper Viséan of North Africa is the first of those. It lacks the pseudocolumella at the growth stage described and illustrated. Its shortened cardinal septum is located in the deep cardinal fossula opened to and continued with the circumaxial structure composed of free inner margins of the major septa, all equal in length. Such a circumaxial structure is not an aulos, whereas an open cardinal fossula is absent from a columnotheca forming taxon. The eccentric longitudinal section (Semenoff-Tian-Chansky 1974, pl. 12, fig. 2) makes uncertain the morphology at the border skeleton of the peripheral and circumaxial part of the tabularium, crucial for the distinction of an aulos from a columnotheca (Fedorowski 2009b). The characters and doubts discussed exclude *A. amarensis* from the Kumpanophyllidae and make its true taxonomic position unknown.

Two following taxa of this group of doubtful solitary corals resemble one another in their morphology and are discussed together as being possibly related. These are: *Paraaulina zhongguoensis* Kuang in Jia *et al*., 1977 from the lower Carboniferous of the Guanxi Province, China, represented by a single incomplete corallite, and *Aulokoninckophyllum ubaghsi* Poty, 1981 from the upper Viséan (middle Warnantien) of Belgium, represented by two incomplete specimens. Both species are probably solitary although the early ontogeny is missing from all specimens illustrated by the authors cited. The pseudocolumella is absent from illustrated parts of all specimens, but both taxa possess carinate septa, the cardinal septum shortened a little, the columnotheca or the aulos indistinct, incomplete and including some additional tabellae. The hemispherical arrangement of dissepiments is the most important character suggesting their probable relationship and excluding them from all higher rank taxa that developed either an aulos or a columnotheca. The arrangement of dissepiments mentioned is typical for corals developing the so-called everted calices. That character, extremely rare in Carboniferous taxa, occurs to my knowledge only in *Sestrophyllum* Fomichev, 1953. Thus, it must be treated as taxonomically important, suggesting the separate family status of the species discussed.

Several taxa either colonial or of growth stage uncertain, but being probably colonial, should also be discussed as either potential relatives of the Kumpanophyllidae, or its homeomorphs. The most important among them in the context of the present paper are the following:

Cyathophyllum echinatum, derived from the lower *Eumorphoceras* Zone (Pendleian, Serpukhovian) of Scotland was diagnosed by Hill (1938–1941, pp. 97, 98, pls 4, figs 19–23; 5, figs 1, 2) as “phaceloid, diphymorphic *Koninckophyllum*”. She confirmed its colonial growth form and established the following characters of that species being of a special value for this discussion: the offsetting peripheral and “parricidal”, the septa weakly carinated, the cardinal septum equal to other major septa in length, the columnotheca (i.e., the aulos according to her) almost complete and the cardinal fossula being absent. Its pseudocolumella occurred as a short thin body in some corallites. Most of those characters, except for the colonial growth form and the septa carinated follow the diagnosis of the Kumpanophyllidae. The mixture of characters resulted in the dubious taxonomic position of *C. echinatum*, but its distant relationship to the colonial Kumpanophyllidae is here considered probable.

Campophyllum carinatum from the upper Viséan and/or lower Namurian of Novaya Zemlya was described by Carruthers (1909, p. 150) as solitary, represented by complete specimens. Unfortunately, that growth habit cannot be established from his illustrations firmly and cannot be checked because the collection has been lost (Smith and Yu 1943, p 53). Despite that loss, Sando (1976) selected *C. carinatum* as the type for his new genus *Aulokoninckophyllum*. That decision and the statement in the diagnosis that either solitary or pseudocolonial corals belong to that genus is unsupported by existing data. Also the assignment to *Aulokoninckophyllum* of *Aulophyllum simplex* Hill, 1934 and *Aulophyllum amarensis*, i.e., taxa with a morphology obviously different from both the type and from each other, is unfortunate. All those decisions made *Aulokonickophyllum* a conglomerate of species rather than a well established genus. It is excluded here from further discussion except for one remark: *Cyathophyllum echinatum* and *Campophyllum carinatum* are perhaps members of a common genus.

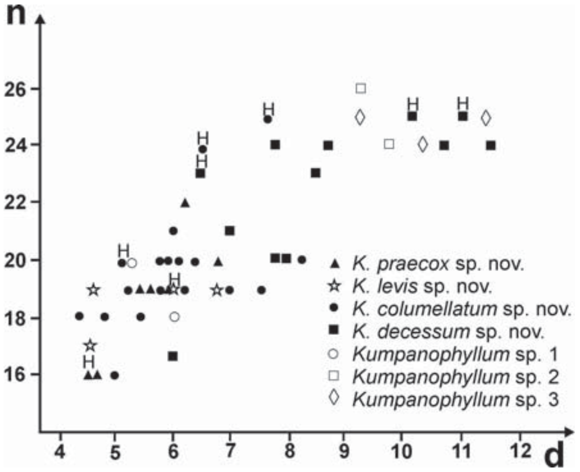
Lithostrotion ineptum from the Bashkirian strata of the Ural Mountains was illustrated by one transverse and one longitudinal thin section of a single corallite (Gorskiy 1978, p. 145, pl. 20, fig. 5, 5a) but his description leaves no doubt that his specimen is colonial. He wrote: “… a view of the colony, consisting of comparatively small number of corallites, does not correspond to the view of colonies from the *Siphonodendron* McCoy, 1849 group …” . Unfortunately, his description missed details important for establishing the offsetting mode. *Lithostrotion ineptum* bears all the most important diagnostic characters of the Kumpanophyllidae and may be related to weakly colonial species discussed here as possibly belonging to this family.

Paradiphyphyllum was introduced for lower Carboniferous (Visean?) fasciculate corals from central Jilin, China. It originally contained two species, *P. fasciculare* Wu and Lin in Lin *et al*., 1984 and *P. dendroideum* Wu and Lin in Lin *et al*., 1984, but was supplemented by Lin and Wu (1988) by *P. guangxiense* from approximately the same age of Guangxi, China. All three species were characterised as colonial (fasciculate) but an offsetting corallite was not illustrated in any of them. Despite poor illustrations and incomplete investigation the main morphological characteristics shown by Wu and Lin (in Lin *et al*. 1984, pl. 1, fig. 2a–f, pl. 3, fig. 6a–c) and Lin and Wu (1988, pl. 2, fig. 3a–e) resemble *Kumpanophyllum*. *Paradiphyphyllum* may be an older synonym of *Diphyphylloides*, but this question cannot be solved on the basis of the existing data. Both genera are questionably included in the Kumpanophyllidae, but their relationship to the Lithostrotionidae is almost equally possible.

Paranemistium typicum Yu, 1985 from the uppermost lower Carboniferous of Zhenan County, Shaanxi Province, China is perhaps a fasciculate colonial coral with many corallites grouped closely to each other in at least some parts of the colony (Yu 1985, pp. 86 and 92, pl. 1, fig. 1a–d). The occurrence of the pseudocolumella and the distinct columnotheca may point either to *Nemistium*, i.e., the Lithostrotionidae or the Kumpanophyllidae. The description and illustrations provided by Yu (1985) are inadequate for solving that question.

Diphyphylloides regularis Wu and Zhao, 1989 from the Weining Formation (Pennsylvanian) of the Panxian County, Guizhou Province, China is described as a fasciculate colony (Wu and Zhao 1989, pp. 118 and 201). However, two small fragments of specimens do not document that statement (Wu and Zhao 1989, pl. 31, fig. 3a, b; pl. 33, fig. 2a, b). The morphology of those fragments closely resembles *Kumpanophyllum*, to which *D. regularis* should be assigned if its growth form is solitary. However, *Diphyphylloides* may be a younger synonym of *Paradiphyphyllum*, as postulated above, if its growth form is truly fasciculate colonial.

A discussion on the genus *Diphyphylloides* is also offered by Igo and Igo (2004, p. 3) in the context of their new species *Nemistium japonicum* from the Serpukhovian of Japan. The radial arrangement of the major septa, all equal in length and thickness, lack of the cardinal fossula, the columnotheca with the pseudocolumella interrupted, the biform tabularium form a set of characters closely resembling *K. decessum* sp. nov. However, a different n:d value (maximum 35:20 mm against maximum 25:11 mm in *K. decessum* sp. nov.; Text-fig. 6) and the colonial growth form of *N. japonicum* are important characters distinguishing those two species. If the Japanese species is a member of the Kumpanophyllidae remains an open question. Its increase, called peripheral by Igo and Igo (2004, p. 5), should rather be called lateral as documented by their fig. 3:8, 9. That mode of increase eliminates the Japanese species from the genus *Nemistium*, which offsets axially.



Text-fig. 6. N:d values of the *Kumpanophyllum* species studied

The colonial growth form and the relationships of most genera discussed above will remain doubtful until at least two generations of offsetting specimens are illustrated and the mode of offsetting (lateral, peripheral or axial) is established. *Nemistium liebanense* discussed above well illustrates the cognitive value of such data. The question of the relationship of solitary and fasciculate colonial taxa, both bearing the main characteristics of the Kumpanophyllidae, is discussed with the Considerations below.

Genus *Kumpanophyllum* Fomichev, 1953

TYPE SPECIES: *Kumpanophyllum kokinense* Fomichev, 1953, p. 257, by original designation.

SYNONYMS:

?e.p. 1945. *Pseudozaphrentoides* Moore and Jeffords, p. 143, non Stuckenberg, 1904
1962. *Koninckophyllum* Armstrong, p. 41, non Thomson and Nicholson, 1876.
?e.p. 1964. *Koninckophyllum* Rowett and Sutherland, p. 55, non Thomson and Nicholson, 1876.
1984. *Nemistium* Rodríguez, p. 229, non Smith, 1928.
?1985. *Pseudosemenoffia* Yu, p. 86.
?1987. *Kapuphyllum* Yu and Wang, p. 78.
?1987. *Semenoffia* Yu and Wang, p. 78, non Poty, 1981.

SPECIES ASSIGNED: *Kumpanophyllum kokinense*; ?*Pseudozaphrentoides nitellus*; *Koninckophyllum elpasoense*; *Nemistium liebanense*; *Nemistium* sp. of Rodríguez (1984); ?*Pseudosemenoffia typica*; ?*Kapuphyllum typicum*; ?*Semenoffia kapuensis*; ?*Semenoffia weiningensis*; *Kumpanophyllum columellatum* sp. nov.; *K. decessum* sp. nov.; *K. praecox* sp. nov.; *K. levis* sp. nov.; *Kumpanophyllum* sp. 1; *Kumpanophyllum* sp. 2; and *Kumpanophyllum* sp. 3.

Notice: The Chinese species may be transferred to *Kumpanophyllum* when their solitary growth form is documented, whereas *Pseudozaphrentoides nitellus* may represent a new genus.

DIAGNOSIS: Solitary Kumpanophyllidae; median lamella elongated towards cardinal septum; solid, simple or incorporating septal lamellae; may be recessed in maturity; dissepiments mostly interseptal, but lonsdaleoid dissepiments commonly occur.

REMARKS: The most substantial remarks are given with the discussion of the family. Only some subjective decisions concerning this genus are briefly explained here. The inner morphology of the pseudocolumella and its permanent occurrence *vs* modifications or reduction should be discussed first since that character is commonly and correctly accepted as important up to the subfamily level (e.g., the Aulophyllidae of Hill 1981).

The pseudocolumella permanent and complex, i.e., incorporating septal lamellae must be accepted as typical for the genus since such a pseudocolumella is described by Fomichev (1953, p. 256) in *K. kokinense* (see above). A complex pseudocolumella is not established in the stratigraphically oldest specimens from the Donets Basin identified so far, i.e., those derived from Limestone D_7^3 (see under *K. praecox* sp. nov.). Also, monoseptal pseudocolumellae are documented so far in almost all specimens from Limestones Group E, up to Limestone E_8^3 inclusively (see under *K. praecox* sp. nov.). Some of those monoseptal pseudocolumellae imitate a complex morphology (see description of *K. praecox* sp. nov.). In some specimens derived from the Limestones Group E, pseudocolumellae are distinct and monoseptal, but very irregular and accompanied by long, irregular septal lamellae and axial tabellae to form an irregular and simple axial structure as seen in the transverse sections, not reflected in the longitudinal section (see under *K. levis* sp. nov.). The pseudocolumella in one specimen from Limestone D_7^3 (see under *K. decessum* sp. nov.) is recessed in the mature growth stage. Three specimens in the collection (see under *Kumpanophyllum* sp. 2) possess a kind of weak axial structure, resembling a different genus (Fedorowski and Ohar, submitted). Their position within the genus *Kumpanophyllum* is discussed below with remarks to *K. levis* sp. nov. Thus, several kinds of modifications in the morphology of pseudocolumellae are established in the Voznesenskian and up to Manuilovian horizons in the Donets Basin.

Specimens described by Rodríguez (1984) as the new species *Nemistium liebanense* and *Nemistium* sp., both from the lower Bashkirian of the Cantabrian Mountains in Spain, possess monoseptal pseudocolumellae (the former) and complex pseudocolumellae (the latter). The stratigraphic position of both Spanish species should be perhaps correlated with one of the lower Bashkirian Horizons of the Donets Basin, but data available are inadequate for a firm decision.

The thin sections of the Chinese specimens described by Yu (1985) and Yu and Wang (1987), restudied by me, possess monoseptal pseudocolumellae. The stratigraphic position of some of them may be as early as lower Serpukhovian, but this has not been re-established (see remarks on the family). The pseudocolumellae in other Chinese species included in the list of species above on the basis of the literature data, look either monoseptal or disintegrated in some, but this statement must be confirmed.

The complex pseudocolumellae present in *K. kokinense*, *K. columellatum* sp. nov. and *Nemistium* sp. of Rodríguez (1984) may be a new evolutionary achievement that appeared comparatively early in the evolution of the group of corals discussed. A subdivision on a subgenus level between bearers of the monoseptal *vs* complex pseudocolumellae may be possible when more data are accomplished.

The connection of the pseudocolumellae to the protosepta varies. Irrespective of its inner morphology, the pseudocolumella is elongated towards the cardinal septum when free. It may be connected to both protosepta for different periods of a corallite growth. It remains connected to the cardinal septum longer than to the counter septum, but can be rarely connected to the counter septum alone (see descriptions of species for details). The variability listed contradicts Fomichev's (1953, p. 256) opinion. He described the pseudocolumella as being connected to the counter septum. That recognition is correct in the case of *K. derevetschkense* but not *K. kokinense*. The pseudocolumella in the latter species is either connected to the cardinal septum or is free. The connection of the pseudocolumella to the protosepta may help in searching for an ancestor of the Kumpanophyllidae (see Considerations) whereas its variable morphology is accepted here as a criterion for the species identification within *Kumpanophyllum*.

The morphology of the dissepimentarium and its width is the next important character. The narrow dissepimentarium, consisting of one or two incomplete rows of regular, interseptal dissepiments occurs in the type species. Narrow dissepimentaria with regular interseptal dissepiments, larger at the periphery if more than one row occurs, are most common in the species described here. The lonsdaleoid dissepiments occur in most species from the Donets Basin, but they differ greatly in their number and size. Such dissepiments are most common in *K. decessum* sp. nov., and *Kumpanophyllum* sp. 2, i.e., the species with wide dissepimentarium. Unfortunately, no sequence in the development of the lonsdaleoid dissepiments can be established.

The n:d value (Text-fig. 6), a character important for the distinction among species in many rugose coral genera, may have a limited value in the case of *Kumpanophyllum* if the species identifications suggested here are correct. The alternative option, i.e., grouping of specimens in accordance to their n:d value, but irrespective of their morphology, will result in an introduction of a single species with an unacceptable variability.

The minor septa in all species studied here and described elsewhere, are well developed, commonly entering tabularia. Their variability in length by comparison to the width of the dissepimentarium and the length of the major septa varies, but it is not large and may be treated as no more than a supplementary distinguishing feature.

The characters of species of the genus *Kumpanophyllum* described in the present paper are compiled in Table 1.

Kumpanophyllum praecox sp. nov.
(Text-fig. 7)

HOLOTYPE: UAM-Tc.Don.1/249.

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

TYPE LOCALITY: Fenine village, Donets Basin, Ukraine.

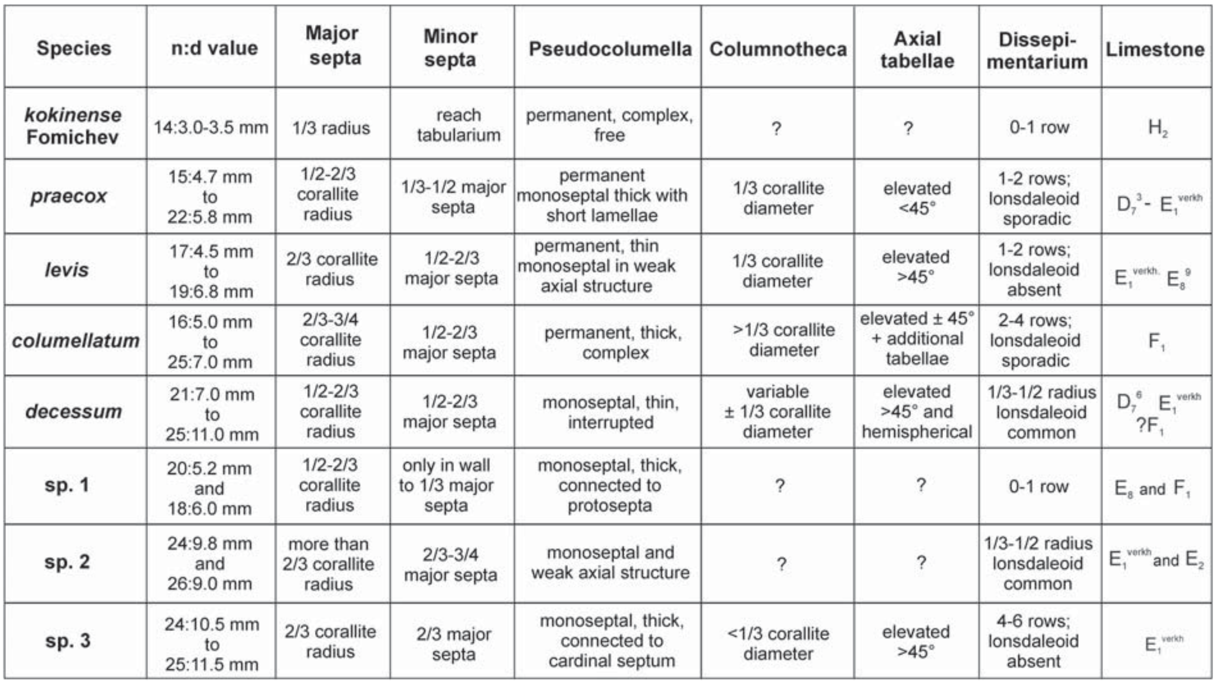
ETYMOLOGY: *Lat. praecox* – early, after an early appearance in the stratigraphic column.

MATERIAL: Holotype UAM-Tc.Don.1/249 and seven paratypes UAM-Tc.Don.1/250–256. All specimens incomplete, some slightly compressed. Brephic and early neanic growth stage missing from all specimens. In two corallites, neanic growth stage preserved. Microstructure of septa in all specimens destroyed by diagenesis. Six thin sections and 18 peels available for study.

DIAGNOSIS: Kumpanophyllidae with mean n:d value in holotype 15:4.7 mm; major septa approximately 2/3 corallite radius in length; pseudocolumella monoseptal, commonly thin, may be met by rare, short septal lamellae; dissepimentarium of one to two rows of rectangular dissepiments; lonsdaleoid dissepiments very rare; tabularium in some septal loculi weakly biform.

DESCRIPTION: Corallites conical when immature (Text-fig. 7N), conic-cylindrical in maturity. Their surfaces almost smooth with delicate growth striae in irregular bands. In neanic growth stage major septa bilaterally arranged; in holotype short; in paratype longer; terminated at sections of axial tabellae of columnotheca. Last pairs of major septa inserted in cardinal quadrants strongly underdeveloped (Text-fig. 7A, G). Axial septum in holotype straight and thin along with three short septal lamellae attached to is middle part. In paratype, counter septum part of axial septum thick (Text-fig. 7A). In late neanic/early mature growth stage of paratype (Text-fig. 7B, upper corallite), major septa remain long, pseudocolumella thick, free. First dissepiments probably appear at this growth stage, but better documented in slightly more advanced growth stage (Text-fig. 7C, upper corallite).

N:d values of paratypes documented in Text-fig. 5. In mature growth stage (Text-fig. 7B, C [lower corallite in both images], F, H, I, L), major septa terminate at sections of axial tabellae. In holotype most of major septa slightly thinner in dissepimentarium; in paratypes either equal in thickness along, or they thicken next to external wall (Text-fig. 7B, C). In holotype both protosepta meet pseudocolu-



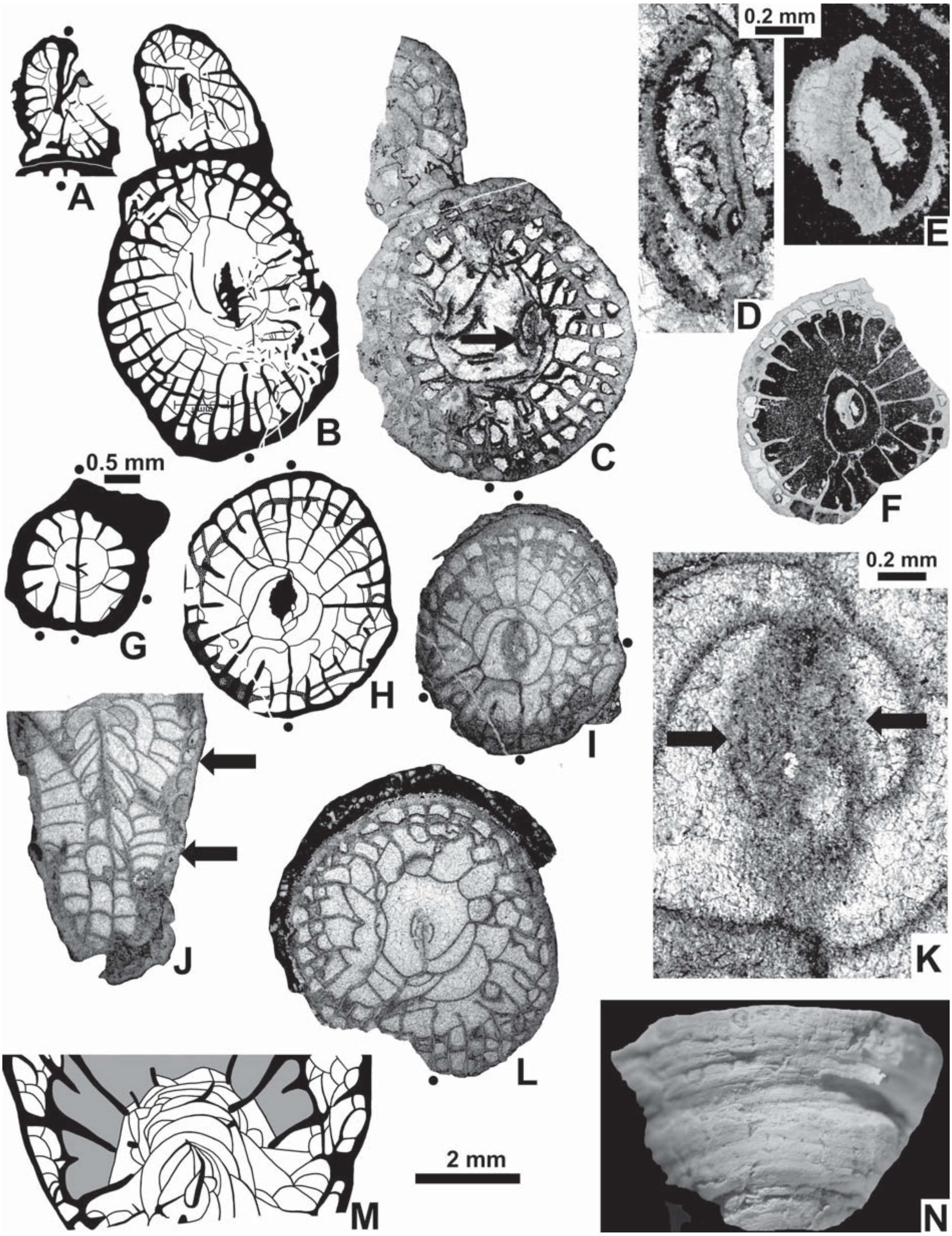
Species	n:d value	Major septa	Minor septa	Pseudocolumella	Columnotheca	Axial tabellae	Dissepi-mentarium	Limestone
***kokinense* Fomichev**	14:3.0-3.5 mm	1/3 radius	reach tabularium	permanent, complex, free	?	?	0-1 row	H_2
praecox	15:4.7 mm to 22:5.8 mm	1/2-2/3 corallite radius	1/3-1/2 major septa	permanent monoseptal thick with short lamellae	1/3 corallite diameter	elevated <45°	1-2 rows; lonsdaleoid sporadic	D_7^3- E_1^{verkh}
levis	17:4.5 mm to 19:6.8 mm	2/3 corallite radius	1/2-2/3 major septa	permanent, thin monoseptal in weak axial structure	1/3 corallite diameter	elevated >45°	1-2 rows; lonsdaleoid absent	$E_1^{verkh.}$ E_8^9
columellatum	16:5.0 mm to 25:7.0 mm	2/3-3/4 corallite radius	1/2-2/3 major septa	permanent, thick, complex	>1/3 corallite diameter	elevated ± 45° + additional tabellae	2-4 rows; lonsdaleoid sporadic	F_1
decessum	21:7.0 mm to 25:11.0 mm	1/2-2/3 corallite radius	1/2-2/3 major septa	monoseptal, thin, interrupted	variable ± 1/3 corallite diameter	elevated >45° and hemispherical	1/3-1/2 radius lonsdaleoid common	D_7^6 E_1^{verkh} ?F_1
sp. 1	20:5.2 mm and 18:6.0 mm	1/2-2/3 corallite radius	only in wall to 1/3 major septa	monoseptal, thick, connected to protosepta	?	?	0-1 row	E_8 and F_1
sp. 2	24:9.8 mm and 26:9.0 mm	more than 2/3 corallite radius	2/3-3/4 major septa	monoseptal and weak axial structure	?	?	1/3-1/2 radius lonsdaleoid common	E_1^{verkh} and E_2
sp. 3	24:10.5 mm to 25:11.5 mm	2/3 corallite radius	2/3 major septa	monoseptal, thick, connected to cardinal septum	<1/3 corallite diameter	elevated >45°	4-6 rows; lonsdaleoid absent	E_1^{verkh}

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

mella, whereas in paratypes they are equal to other major septa in length and thickness. Minor septa approximately 1/2 length of major septa, enter tabularium. Pseudocolumella monoseptal, moderately thickened. Its strong thickening and wavy outline in holotype apparent, resulting from attachment of innermost parts of thickened axial tabellae (Text-fig. 7K, arrowed). Short septal lamellae may temporarily attach pseudocolumella (Fig. 7B, C [lower corallite], D, G). Dissepimentarium 1/5–1/6 corallite radius in width. Dissepiments interseptal, rectangular or slightly irregular, in single row, or two rows in parts of transverse sections or around corallite. Inner wall slightly thickened. Rare lonsdaleoid dissepiments present in holotype (Text-fig. 7H, I, lower right) and in some paratypes. Tabularium in longitudinal section of holotype (Text-fig. 7J) tripartite with columnotheca clearly separated from peripheral tabularium. Tabellae in columnotheca steeply elevated to meet pseudocolumella. Peripheral tabellae almost horizontal to slightly elevated. Their possible biformity demonstrated by slightly different position in lower and upper right side of picture (Text-fig. 7J, arrowed) and confirmed in transverse sections by unequal number of sections of peripheral tabellae at left and right side of minor septa in some septal loculi (Text-fig. 7B, C, H, I, L). Oblique section of one paratype (Text-fig. 7M) confirms both occurrence of columnotheca with axial tabellae elevated towards pseudocolumella (lower middle part of picture) and elevation of columnotheca above calice floor (white and gray respectively in upper part of picture).

REMARKS: Differences of the holotype from all paratypes in the length of the protosepta, in the occurrence of lonsdaleoid dissepiments and in its smaller diameter and number of septa may suggest its separate species position. However, a close similarity in all remaining characters of all specimens and my reluctance to create new taxa based on inadequately documented characters preclude a species diversification of the specimens.

Nemistium liebanense (Text-fig. 8A–C) is morphologically similar to *K. praecox* sp. nov. in possessing a monoseptal pseudocolumella, accompanied by short septal lamellae in some corallites (Text-fig. 8B, corallites a and c) and in major septa equal in length, terminating at sections of axial tabellae. Also, its stratigraphic position and solitary growth form is similar as specified by Prof. Sergio Rodríguez in his letter cited above. *Kumpanophyllum liebanense* differs from *K. praecox* sp. nov. in the morphology and width of the dissepimentarium comprising 2–4 rows of dissepiments, several of which are irregular and some pseudo-herringbone. *Kapuphyllum typicum* Yu and Wang, 1987 resem-



Text-fig. 7. *Kumpanophyllum praecox* sp. nov. Transverse sections, except when stated otherwise. A-D – Specimen UAM-Tc.Don.1/256. Paratype. A – neanic growth stage, B – neanic growth stage attached to mature corallite (A, B – peels with drawings), C – fragment of neanic growth stage attached to mature corallite with pseudocolumella (arrowed) pushed aside by pressure (thin section), D – solitary pseudocolumella with two septal lamellae attached (enlarged from C). E, F – Specimen UAM-Tc.Don.1/255. Paratype. E – solitary pseudocolumella →

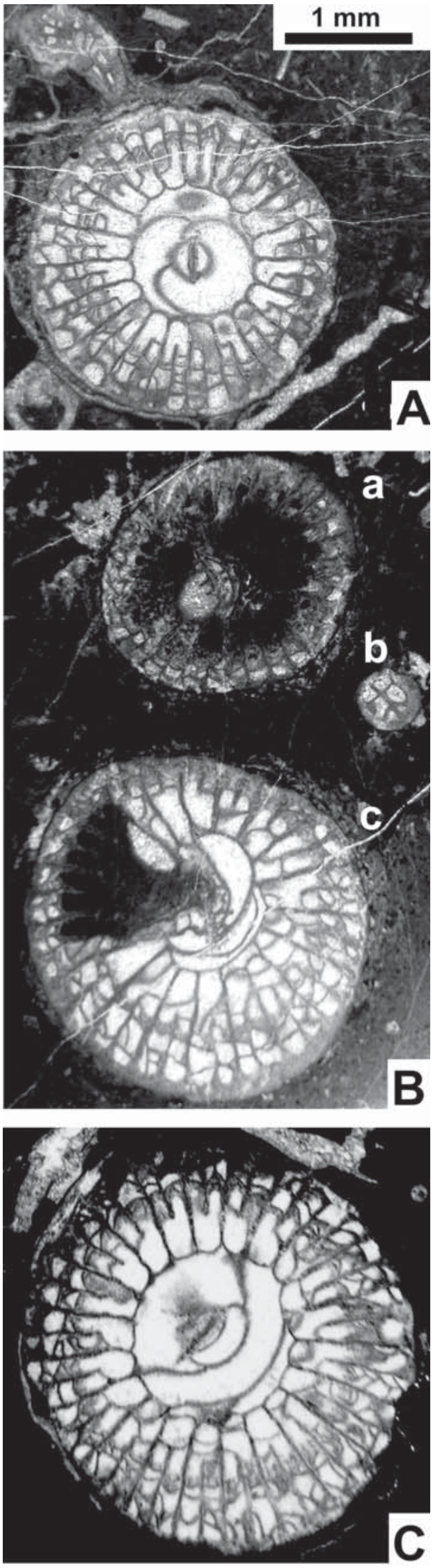
bles *K. praecox* sp. nov. in having a thin and most probably monoseptal, continuous pseudocolumella and in the tabellae within the columnotheca elevated comparatively steeply. It differs in larger n:d value and wider dissepimentarium, but those differences are rather small. Unfortunately, the existing data are inadequate for suggesting their co-specificity. The differences of *K. praecox* sp. nov. from *K. levis* sp. nov. and *K. columellatum* sp. nov., other similar taxa, are discussed with the latter species.

OCCURRENCE: Holotype UAM-Tc.Don.1/249 and Paratypes UAM-Tc.Don.1/250–253: Kalmius River Area. Fenine Village. Limestone E_1^{vyzh}. Lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus* conodont Biozone. Upper lower Bashkirian. Paratypes UAM-Tc.Don.1/254–256: Voznesenka Village, Limestone D_7^3, lower Voznesenskian Horizon, *Homoceras–Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lower Bashkirian.

Kumpanophyllum levis sp. nov.
(Text-fig. 9)

HOLOTYPE: UAM-Tc.Don.1/257.

TYPE STRATUM: Limestone E_9^1, Manuilovian Horizon, lower middle Bashkirian.



Text-fig. 8. *Kumpanophyllum liebanense* (Rodríguez, 1984). Transverse thin sections of five corallites. A, C – mature growth stage, B, corallite **a** – calice of probably early mature corallite, B, corallite **b** – brephic, six-septal growth stage of a corallite that belongs perhaps to *K. liebanense*, B, corallite **c** – mature growth stage, destroyed in part. All pictures provided with the courtesy of Prof. Sergio Rodríguez. Originally assigned to the upper Serpukhovian (Rodríguez 1984, p. 229), stratigraphic position corrected to lower Bashkirian by Prof. Sergio Rodríguez (in letter from 2018). Scale bar at upper right of A corresponds to all figures

→

(enlarged from F), F – lower part of calice (thin section). G-K – Specimen UAM-Tc.Don.1/249. Holotype. G – neanic growth stage, H, I – mature growth stage, J – slightly oblique longitudinal thin section; Positions I and II of Sutherland (1965) arrowed, K – solitary pseudocolumella with sections of tabellae closely attached (arrowed; enlarged from I) (G, H peels with drawings, I-K thin sections). L, M – Specimen UAM-Tc.Don.1/250. Paratype. L – mature growth stage overgrown by bryozoan colony (thin section), M – oblique section close to and through lower part of calice (drawing on peel image), N – Specimen UAM-Tc.Don.1/254. Side view. For stratigraphic position see text. Protosepta marked by black dots when recognisable. Scale bar between M and N corresponds to all images except for those marked separately.

TYPE LOCALITY: Krynka River Area, Amvrosiivka Village, Ukraine.

ETYMOLOGY: *Lat. levis, e* – insignificant, variable, after the morphology of the axial structure

MATERIAL: Four specimens. Holotype UAM-Tc. Don.1/257 almost complete with only calice lacking. Microstructure diagenetically destroyed. Three paratypes incomplete. Paratype UAM-Tc.Don.1/258 is a small fragment embedded in rock. Paratype UAM-Tc. Don.1/259 shows a mature growth stage and lower part of calice. Paratype UAM-Tc.Don.1/260 shows lower part of calice. Seven transverse thin sections, two longitudinal and five transverse peels available for study.

DIAGNOSIS: *Kumpanophyllum* with neanic growth stage rotiphylloid; n:d value 17–19:4.5–6.0 mm; major septa thin, approximately 1/2 corallite radius in length; minor septa enter tabularium, approximately 1/2 major septa in length; weak axial structure comprises irregular, monoseptal median lamella, 1–3 septal lamellae and some axial tabellae; columnotheca more than 1/3 corallite diameter in width; dissepiments interseptal, mostly regular.

DESCRIPTION: Corallite surface almost smooth, with delicate growth striae arranged in bunches. Septal ribbing hardly distinguishable. Talon very strong (Text-fig. 9N). Neanic growth stage with n:d value 12:1.5×1.0 mm when elongated towards talon and 12:1.6 mm immediately above talon. Arrangement of major septa in that growth stage rotiphylloid (Text-fig. 9G, H) with axial septum curved in its axial part, making it asymmetrical. Number of major septa in left and right quadrants equal: two in each cardinal quadrant and three in each counter quadrant. Minor septa not recognised. In mature growth stage (Text-fig. 9A, B, I, J), major septa radially arranged, in tabularium of holotype and one paratype equal in length, slightly thickened, approximately 1/2 corallite radius in length, terminated at lateral sections of axial tabellae. In lower part of calice of paratype UAM-Tc. Don.1/260 (Text-fig. 9F) major septa differentiated in length. Most of them less than 1/2 corallite radius in length, but some elongated so as to meet tabellae of axial structure. Minor septa in all corallites enter tabularium, approximately 1/2 length of major septa; their inner margins thin. Weak axial structure observed only in transverse sections (Text-fig. 9C–E, K) comprises median lamella free from protosepta, 1–2 slightly thickened, comparatively long, irregularly curved septal lamellae, rare short septal lamellae and sections of axial tabellae. It elevates above peripheral parts of calice (Text-fig. 9B, E, F). Dissepimentarium 1/4–1/6 corallite radius in width. Dissepiments interseptal, most regular, in 1–3 rows within given transverse section. In longitudinal section (Text-fig. 9L, M) columnotheca continuous, occupies slightly more than 1/3 corallite diameter. Axial tabellae at periphery curved down to rest on underlying tabellae, in remaining part elevated gently towards median lamella, may bear rare, short additional tabellae. Peripheral tabellae shorter than axial tabellae, flat, elevated towards columnotheca at an angle approximately equal to elevation of axial tabellae. A part of the holotype damaged at the polyp's life time (Text-fig. 9I, J, L, M, right), but its major part continued to grow.

REMARKS: The transverse sections of *K. levis* sp. nov. resemble those of a new genus established by Fedorowski and Ohar (submitted) in possessing a weak and irregular axial structure. However, that structure did not appear as a result of disintegration of a complex pseudocolumella as in that new genus, but is formed by loose septal lamellae, only joining the median lamella. Its thick immature pseudocolumella is monoseptal. Also, its morphology in the longitudinal section is typical for the genus *Kumpanophyllum*.

Kumpanophyllum levis sp. nov. shows the closest morphological and dimensional similarity to *K. praecox* sp. nov., but differs from the latter in the morphology of the median lamella, development of weak axial structure, wider columnotheca with axial tabellae elevated less steeply and by lack of determinable biformity of its tabularium. Its difference from remaining species of *Kumpanophyllum* is discussed under those species.

OCCURRENCE: Holotype UAM-Tc.Don.1/257 and paratype UAM-Tc.Don.1/258: Krynka River Area. Amvrosiivka Village, Limestone E_8^9. Manuilovian Horizon, lower *Bilinguites–Cancelloceras* ammonite Biozone, upper *Pseudostaffella antiqua* foraminiferal Biozone, upper *Neognathodus askynensis* conodont Biozone. Lower middle Bashkirian. Paratypes

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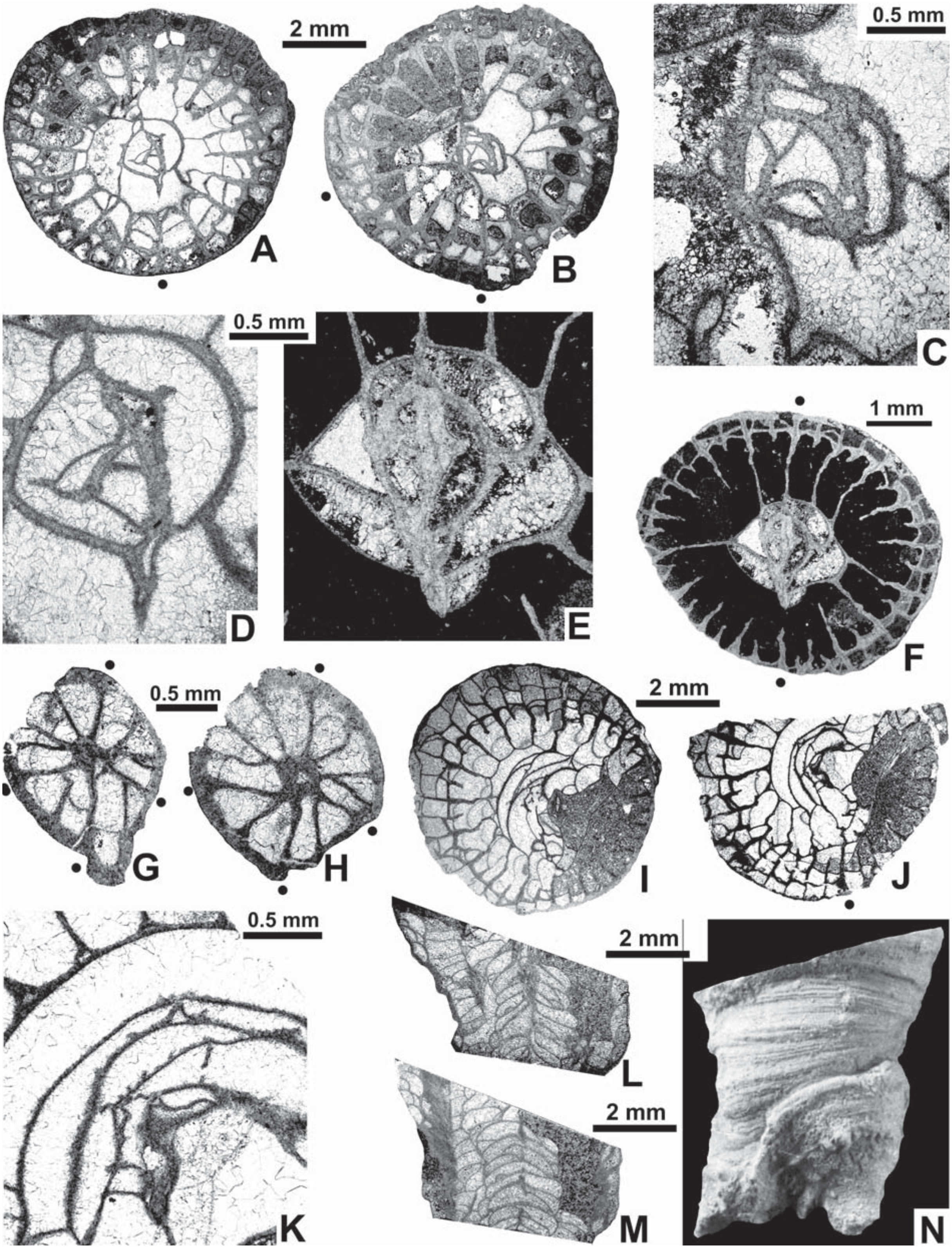
Text-fig. 9. *Kumpanophyllum levis* sp. nov. Transverse thin sections except when stated otherwise. A-D – Specimen UAM-Tc.Don.1/260. Paratype. A, B – mature growth stage; B – above calice floor in part (grey in image); C, D – axial structure (enlarged from B and A respectively). E, F – Specimen UAM-Tc.Don.1/259. Paratype. E – axial structure (enlarged from F), F – mature growth stage above calice floor in most part. G-N – Specimen UAM-Tc.Don.1/257. Holotype. G, H – neanic growth stage, I, J – mature growth stage partly damaged at life time →



as suggested by rejuvenation (J, lower), K – axial structure (enlarged from J), L, M – longitudinal sections made approximately 0.7 mm apart; L – centric, M – slightly eccentric (peels), N – side view. Protosepta and alar septa marked by black dots when recognisable. For stratigraphic position see text. Scale bars between two images correspond to both, scale bar corresponding to a given image located in its upper right or left

UAM-Tc.Don.1/259, 260: Kalmius River Area. Fenine Village, Limestone $E_1^{vyzh.}$, lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus* conodont Biozone. Upper lower Bashkirian.

Kumpanophyllum columellatum sp. nov.
(Text-figs 10, 11)

HOLOTYPE: UAM-Tc.Don.1/261.

TYPE STRATUM: Limestone F_1, Blagodatnian Horizon, upper middle Bashkirian.

TYPE LOCALITY: Solona River bank, Novotroitske Village, Ukraine.

ETYMOLOGY: *lat. columna* – column, after development of permanent pseudocolumella.

MATERIAL: Holotype UAM-Tc.Don.1/261 with both early growth stage and calice preserved and 22 paratypes mostly incomplete, diagenetically altered, UAM-Tc.Don.1/262–283. Measurements shown in Text-fig. 6. 17 thin sections and 20 peels available for study.

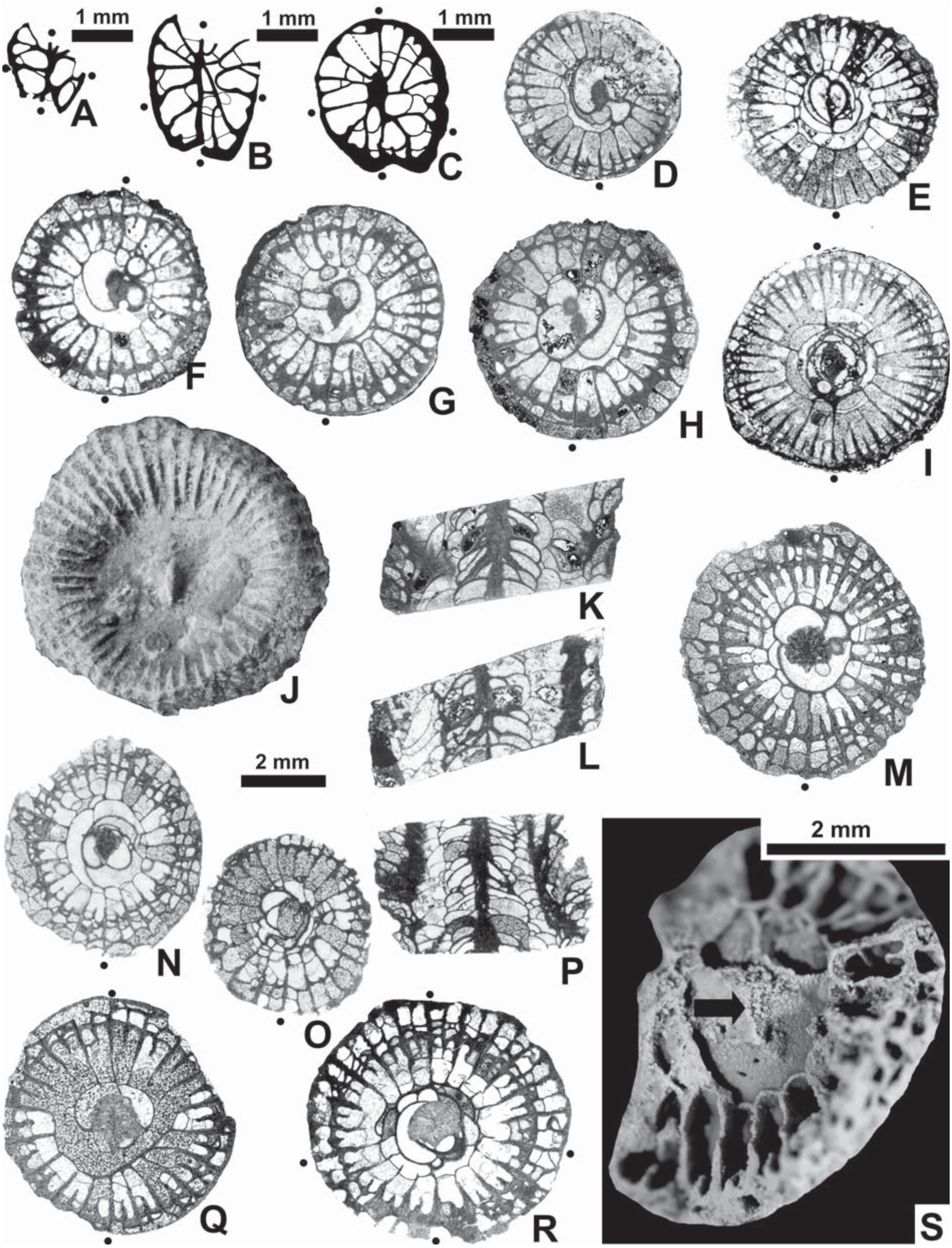
DIAGNOSIS: *Kumpanophyllum* with most common n:d value 19–20:5–6 mm, maximum in holotype 25:7.0 mm beneath calice and 26:9.5 mm at calice margin; median lamella continuous, complex, thick, with septal lamellae incorporated; minor septa 1/2–2/3 of major septa in length, enter tabularium deeply; columnotheca occupies less than 1/3 corallite diameter; dissepimentarium 1/4–1/3 corallite radius width; dissepiments mostly regular, interseptal; small lonsdaleoid dissepiments may rarely appear at periphery.

DESCRIPTION OF HOLOTYPE: Calice (Text-fig. 10J) with peripheral part almost flat and inner part steeply down-sloping. Hemispherical upper margin seen in part of calice apparent, resulted from corrosion. All septa radially arranged. Slight waviness of their margins may reflect remnants of trabeculae. Minor septa in upper part of calice almost as long as major septa. Cardinal fossula absent. Pseudocolumella extends up to 2/3 of calice depth.

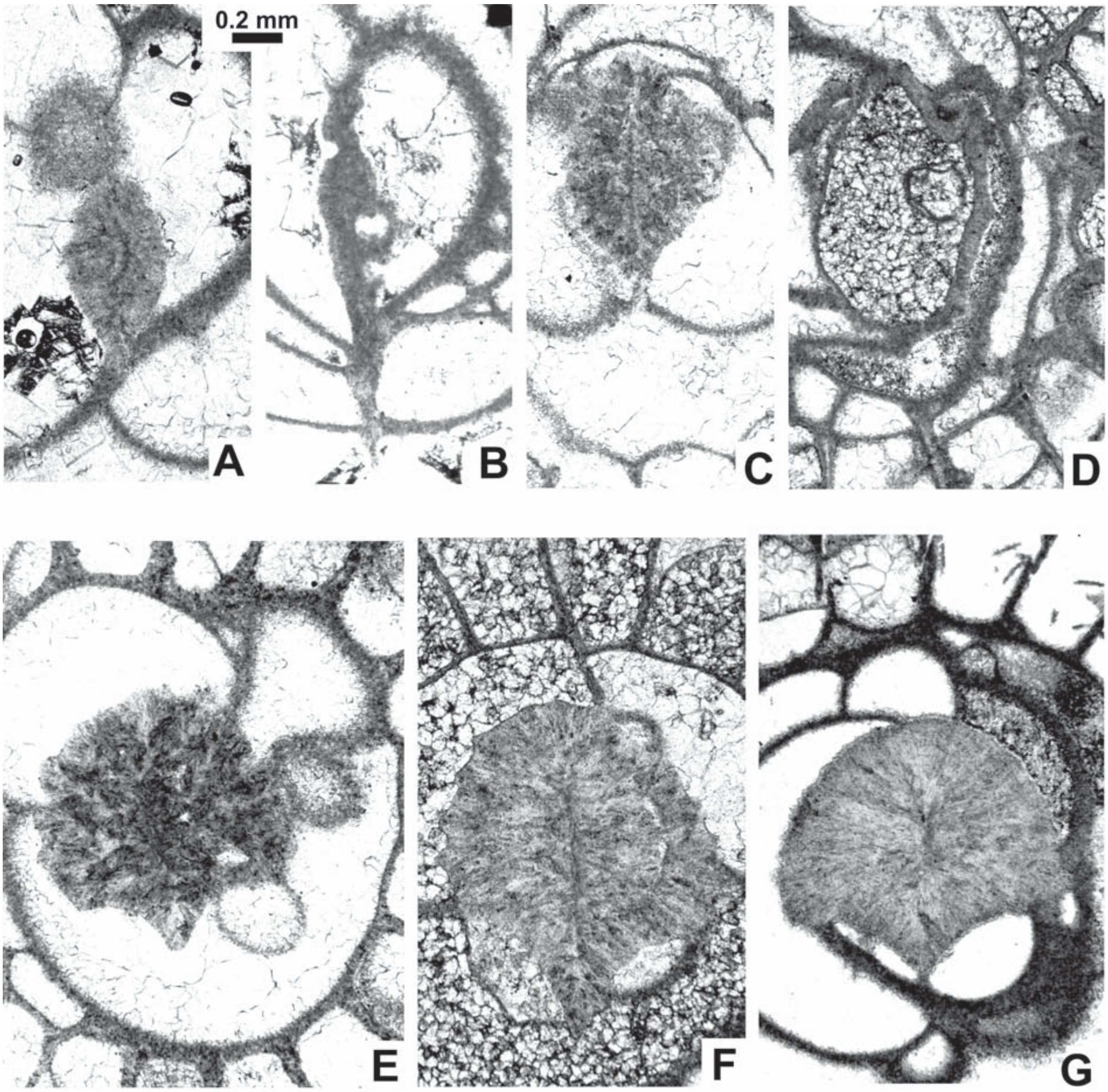
Brephic growth stage missing. Elongation of corallite in early neanic growth stage resulted from attachment to substrate (Text-fig. 10A, B). Major septa bilaterally arranged with axial septum as symmetry axis. Most major septa attached to axial septum. Cardinal fossula absent. Minor septa not yet appearing in corallite lumen. In late neanic growth stage, sectioned immediately above attachment scar (Text-fig. 10C), arrangement of major septa resembles rotiphylloid due to underdevelopment of last septa inserted in individual quadrants, but bilateral symmetry in their arrangement continued. Axial part of axial septum strongly thickened. First minor septa appear in some septal loculi, but dissepiments not yet developed.

Morphology of early to advanced mature growth stage similar (Text-fig. 10D–I) except for thickness of pseudocolumella (Text-figs 10E *vs* Text-figs 10D, F–I; 11A, B). Major septa amplexoid, beneath tabulae equal in length, reaching border of columnotheca; some slightly, other distinctly, elongated near and along upper surfaces of inner tabellae; longest of them almost reach corallite axis as demonstrated by short septal crests attached to sections of inner tabellae (Text-fig. 10E, I). Protosepta indistinguishable by length and/or thickness except for short time of growth when elongated so as to approach pseudocolumella. (Text-fig. 10I). Minor septa non-amplexoid, enter tabularium to reach 1/2 length of major septa beneath tabulae and slightly less when major septa elongated along tabulae surfaces. Cardinal fossula absent. Median lamella derived from axial septum, but incorporates a few septal lamellae soon after its isolation from protosepta and forms complex pseudocolumella (Text-fig. 11A). It resembles a wheat grain shape during most part of corallite growth (Text-fig. 10D, F–I). Temporary thinning of pseudocolumella (Text-figs 10E, K, L; 11B) perhaps environmentally caused. Septal lamellae in such thin pseudocolumella free in their outer parts (Text-fig. 11B). Dissepimentarium approximately 1/5 corallite radius in width varies slightly both during corallite growth and within given transverse section; consists of one to four rows of interseptal dissepiments within a given transverse section. Near calice and in calice widest. Peripheral dissepiments largest.

Text-fig. 10. *Kumpanophyllum columellatum* sp. nov. Transverse thin sections except when stated otherwise. A-L – Specimen UAM-Tc. Don.1/261. Holotype. A-C – early to late neanic growth stage (drawings), D – early mature growth stage, E-I – mature growth stage (C, D, F, G, I peels), J – calice, K, L – longitudinal sections; K – centric, L – slightly eccentric (peel). M – Specimen UAM-Tc.Don.1/265. Paratype. Mature growth stage. N-P – Specimen UAM-Tc.Don.1/264. Paratype. N, O – advanced (N) and early (O) mature growth stage, P – centric longitudinal section. Q – Specimen UAM-Tc.Don.1/273. Paratype. Mature growth stage. R – Specimen UAM-Tc.Don.1/266. Paratype. Mature →



growth stage. S – Specimen UAM-Tc.Don.1/272. Paratype. Broken and weathered corallite documenting relationships of major septa, pseudocolumella (arrowed) and tabulae. Protosepta and alar septa marked by black dots when recognisable. For stratigraphic position see text. Scale bars corresponding to given images located in their upper right. Scale bar below J corresponds to all remaining images



Text-fig. 11. *Kumpanophyllum columellatum* sp. nov. Transverse thin sections of pseudocolumellae. A, B – Specimen UAM-Tc.Don.1/261. Holotype. C, D – Specimen UAM-Tc.Don.1/264. Paratype. D – inner part of pseudocolumella damaged by dolomite replacement. E – Specimen UAM-Tc.Don.1/265. Paratype. F – Specimen UAM-Tc.Don.1/273. Paratype. G – Specimen UAM-Tc.Don.1/266. Paratype. For images of complete specimens see Text-fig. 10. For stratigraphic positions see text. Scale bar between A and B corresponds to all images

Inner row thickened to various extent to form inner wall. Rare lonsdaleoid dissepiments incidentally interrupt minor septa (Text-fig. 10E, H lower).

Longitudinal sections clearly tripartite. Columnotheca bordered by down-curved, convex parts of long axial tabellae. Inner parts of axial tabellae slightly convex, elevated at low angle towards pseudocolumella, supplemented by rare, bubble-like additional tabellae. Biform morphology of peripheral tabularium weakly accentuated, best seen in left and right side of slightly eccentric longitudinal section (Text-fig. 10L). Long, slightly concave or convex peripheral tabellae, elevated towards columnotheca at left side of picture correspond to Position II of Sutherland (1965), whereas shorter, commonly convex, horizontal or slightly down slopping tabellae at right side of picture corresponds to Position I. Dissepimentarium of 2–3 rows of bubble-like dissepiments, differentiated in shape.

INTRASPECIFIC VARIABILITY: General morphology of paratypes in both transverse (Text-fig. 10M–O, Q, R) and longitudinal sections (Text-fig. 10P) strikingly similar to holotype and to each other making detailed description unnecessary. Only two characters, i.e., much larger number of septa in holotype at its diameter corresponding to largest paratypes and variability in morphology and shape of pseudocolumella (Text-fig. 11C–G) should be elevated. The different n:d value (Text-fig. 5) apparently contests the co-specific position of holotype and specimens considered as paratypes. Close morphological similarity documented above by numerous images (Text-fig. 10M–S) allows the rejection of that option.

The differentiation of pseudocolumellae requires some discussion. All of them are complex, i.e., they incorporate septal lamellae during their mature growth and all point towards the cardinal septum by their elongated and thinning margins (Text-fig. 11A–G). That elongation resulted in a fan-shape of the pseudocolumella when strongly thickened (Text-fig. 11E–G). All pseudocolumellae, including the holotype, underwent diagenetic alterations, but advancement of that process differs. Inner morphology recognisable in most specimens (Text-fig. 11A–C, E, F). Some pseudocolumellae apparently monoseptal (Text-fig. 11D, G). In one corallite, pseudocolumella in part of its growth only slightly recrystallised, whereas coarse dolomite crystals replace calcite in inner part of pseudocolumella in its adjacent part. Frame of that part of pseudocolumella remains calcitic (Text-fig. 11C and D respectively). In some instances, recrystallisation may lead to apparent absence of median lamella, recrystallised together with septal lamellae to form centripetally arranged fan of secondary calcite fibres (Text-fig. 11G).

REMARKS: The holotype and the paratypes of *K. columellatum* sp. nov. resemble the type species of the genus in possessing a complex pseudocolumella, but differ from it in their larger diameters and number of septa, wider dissepimentarium and the minor septa much longer, deeply entering the tabularium. *Nemistium liebanense* differs from *K. columellatum* sp. nov. in the n:d value (18–20:6–7 mm), in possessing a monoseptal and interrupted pseudocolumella. *Nemistium* sp. of Rodríguez (1984, text-fig. 98, pl. 7, figs 5, 6) resembles *K. columellatum* sp. nov. in the complex pseudocolumella, the minor septa penetrating the tabularium deeply and in the morphology and width of the dissepimentarium. The probably interrupted pseudocolumella forms the only important difference between those two taxa. *Nemistium* sp. of Rodríguez (1984) may appear conspecific with *K. columellatum* sp. nov. when/if the interruption of its pseudocolumella appears apparent, resulting from the eccentric longitudinal section illustrated.

Small specimens of *K. columellatum* sp. nov. display the n:d value similar to *K. levis* sp. nov. and *K. praecox* sp. nov. (Text-fig. 6) but they differ from both species mentioned in possessing a strong, solid and complex pseudocolumella. Slightly longer major and minor septa and the tabellae in the columnotheca less strongly elevated towards the pseudocolumella are additional features distinguishing *K. columellatum* sp. nov. from those two species.

OCCURRENCE: Holotype UAM-Tc.Don.1/261 and paratypes (UAM-Tc.Don.1/262-283): Solona River Area. 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.

Kumpanophyllum decessum sp. nov.
(Text-figs 12, 13)

HOLOTYPE: UAM-Tc.Don.1/284.

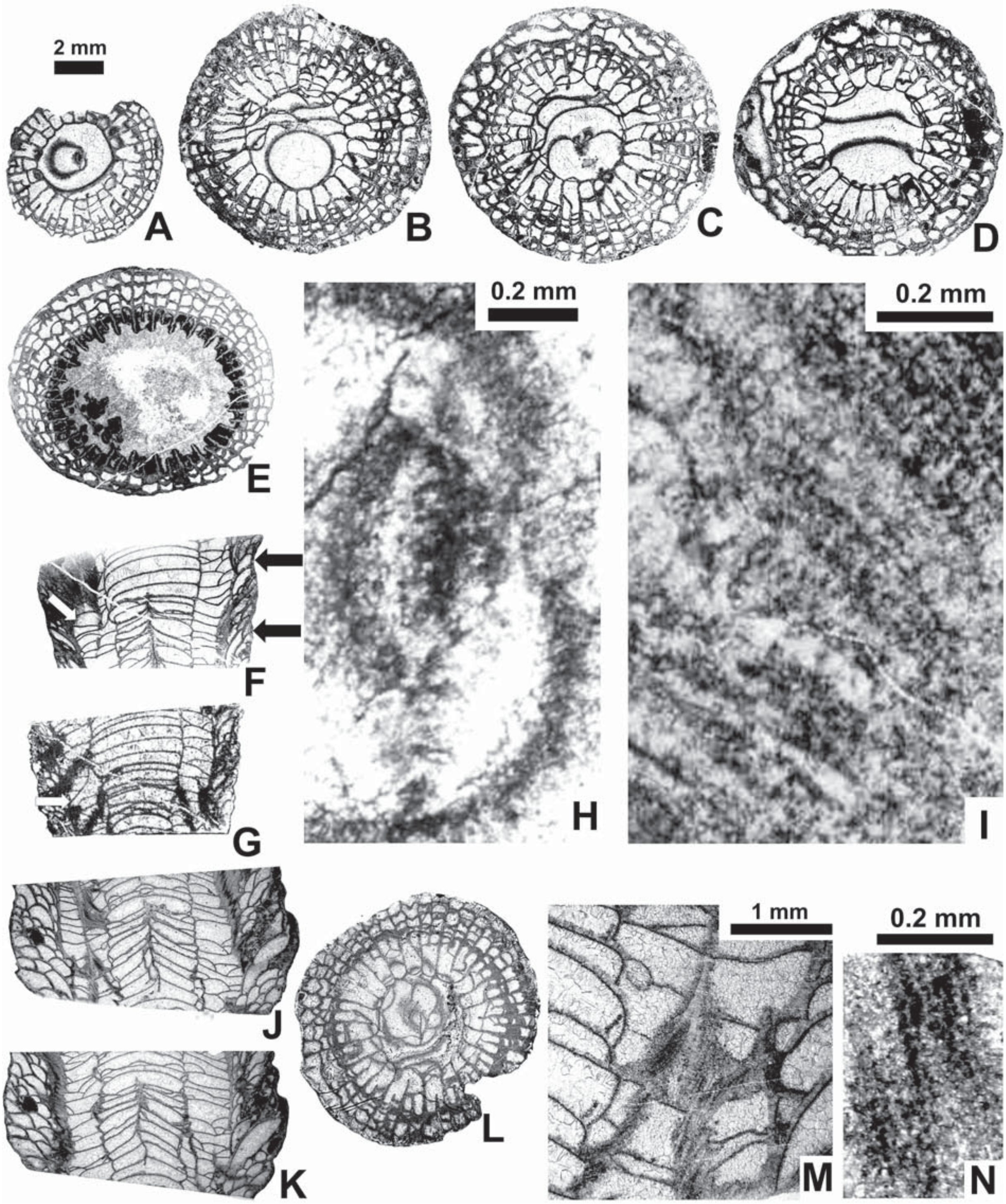
TYPE LOCALITY: Krynka River Area, Amvrosiivskyi Kupol, Velyka Shyshivka Ravine (Balka), Ukraine.

TYPE HORIZON: Limestone E_1^{vyzh}. Feninian Horizon, upper lower Bashkirian.

ETYMOLOGY: *Lat. decessio*, *onis* – diminution, after temporary or permanent atrophy of pseudocolumella in advanced maturity.

MATERIAL: Holotype UAM-Tc.Don.1/284 and twelve specimens; most incomplete; two with early ontogeny and one with part of calice preserved. Paratypes:UAM-Tc.Don.1/285–295a, b (2 specimens in one thin section). 16 thin sections and 29 peels available for study.

DIAGNOSIS: *Kumpanophyllum* with 22–26×2 septa at 6.5–11.5 mm corallite diameter; most commonly 24–26:8–11 mm; pseudocolumella indistinct, monoseptal, interrupted, commonly disappear at advanced mature growth stage; minor septa 1/2–2/3 of major septa in length, enter tabularium; dissepimentarium 1/3–1/2 corallite radius in width; dissepiments



Text-fig. 12. *Kumpanophyllum decessum* sp. nov. Transverse thin sections except when stated otherwise. A-I – Specimen UAM-Tc.Don.1/284. Holotype. A – early mature growth stage, B-D – mature growth stage, E – lower part of calice, F, G – longitudinal sections; F – centric; different positions of peripheral tabellae pointed by arrows, G – slightly eccentric (peel), H – pseudocolumella and axial tabellae (enlarged from A), I – rudiments of very fine trabeculae in longitudinal section (enlarged from F). J-N – Specimen UAM-Tc.Don.1/286. Paratype. J, K – longitudinal thin sections at distance of approximately 1 mm apart; J – centric, K – slightly eccentric, L – mature growth stage, transverse section (peel), M – longitudinal thin section. Biform tabularium (lower right) and relationship of peripheral parts of tabellae in columnotheca (left), N – rudiments of very fine trabeculae in longitudinal section (enlarged from J). For stratigraphic position see text. Scale bars corresponding to given images located in their upper right. Scale bar above A corresponds to all other images mostly interseptal, regular; lonsdaleoid dissepiments common at periphery.

DESCRIPTION OF HOLOTYPE: Neanic growth stage lacking. In early mature growth stage (Text-fig. 12A) with n:d value 23:6.5 mm, major septa radially arranged, thin, equal in length, approximately 2/3 corallite radius in length, terminated at sections of tabellae of columnotheca. Protosepta indistinguishable. Cardinal fossula absent. Pseudocolumella thin and short (Text-fig. 12A, H). Minor septa thin, barely enter tabularium; their inner margins thin. Dissepimentarium approximately 1/3 length of major septa. Dissepiments interseptal.

In mature growth stage with n:d value 25:10–11.5 mm, general morphology similar to that in early mature growth stage. Three transverse sections along approximately 10 mm corallite growth and through lower part of calice (Text-fig. 12B–E) confirm amplexoid character of major septa. Although weakly accentuated, that character results in slight differences in length of major septa in particular transverse sections. Dissepimentarium slightly wider than in early mature growth stage, reach 1/3 corallite radius in width. Lonsdaleoid dissepiments increase in number and size during corallite growth. In addition to larger size and slightly larger number of septa, development of lonsdaleoid dissepiments form main difference when compared to early mature growth stage. However, lonsdaleoid dissepiments almost absent from calice surrounding dissepimentarium (Text-fig. 12E). Pseudocolumella monoseptal, short and thin, appeared as ephemeral structure developed during short distance of corallite growth. Minor septa penetrate tabularium deeper than in early mature growth stage, but remain thin-ended. In calice major septa shortened, making minor septa almost equal to them as a result.

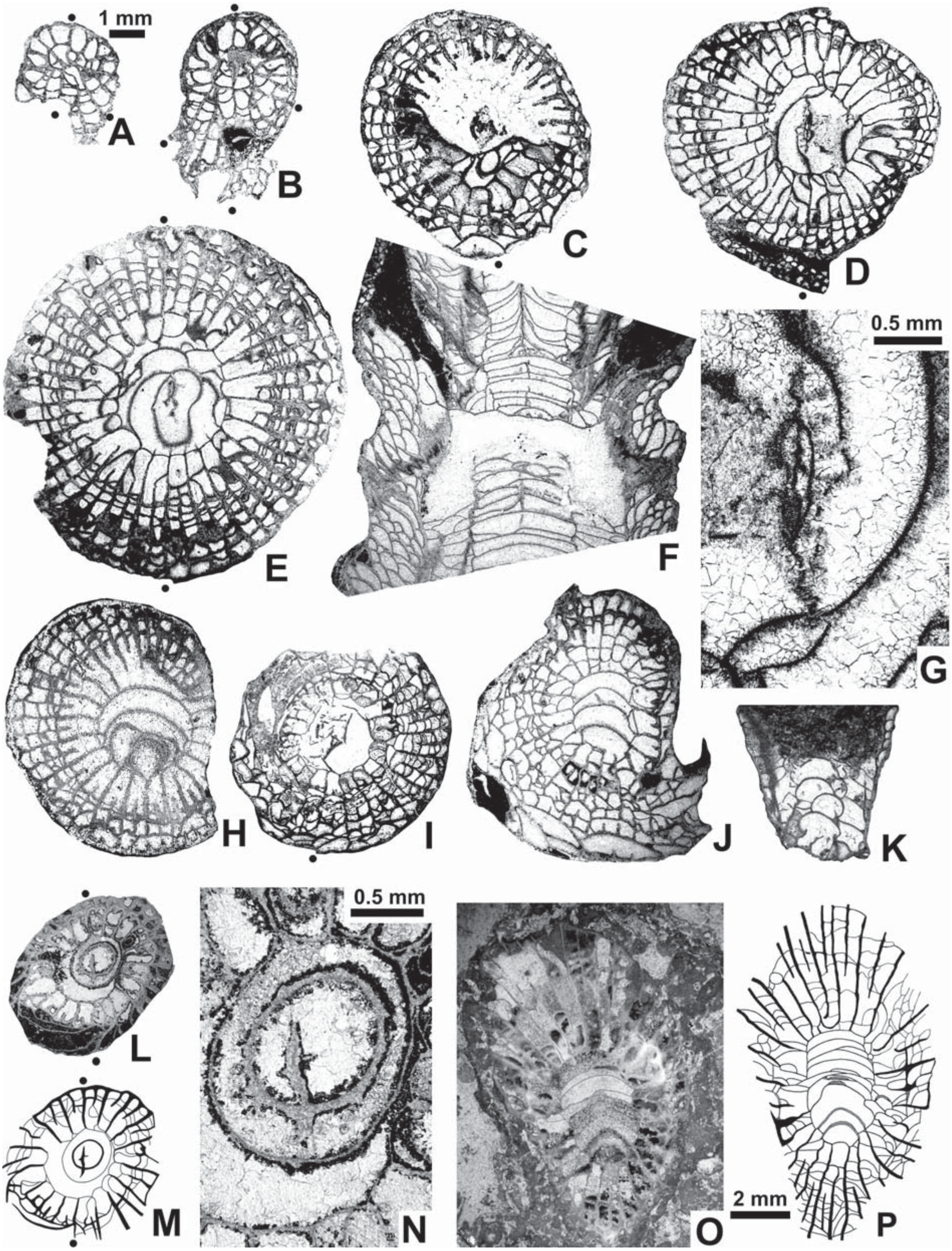
Tabularium clearly bipartite with columnotheca occupying approximately 1/3 corallite diameter. Axial tabellae slightly convex in axial part when pseudocolumella absent, elevated towards it, when present (Text-fig. 12F, G). Their peripheral parts turned abruptly down to rest on underlying axial tabellae to form border of columnotheca. Columnotheca of this species was earlier described in detail and selected as typical (Fedorowski 2009b, fig. 6A, E, F). Peripheral tabularium biform. Arrangement of peripheral tabellae (Text-fig. 12F, G, white arrows) depends on positions against minor septa. Those tabellae look complete when sectioned exactly in Position II of Sutherland (1965) and look as bearing additional tabellae when sectioned through both Positions (Text-fig. 12F, lower and upper black arrow respectively). Dissepiments differ in shape and size being small and globose when corresponding to interseptal dissepiments seen in transverse section and large, elongated when corresponding to lonsdaleoid dissepiments.

Microstructure of septa (Text-fig. 12I) finely trabecular with individual trabeculae approximately 0.03 mm wide, differentiated in length, but invariably crossing several incremental lines. Details in their morphology and true length camouflaged by diagenesis.

INTRASPECIFIC VARIABILITY: Early neanic and neanic growth stage, lacking from holotype, best preserved in paratype UAM-Tc.Don.1/290 (Text-fig. 13A, B). Elongated shape and other irregularities resulted from attachments to substrate. Arrangement of major septa rotiphylloid, with axial septum crossing distinct cardinal fossula that extends up to corallite axis. Incomplete row of dissepiments appear in advanced neanic growth stage (Text-fig. 13B, right).

N:d ratios of paratypes documented in Text-fig. 6. Mature growth stages of most paratypes (Text-figs 12L; 13C–E, H–J, N) resemble holotype in their general morphology. Major septa amplexoid, arranged radially with protosepta indistinguishable by length and/or thickness. Minor septa thin-ended, penetrate peripheral tabularium. Microstructure of septa destroyed by diagenesis in most instances. Some best preserved fragments resemble that in holotype (Text-fig. 12N). Cardinal fossula absent. Most paratypes differ from holotype in better developed and longer lasting pseudocolumella. Short septal crests (Text-fig. 13G) attach its surface in several corallites. Columnotheca continuous (Text-figs 12J, K; 13F). Arrangement of axial tabellae depends on presence or absence of pseudocolumella in given part of corallite growth. Axial tabellae gently convex when pseudocolumella absent, elevate to pseudocolumella under low angle in most instances, but may elevate very steeply in some part of corallite growth (Text-fig. 13F, upper part of image). Peripheral tabularium biform; arrangement of peripheral tabellae depends on Positions of Sutherland (1965) the same way as in holotype (Text-figs 12J, K, M; 13F *vs* Text-fig. 12F, G) with details illustrated in Text-fig. 12M. Dissepimentarium slightly more or slightly less than 1/3 corallite radius in width. Dissepiments mostly interseptal, regular, some irregular. Lonsdaleoid dissepiments rare and small in most paratypes, may be numerous and large in some (Text-fig. 13J).

Specimen UAM-Tc.Don.1/294 (Text-fig. 13L–P) requires separate treatment as being collected from



Text-fig. 13. *Kumpanophyllum decessum* sp. nov. Transverse thin sections except when stated otherwise. A-C – Specimen UAM-Tc.Don.1/290. Paratype. A – early neanic growth stage, B – neanic growth stage, C – mature growth stage. D-G – Specimen UAM-Tc.Don.1/285. D, E – mature growth stage, F – rejuvenated corallite, longitudinal thin section, G – axial structure; most inner margins of major septa or septal →

Limestone D_7^6. Despite occurrences older than remaining representatives of *K. decessum* sp. nov., it closely resembles holotype and most paratypes in morphology and n:d value, allowing to consider appearance of *K. decessum* sp. nov. very early in stratigraphic column.

REMARKS: The corallites assigned by Fomichev (1953, p. 257) to the type species *K. kokinense* are very tiny specimens. The holotype is only 4 mm wide in the calice and 3.5 mm wide beneath the calice. This feature, a small number of septa (14), their short length and the dissepimentarium restricted to one, incomplete row of dissepiments are characters very distant from those of *K. decessum* sp. nov. Thus, a new subgeneric or generic position of the latter species may appear. Its morphology is intermediate between other species of *Kumpanophyllum* and such species as *Pseudozaphrentoides nitellus* from the Hale Formation in SW Texas and the Wapanucka Formation in Oklahoma.

Koninckophyllum elpasoense from the Helms Formation (Chesterian) of the Franklin Mountains in SW Texas, USA resembles *K. decessum* sp. nov. mainly in the monoseptal and interrupted pseudocolumella, and in the wide dissepimentarium. It differs in the much larger number of septa and corallite diameters (30–34:15–22 mm) and in most minor septa not entering the tabularium.

Nemistium liebanense resembles *K. decessum* sp. nov. in the morphology and width of the columnotheca, with the monoseptal pseudocolumella either interrupted or reduced in an advanced mature growth stage. It differs from *K. decessum* sp. nov. in much smaller dimensions (n:d value 18–20:6–7 mm), the lonsdaleoid dissepiments sparse or absent and in peripheral tabellae more densely packed.

The acolumellate growth stage of *K. decessum* sp. nov. resembles *Semenoffia weiningensis* from the *Profusulinella* Zone of Guizhou Province, South China in reduction of the columella and a common development of lonsdaleoid dissepiments at the periphery. It differs from that Chinese species in the minor septa penetrating the tabularium deeper, in the wider dissepimentarium and (perhaps) in the columella reduced to a lesser degree. The character of the pseudocolumella is impossible to check in the Chinese species, represented by a single, incomplete specimen with only one transverse thin section illustrated. The morphology in the longitudinal section (Yu and Wang 1987, pl. 2, fig. 4b), closely resembles that in the acolumellate part of specimens of *K. decessum* sp. nov. (Text-fig. 12F, G).

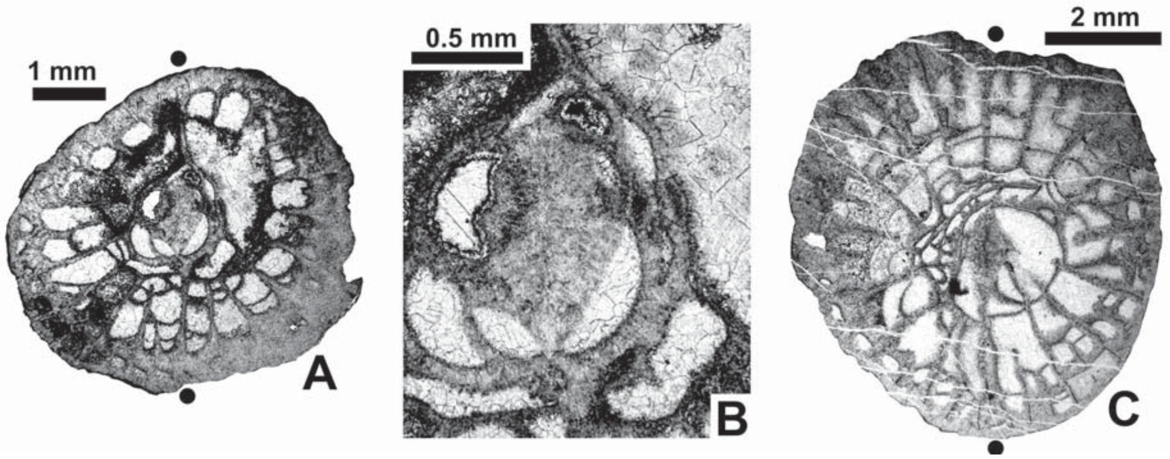
OCCURRENCE: Holotype UAM-Tc.Don.1/284 and paratypes UAM-Tc.Don.1/285–290: Krynka River Area, Svistuny Village, Velyka Shyshivka Ravine (Balka). Paratypes UAM-Tc.Don.1/291, 292, 293a, b: Kalmius River Area, Fenine Village. All from Limestone E_1^{vyzh}. Lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus* conodont Biozone. Upper lower Bashkirian. Paratype UAM-Tc.Don.1/294: Kalmius/Berestova Rivers Head, Limestone D_7^6. Lower Voznesenskian Horizon, *Homoceras–Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lower Bashkirian.

Kumpanophyllum sp. 1
(Text-fig. 14)

MATERIAL: Two incomplete specimens UAM-Tc.Don.1/296, 297, both diagenetically altered. Fragment of specimen UAM-Tc.Don.1/296 restricted to early mature growth stage. Fragment of specimen UAM-Tc.Don.1/297 represents mature growth stage. Two transverse thin sections and two peels available for study.

DESCRIPTION: N:d values 20:5.2 mm and 18:7.0 mm. Major septa amplexoid, approximately 2/3 corallite radius in length, slightly thickened, thickest at periphery. Cardinal septum reaches thick, monoseptal pseudocolumella. Counter septum terminated at section of tabellae located close to pseudocolumella or forms one of several septal crests attached to inner tabellae intercepts (Text-fig. 14A, B *vs* C). Minor septa differentiated in length, hidden in thick external wall where dissepiments lacking in early mature growth stage. In mature growth stage developed prior to formation of dissepiments; penetrate outer tabular-

lamellae attached to tabula and some to thin pseudocolumella (enlarged from D). H – Specimen UAM-Tc.Don.1/288. Mature growth stage (peel). I – Specimen UAM-Tc.Don.1/293a. Mature growth stage. J – Specimen UAM-Tc.Don.1/287. Mature growth stage. K – Specimen UAM-Tc.Don.1/293b. Longitudinal thin section of immature corallite. L-P – Specimen UAM-Tc.Don.1/294. L, M – early mature growth stage (M – drawing on peel), N – corallite axial area; monoseptal pseudocolumella with two septal lamellae attached (enlarged from L), O, P – mature growth stage (O – polished surface, P – drawing on image taken from that surface). Protosepta and alar septa marked by black dots when recognisable. For stratigraphic position see text. Scale bars corresponding to given images located in their upper right. Scale bar between O and P corresponds to all other images



Text-fig. 14. *Kumpanophyllum* sp. 1. Transverse thin sections. A, B – Specimen UAM-Tc.Don.1/296. A – early mature growth stage, B – pseudocolumella (enlarged from A). C – Specimen UAM-Tc.Don.1/297. Mature growth stage. Protosepta marked by black dots. For stratigraphic position see text

ium where dissepimentarium present. Dissepiments rectangular and oblique. In early mature growth stage sclerenchyme filled some of them completely.

REMARKS: Two corallites assigned to this unnamed species differ in their n:d values, but are comparable to one another in their main morphological characteristics that differ at the same time from all specimens described herein. The thick monoseptal pseudocolumella probably permanently connected to the cardinal septum, the incomplete dissepimentarium and strong sclerenchymal thickening are the distinguishing characters of *Kumpanophyllum* sp. 1. The first of those characters resembles the holotype of *K. praecox* sp. nov.

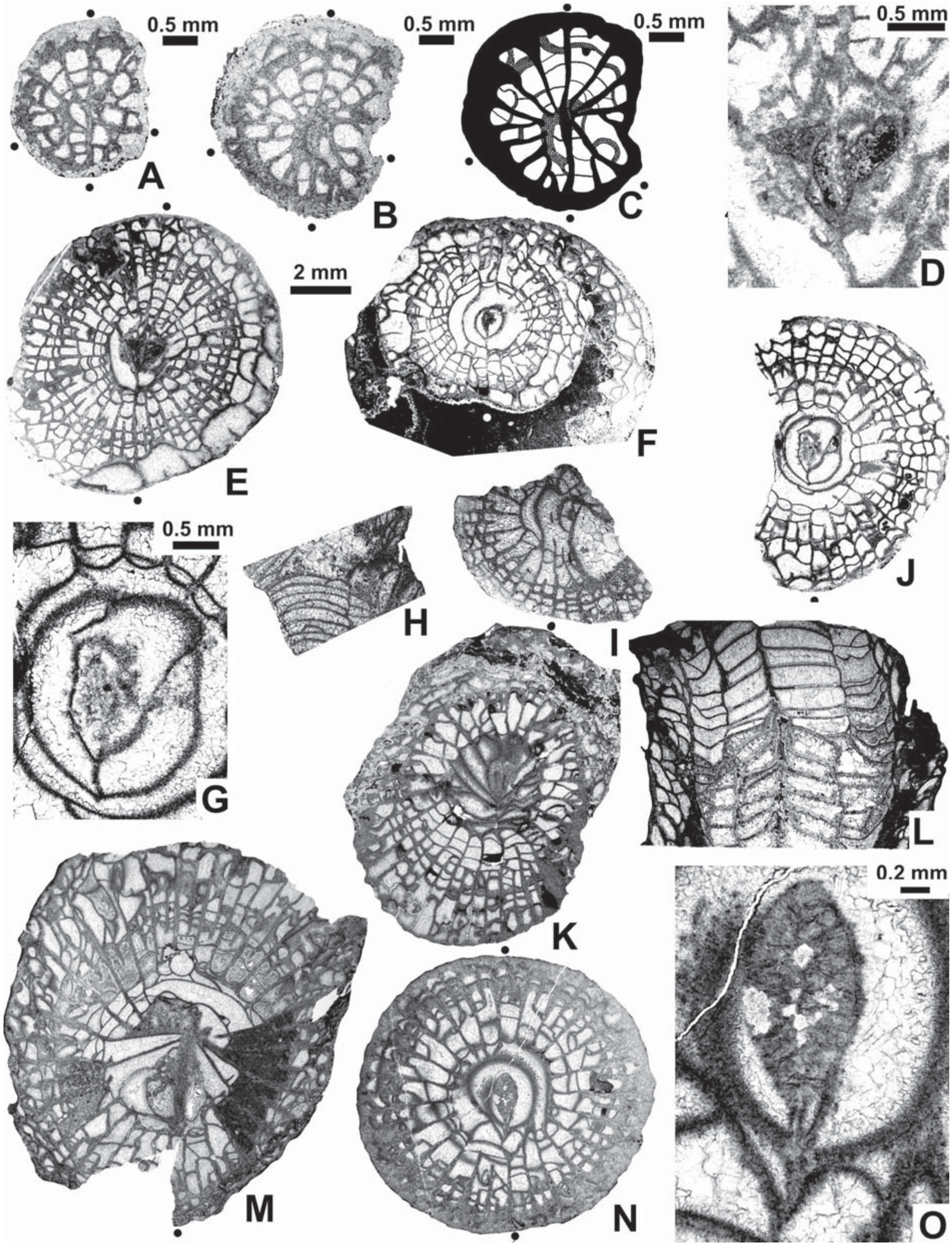
OCCURRENCE: Specimen UAM-Tc.Don.1/296: Blagodatne Village, Dubova Balka (Ravine), Limestone E_8. Lower Manuilovian Horizon, Specimen UAM-Tc.Don.1/297: Luhanchyk River Area, Volnukhine Village, Limestone F_1. Blagodatnian Horizon. Lower and upper *Bilinguites–Cancelloceras* ammonite Biozone, *Pseudostaffella praegorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Middle Bashkirian.

Kumpanophyllum sp. 2
(Text-fig. 15A–J)

MATERIAL: Three corallites. Specimen UAM-Tc.Don.1/298 with neanic and mature growth stage preserved. Its widely cone-shape makes rudiment left from thin sectioning too short for longitudinal section. Specimen UAM-Tc.Don.1/299 restricted to rejuvenated part with remnants of corallite lacking. Specimen UAM-Tc.Don.1/300 lacks almost whole left quadrants of septa. Microstructure of all corallites recrystallised. Five thin sections and eight peels available for study.

DESCRIPTION: In neanic growth stage of specimen UAM-Tc.Don.1/298 (Text-fig. 15A–C) arrangement of major septa rotiphylloid, with axial septum distinct. Major septa last inserted in quadrants underdeveloped. Cardinal fossula present. Minor septa recognisable in external wall of counter quadrants where first dissepiments appear. In mature growth stage of the same specimen (Text-fig. 15E) with n:d value 26:9.0 mm, major septa radially arranged, most 4/5 corallite radius in length, leave narrow area around axial structure free. Some major septa in counter quadrants closely approach thin, median lamella, united with protosepta to form continuous axial septum.

Text-fig. 15. **A-J**. *Kumpanophyllum* sp. 2. A-E – Specimen UAM-Tc.Don.1/298. A-C – neanic growth stage (C – drawing on B), D – weak axial structure (enlarged from E), E – mature growth stage. F – Specimen UAM-Tc.Don.1/299. Rejuvenated corallite. G-J – Specimen UAM-Tc.Don.1/300. G – weak axial structure (enlarged from J), H – fragment of longitudinal section (peel), I – fragment of transverse section with thin, short median lamella (peel), J – mature growth stage. **K-O** – *Kumpanophyllum* sp. 3. K – Specimen UAM-Tc.Don.1/303. Mature growth stage. L, M – Specimen UAM-Tc.Don.1/301. L – longitudinal section, M – mature growth stage. N, O – Specimen UAM-Tc.Don.1/302. N – ma- →



ture growth stage, O – solid, monoseptal pseudocolumella (enlarged from L). Transverse thin sections except when stated otherwise. Protosepta and alar septa marked by black dots when recognisable. For stratigraphic position see text. Scale bars corresponding to given images located in their upper right. Scale bar between E and F corresponds to all other images

Inner margins of major septa, short septal lamellae and intercepts of axial parts of tabellae form a kind of loose axial structure (Text-fig. 15D). In two remaining corallites, axial structure narrow, more compact, isolated from inner margins of major septa completely, reduced to simple median lamella in part of growth of one of them (Text-fig. 15F, G, J and I respectively). Minor septa in all corallites equally thin, reach approximately 3/4 length of major septa, penetrate peripheral tabularium. Dissepimentarium 1/2 to more than 1/3 corallite radius in width. In one corallite (Text-fig. 15J) almost all dissepiments interseptal, rectangular; lonsdaleoid dissepiments rare. In remaining two specimens (Text-fig. 15E, F), inner dissepiments interseptal, rectangular. Peripheral dissepiments mostly lonsdaleoid and large, present around most part of corallite periphery. Some may extent to tabularium border (Text-fig. 15F, lower right).

REMARKS: The corallites described resemble *K. decessum* sp. nov. in thin minor and major septa, long length of minor septa, large width and morphology of dissepimentarium and a temporary atrophy of the pseudocolumella (Text-fig. 15H). They differ in developing a kind of axial structure and in the median lamella being connected either to both protosepta, or to the cardinal septum, or at least elongated to the latter septum in mature growth stage. The morphology of specimen UAM-Tc.Don.1/300 (Text-fig. 15G–J), derived from the same locality as most specimens of *K. decessum* sp. nov., resembles that species most closely. Specimen UAM-Tc.Don.1/298 (Text-fig. 15A–E) is morphologically most distant from *Kumpanophyllum* and most similar to a new genus collected from the Limestone F_1 of the Donets Basin, introduced by Fedorowski and Ohar (submitted). The occurrence in Limestone E_1^{sred} may suggest an intermediate position of that species between the two genera mentioned.

OCCURRENCE: Specimen UAM-Tc.Don.1/298: Krynka River Area, Svistuny Village, Velyka Shyshivka Ravine (Balka). Specimens UAM-Tc.Don.1/299, 300: Blagodatne Village, Dubova Ravine (Balka). All from Limestone $E_1^{sred.}$. Lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus* conodont Biozone. Upper lower Bashkirian.

Kumpanophyllum sp. 3
(Text-fig. 15K–O)

MATERIAL: Three incomplete specimens UAM-Tc.Don.1/301–303. Only mature growth stage preserved. All diagenetically altered. One corallite rejuvenated. Its skeleton left by polyp damaged (Text-fig. 15K, upper). Three transverse thin sections (two slightly oblique), one longitudinal thin section and five peels available for study.

DESCRIPTION: Corallites with mean n:d values 24:10.5 mm, 25:9.0 mm and 25:11.5 mm. Major septa 2/3 corallite radius in length, equal in length and thickness except for long cardinal septum that meets pseudocolumella. Minor septa 2/3–1/2 major septa in length, enter peripheral tabularium. Pseudocolumella monoseptal, continuous, much thicker than major septa, oval or lath-like (Text-fig. 15K, N, O and M respectively). Dissepimentarium approximately 1/4 corallite radius in width. Dissepiments exclusively interseptal, rectangular and slightly irregular, arranged in steep rows (Text-fig. 15L). Tabularium bipartite. Columnotheca wider than outer tabularium. Inner tabellae reach continuous pseudocolumella at low angle. Most of their length flat; only peripheral parts steeply down turned, rest on underlying tabellae. Peripheral tabularium biform. Peripheral tabellae in Position II of Sutherland (1965) elevated towards columnotheca at angle similar to elevation of inner tabellae towards pseudocolumella. Peripheral tabellae in Position I down-sloping (Text-fig. 15L).

REMARKS: *Kumpanophyllum* sp. 3 resembles *K. decessum* sp. nov. and *Kumpanophyllum* sp. 2 closer than any of the remaining species of that genus. Thus, only its difference from those two are mentioned. It differs from *K. decessum* sp. nov. in the thick, continuous pseudocolumella, permanently united with the long cardinal septum, and in the absence of lonsdaleoid dissepiments. Its slightly narrower dissepimentarium and wider columnotheca are additional characters distinguishing it from *K. decessum* sp. nov. The weak axial structure with median lamella thin, the dissepimentarium wide and the lonsdaleoid dissepiments commonly developed are the main characters distinguishing *Kumpanophyllum* sp. 2 from *Kumpanophyllum* sp. 3.

OCCURRENCE: Specimen UAM-Tc.Don.1/301: Krynka River Area. Amvrosiivka Village, Limestone E_2. Specimens UAM-Tc.Don.1/302, 303: Velyke Mishkove Village, Limestone E_1^{vyzh}. Lower Feninian Horizon, lower *Reticuloceras–Bashkortoceras* ammonite Biozone, lower *Semistaffella variabilis–S. minuscularia* foraminiferal Biozone, lower *Idiognathodus sinuatus* conodont Biozone. Upper lower Bashkirian.

?*Kumpanophyllum* sp.
(Text-fig.16)

MATERIAL: One fragment of offsetting specimen UAM-Tc.Don.1/304, approximately 9 mm long, all used to make seven thin sections. Skeleton damaged in part of corallite. Microstructure of septa destroyed by diagenesis.

DESCRIPTION: Corallite with n:d value 24:9.5 mm mean diameter. Major septa equal in length and equally thin along their length, amplexoid, terminate at vertical part of columnotheca, but elongated along weakly convex parts of axial tabellae (Text-fig. 16A–C, lower part of image). Protosepta indistinguishable from remaining major septa. Pseudocolumella and cardinal fossula absent. Minor septa thin, penetrate peripheral tabularium. Columnotheca more than 1/3 corallite diameter in width. Axial tabellae distant for approximately 1.7 mm. Peripheral tabularium biform as suggested by unequal number of sections of tabellae in septal loculi right and left of minor septa.

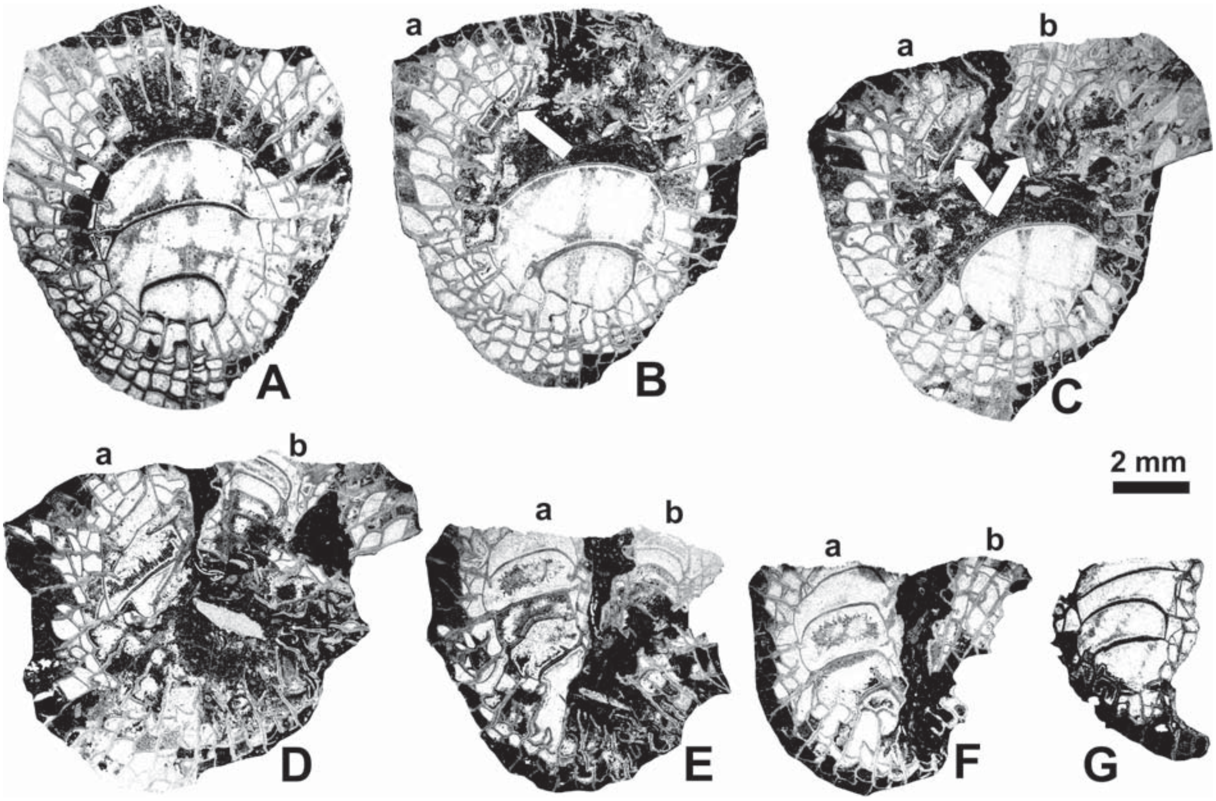
Corallite offsets peripherally (Text-fig. 16B, C, white arrows). However, direction of offset's growth, perpendicular to growth of parent's specimen suggests overturn of the latter. Remnants of polyp that survived created two individuals. Thus, rejuvenation forced by extrinsic factors took place rather than offsetting leading to colony formation. Derivation of corallite "b" uncertain and not discussed, whereas corallite "a" utilises parental body and skeleton to built its peripheral part (Text-fig. 16B–F), confirming interpretation suggested. It remains uncertain whether offsets maturated. In their preserved parts, major septa reach 1/3 corallite radius or less. Some minor septa recognisable in most advanced growth stage (Text-fig. 16G). Pseudocolumella or axial septum absent from both young corallites studied. Columnotheca 1/2–2/3 corallite diameter in width. Axial tabellae convex, widely spaced, approximately 1.0–1.5 mm apart. Peripheral tabularium very narrow. Dissepimentarium restricted to single row of dissepiments.

REMARKS: The specimen described is stratigraphically the oldest among the Bashkirian specimens described in the present paper and is the only offsetting specimen among those bearing characters of the Kumpanophyllidae. The parent corallite resembles the pseudocolumella lacking growth stages of *K. decessum* sp. nov. in both the morphology and the n:d value. Lack of pseudocolumella at any growth stage studied, the possible absence of lonsdaleoid dissepiments and the very wide columnotheca with axial tabellae widely spaced constitute a set of characters that distinguish ?*Kumpanophyllum* sp. from *K. decessum* sp. nov. Absence of pseudocolumella or axial septum from early growth stage makes the taxonomic position of that specimen within the Kumpanophyllidae doubtful. That character in turn points to *Diphyphyllum*, whereas the peripheral offsetting or, more probably, only the multiple rejuvenation, excludes such an option. Although doubtful in the systematic position and despite its incompleteness, the specimen in question is described here and illustrated as belonging to a restricted rugose coral taxon that survived the end Mississippian extinction event. It occurs almost immediately above the Serpukhovian/Bashkirian boundary,

OCCURRENCE: Specimen UAM-Tc.Don.1/304: Kalmius River Area. Berestova River mouth. Limestone D_5^9. *Homoceras–Hudsonoceras* ammonite Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Lowermost Bashkirian.

CONSIDERATIONS

The close relationship of the Kumpanophyllidae to the Aulophyllidae, clearly suggested by Hill (1981) who synonymised the former with the latter, cannot be documented by indisputable data. However, a relationship of those two families can be considered as a possible option. The Lithostrotionidae/Kumpanophyllidae relationship is the second possible option, supported by fasciculate colonial taxa tentatively included here in the Kumpanophyllidae. The close Aulophyllidae/Lithostrotionidae relationship suggested by Vaughan (1915, pp. 39, 40) may form an additional argument for placing Kumpanophyllidae in that group of families. Vaughan (1915) pointed out an ancestral role of his new genus *Eostrotion* to both *Koninckophyllum* and *Lithostrotion* Fleming, 1828 in his meaning, i.e., including *Siphonodendron*. He selected *Cyathaxonia tortuosa* Michelin, 1846 as the type species of *Eostrotion* and referred to the illustrations and descriptions by Carruthers (1913). Thus, those data should be considered typical for *Eostrotion*. The following characters of *E. tortuosum* are most important in the context of this discussion: 1) the major septa in the early mature growth stage long, zaphrentoidally arranged with the cardinal fossula well developed; the axial septum in that growth stage strongly thickened in the middle to form the



Text-fig. 16. ?*Kumpanophyllum* sp. Specimen UAM-Tc.Don.1/304. Successive transverse thin sections of incomplete, offsetting specimen. A – protocorallite, B – very beginning of peripheral offsetting (arrowed), C-G – successive sections of developing offsets (arrowed) with only offset a survived. For stratigraphic position see text

pseudocolumella (Carruthers 1913, pl. 3, fig. 1a, b); and 2) in the mature growth stage, the free major septa shorten successively during corallite growth, becoming eventually arranged radially and equal in length. The latter statement includes the counter septum. The cardinal septum is slightly shortened and located within the cardinal fossula. The monoseptal pseudocolumella becomes free. Dissepiments are exclusively interseptal and regular. The tabularium is probably biform. Tabulae are mostly tent-shaped, complete, with rare additional tabellae, but without any trend to form columnotheca. Two of the characters listed, i.e., the occurrence of the cardinal fossula and the absence of a trend to form the columnotheca eliminate *Eostrotion* from a list of potential ancestors of *Kumpanophyllum* despite such characters in common as the axial septum, the pseudocolumella and the biform tabularium.

The question of the Aulophyllidae/Lithostrotionidae relationship is beyond the scope of the present paper. Hill (1981, pp. *F*352 and *F*379, respectively) assigned these families to different suborders. That assignment does not contradict the derivation of the Lithostrotionidae from the Aulophyllidae, but made their relationship distant.

Only fasciculate Lithostrotionidae with major septa equal in length, with a columnotheca present but a cardinal fossula lacking and with a pseudocolumella derived from an axial septum and occurring at least in the early growth stage, can be considered when searching for an ancestor of *Kumpanophyllum*. There is no taxon known to me that fulfils all the conditions listed. Several species assigned to various genera of the fasciculate Lithostrotionidae follows the first of the two conditions, but none of the completely investigated ones possesses the axial septum present early in the hystero-ontogeny. The hystero-ontogeny in most of the potential candidates for the Kumpanophyllidae ancestors, assigned to such genera as *Siphonodendron*, *Diphyphyllum* or *Nemistium* remains unknown. The early growth stages thoroughly investigated by Khoa (1977, text-fig. 19) in his new species *Lithostrotion* (*Siphonodendron*) *dobroljubovae* from the upper Brigantian of eastern Poland lacks an axial septum. The same is true for *Nemistium* from the Mattson Formation in Canada (Fedorowski *et al*., submitted), whereas the hystero-ontogeny in *Nemistium edmondsi* Smith, 1928, the type species for the genus, remains unknown. Lack of data in most columnotheca bearing colonial Lithostrotionidae does not eliminate that family from the list of the Kumpanophyllidae ancestors rigorously, but the examples cited made that elimination probable.

The discussion above and the remarks concerning the Kumpanophyllidae which consider all taxa known to me as exposing characters comparable to that family, allow the conclusion that there is an absence in the existing literature of a taxon undoubtedly ancestral to the Kumpanophyllidae. Moreover, the lack of hystero-ontogenetic data in all the fasciculate colonial taxa, conditionally included here in that family, makes that assignment doubtful. Those taxa may expose characters of the Lithostrotionidae when studied comprehensively enough.

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