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Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 11. The Family Pentaphyllidae Schindewolf, 1942 and considerations on the Suborder Tachylasmatina Fedorowski, 1973

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ABSTRACT:

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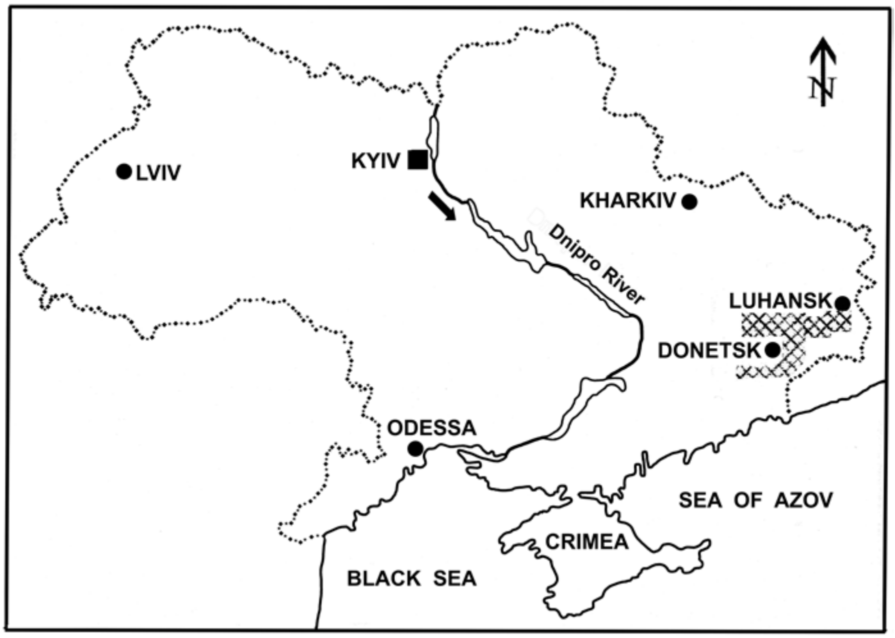
Inconsistency in the approach to the corals included by different authors in the families Tachylasmatidae Grabau, 1928 and Pentaphyllidae Schindewolf, 1942 are discussed in the context of their relationship *vs* homeomorphy to the Family Plerophyllidae Koker, 1924. Following Schindewolf (1942), the pentaphylloid or cryptophylloid early ontogeny, typical of the former two families, is contrasted with the zaphrentoid ontogeny typical of the latter family. Comprehensive analysis proves the independent taxonomic position of the Suborder Tachylasmatina Fedorowski, 1973. The taxa described herein support this idea. The relationship of the two families: Tachylasmatidae and Pentaphyllidae within the framework of this suborder are suggested. A new genus left in open nomenclature (represented by a single specimen) and three new species, *Pentaphyllum* sp. nov. 1, ?*Pentaphyllum* sp. nov. 2 and Gen. et sp. nov. 1 are described from lower Bashkirian deposits.

Key words: Anthozoa (Rugosa); validity of Suborder Tachylasmatina; Lower Bashkirian (Carboniferous); Ukraine.

INTRODUCTION

The specimens described herein belong to morphotypes of the Rugosa, the taxonomy of which remains disputable. Known from the upper Silurian up to the upper Permian inclusively, representatives of this morphotype have seldom been found in large numbers and as complete corallites. The rich collections of well-preserved specimens from the upper Permian deposits of Armenia (Ilina 1965) and Iran (Ezaki 1991) are exceptional, whereas specimens studied from individual sites were usually very restricted in number. Sixteen named species of the genus *Cryptophyllum* Carruthers, 1919, ten of which were based on a single specimen each (Fedorowski 2009b, table 2), clearly exemplify this situation. A very individualized evaluation of the characters (see remarks on the family), a differentiated distribution of taxa both in time and space, commonly disregarded in descriptions and discussions, and the incomplete knowledge of the immature ontogeny of some important type species, has resulted in several taxonomical controversies lasting up till today. The present paper does not attempt to fully clarify these controversies and to suggest a taxonomic solution, although some suggestions are raised in the discussion. Its main aim is rather to support the independent taxonomic status of the Suborder Tachylasmatina Fedorowski, 1973 and to



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

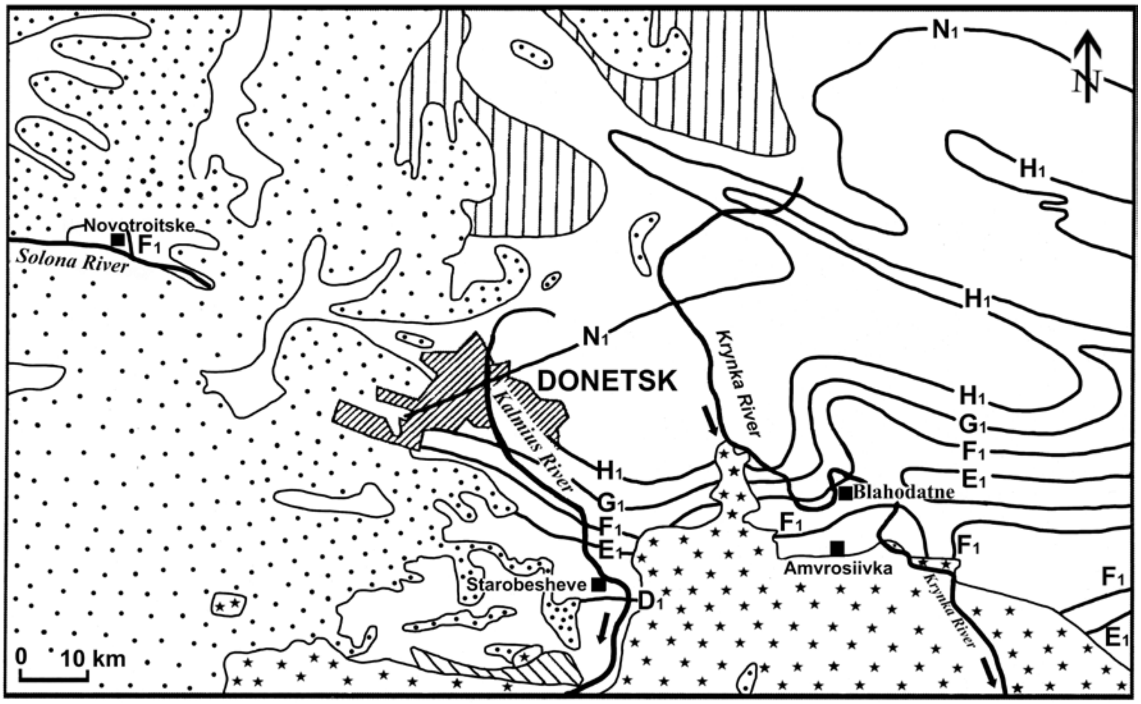
document the occurrence of *Pentaphyllum*-like corals in the lower Bashkirian of eastern Europe.

The history of the studies on *Pentaphyllum*-like corals goes back to the second half of the 19th century, when de Koninck (1872) introduced the new genus *Pentaphyllum* with two new species, *P. armatum* and *P. caryophyllatum*. Both those species were based on a single specimen each and were described on the basis of their external characters, including calices (de Koninck 1872, p. 58, pl. 4, figs 8, 8a, 8b). Hinde (1890) suspected the preoccupation of the name *Pentaphyllum* and replaced it by *Plerophyllum*, based on a Permian species from Australia. He questionably included the European Tournaisian *Pentaphyllum* in *Plerophyllum*. Koker (1924) accepted the name *Plerophyllum*, described several specimens from Permian strata of Timor Island and introduced the new Family Plerophyllidae; however, she did not offer a discussion supporting her decisions. Such a discussion was subsequently presented by Grabau (1928) and Schindewolf (1942) with the suggestions of the second author being crucial for the taxonomy of this group of corals. Schindewolf (1942, p. 172) demonstrated the validity of the name *Pentaphyllum* which differs in one letter from the coleopteran genus *Pentaphyllus*. However, he accepted the genus *Plerophyllum* as well, documenting a difference in the early ontogeny between the two genera adequate for a distinction at subfamily level. Fedorowski (1973) expanded Schindewolf's (1942) idea and introduced the new suborder Tachylasmatina. Later, Fedorowski (2009b) restudied the type specimens of both de Koninck's (1872) species, re-capitulated the history of the investigations on corals similar to or related to *Pentaphyllum*, proposed models of pentaphylloid or cryptophylloid *vs* zaphrentoid ontogeny, and suggested the *incertae sedis* taxonomic status of *Pentaphyllum*-like corals. The models remain valid, but the *incertae sedis* position of these taxa is not followed herein (see discussion on the family).

Following Hudson (1936b) and Fedorowski (1997), only the cardinal and the counter major septa are considered as protosepta. As in my earlier papers, the microstructure of septa, if recognisable, is described on the basis of the so-called 'dark lines': i.e., the primary septa created within septal pockets prior to secretion of the sclerenchymal covers.

MATERIAL AND METHODS

The specimens described in this paper belong to the collection offered to me by the late Dr. N.P. Vassilyuk, former professor of the Donetsk Polytechnic, Ukraine. The number of specimens is restricted to only three, each of which differs from the other two. However, their



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

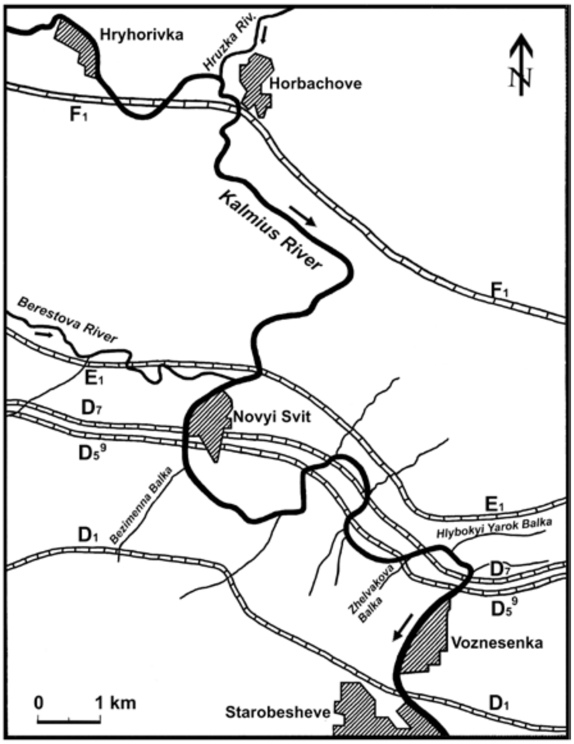
completeness and the state of preservation allows for a fairly complete study and taxonomic identification. In addition, their stratigraphic position (Limestone D_7^7), i.e., close to the base of the Bashkirian, i.e., immediately after the Serpukhovian mass extinction, makes them important for the re-capitulation of the phylogeny of rugose corals.

All specimens were cut using a cutting machine equipped with a 0.03 mm wire. Subsequently, they were either thin-sectioned, acetate-peeled, or both. All specimens were illustrated. Images of poorly preserved fragments of corallites are augmented by computer drawings based on highly enlarged images.

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

GEOLOGICAL SETTING

All specimens were derived from the site in Voznesenka Village (Text-figs 1–3), the stratotype for the Voznesenkian Horizon. The history of the investigation of that horizon and the detailed succession



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

of strata were described by Poletaev *et al*. (2011, pp. 60–64, fig. 10). The horizon comprises mostly argillites and aleurites with limestone intercalations varying from 0.1 m to 1.7 m in thickness. In the type area the succession begins with 0.6 m thick Limestone D_5^{8verkh} and terminates with an approximately 20 m thick set of argillites with sandstone intercalations that overly the 0.1 m thick Limestone D_8, the last limestone intercalation bearing the index D. The corallites studied herein derive from the base of the argillite cover of Limestone D_7^7, occurring slightly higher than the 2/3 thickness of the Voznesenkian Horizon. That limestone comprises two limestone layers, 0.3 m and 0.15 m thick, respectively, separated by a thin argillite layer similar to that of the argillite cover mentioned.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugose Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder Tachylasmatina Fedorowski, 1973
Family Pentaphyllidae Schindewolf, 1942
Subfamily Pentaphyllinae Schindewolf, 1942

REMARKS: Rugose corals with the protosepta, the alar and the counter-lateral septa variously differentiating in length were all included by Hill (1981) in the suborder Plerophyllina Sokolov, 1960. From several families included by her in that suborder, only the Family Pentaphyllidae (in Hill's 1981 meaning) and the two oldest genera with the major septa differentiating in length are considered in this discussion. The genus *Pentaphyllum*, i.e., the nominative genus for the family, is considered as the reference taxon. Hudson (1936a) re-studied de Koninck's specimens, recognised their poor preservation and transferred *P. caryophyllatum* to *Cryptophyllum* (see Fedorowski 2009b, p. 570). I have repeated that revision (Fedorowski 2009b) and confirmed both the transfer of *P. caryophyllatum* to *Cryptophyllum* and the diagenetic alterations (silicification and partial dissolution) of both types and the only specimens representing de Koninck's (1872) species. Destruction of the early ontogeny is observed in both specimens, but that failure in *P. armatum* is especially important since it occurs in the type species of *Pentaphyllum*. This failure makes the entire concept of the taxonomy within that group of corals dubious (see below). The history of the study on the *Pentaphyllum*-like corals, descriptions of morphological details of the holotypes of *P. armatum* and *P. caryophyllatum* and the detailed discussion on the zaphrentoid *vs* the cryptophylloid (= pentaphylloid) early ontogeny reported by Fedorowski (2009b) makes that paper a reference point in this discussion. However, several issues not dealt with that paper should be and are discussed here. Moreover, I have changed my mind with regard to the *incertae sedis* position of the Suborder Tachylasmatina. Such an expression is misleading when I am now convinced about the taxonomically independent position of at least Carboniferous and Permian taxa passing through a cryptophylloid early ontogeny stage (see below).

Pre-Carboniferous taxa with major septa differentiating in length are only mentioned here. The stratigraphically oldest among them, i.e., *Anisophyllum* Milne Edwards and Haime, 1850 from the upper Silurian of Tennessee and Oklahoma (USA) and *Amandaria* Lavrusevich, 1968 from the upper Silurian or the Lower Devonian from Tadzhikistan, are morphologically so distant from one another and from other *Pentaphyllum*-like taxa that their different position at the family level (Hill 1981) is indisputable. Moreover, the morphological differences between those two taxa and the distant geographic positions during their life time makes their relationship at suborder level doubtful.

The generic name *Oligophyllum* Počta, 1902 has been differently treated by particular researchers (e.g., Grabau 1928; Schindewolf 1942; Kullmann 1965; Weyer 1973; Ilina 1984). These remarks are restricted to the holotype *Oligophyllum quinqueseptatum* Počta, 1902, the type species for the genus from the Dvorce Limestone (Pragian, middle Lower Devonian) and the holotype of *O. permirum* Počta, 1902 from the Lochkovian (lower Lower Devonian), both from the Czech Republic. *Oligophyllum quinqueseptatum* is preserved only in a mature growth stage. The earliest growth stage was restudied by Schindewolf (1942, fig. 75a, b) from the holotype of *O. permirum*. He recognised a septal structure hidden in the external wall in the middle of an apparently single, very thick and dominating septum that according to him represents two counter-lateral septa. Vestigial data provided by those two specimens, both diagenetically altered, cannot serve as a basis for a reliable interpretation. However, the ancestral position of *Oligophyllum* to *Pentaphyllum* and the relationship of those two genera, suggested by Schindewolf (1942), cannot be excluded despite the long gap between their occurrences.

Upper Lower Devonian (Emsian) Spanish taxa (Kullmann 1965) have been described on the basis of incomplete specimens, with the early ontogeny unknown. Despite that incompleteness, Kullmann

(1965) identified some specimens as *Oligophyllum s.s.* and distinguished some other ones as the new subgenus *Pentelasma*. Hill (1981) synonymised these two subgenera and accepted them as *Oligophyllum*. Kullmann's (1965) taxa bear some common characters with the Carboniferous *Cryptophyllum*-like corals. However, the level of knowledge of all pre-Carboniferous taxa is inadequate for a detailed analysis and they are omitted from this discussion.

The Carboniferous and Permian taxa passing through the cryptophylloid early ontogeny stage were treated before (Fedorowski 1973) and herein as members of the independent Suborder Tachylasmatina. That distinction is neglected by most researchers (e.g., Ilina 1965, 1984; Flügel 1968, 1972; Weyer 1972, 1975, 1994; Weyer and Ilina 1979; Hill 1981; Ezaki 1991; Fan *et al*. 2003; Wang *et al*. 2004). The taxa described by those and other authors (see complete list in Fedorowski 2009b) have been most commonly placed within the Family Plerophyllidae, in the Suborder Plerophyllina.

A methodological error by Schindewolf (1942), who took no account of the lack of the early ontogeny in the holotypes of both *Pentaphyllum armatum* and *Tachylasma cha* Grabau, 1922, i.e., the type species of the eponymous genera for the families, may be one of the most important reasons for neglecting the independent status of the Suborder Tachylasmatina. Schindewolf (1942, fig. 72) re-drew the ontogeny established by Carruthers (1919) in his new genus and species *Cryptophyllum hibernicum* and accepted it as typical of the Subfamily Pentaphyllinae. He made the same methodological error by not taking into account the lack of early ontogenetic data from *Tachylasma cha*. Moreover, he illustrated the early ontogeny of his own species arbitrarily accepted by him as *Tachylasma* (e.g., Schindewolf 1942, fig. 85). I did not recognise these errors when introducing the Suborder Tachylasmatina. Fortunately, Schindewolf (1942, figs 41, 42) studied and illustrated the early ontogeny of the topotypes of *Plerophyllum australe* Hinde, 1890 and clearly documented its zaphrentoid ontogeny. Thus, the documented zaphrentoid early ontogeny in the Family Plerophyllidae and the Suborder Plerophyllina is superimposed onto numerous data of the parallel occurrence of cryptophylloid ontogeny. Unfortunately, none of these studies are based on the type species as mentioned above. This strange situation was obvious to Hill (1981, p. *F*330), who pointed out the lack of ontogenetic studies in the type species of both *Pentaphyllum* and *Tachylasma* Grabau, 1922 and concluded her comments as follows: "this Treatise tentatively gives family value to Pentaphyllidae". Hill (1981) accepted three subfamilies within that family: Pentaphyllinae, Commutinae Fedorowski, 1973 and Dalniinae Fedorowski, 1973, a position tentatively followed here. However, Hill's (1981, p. *F*330) diagnoses of both the Family Pentaphyllidae and the Subfamily Pentaphyllinae are not recommended, but an alternative diagnosis for both these taxa cannot be suggested on the data available so far.

The different approach of particular researchers to the taxonomic value of given characters, early ontogeny in particular, forms the next important reason for neglecting the independent status of the Suborder Tachylasmatina. Ezaki's (1991) suggestions form an extreme position in that matter, totally rejected here as being contradictory to biological rules. He attempted to apply the morphological variations established by him in the upper Permian specimens from Iran to the lower Carboniferous European species. An obvious similarity in the mature morphology of such pairs of genera, representing Plerophyllidae *vs* Pentaphyllidae, as *Plerophyllum* and *Cryptophyllum* or *Ufimia* Stuckenberg, 1904 and *Tachylasma* is perhaps the next reason for neglecting the independent status of the Suborder Tachylasmatina, if the early ontogeny of these genera is unknown or neglected. However, repetition of mature skeletal structures following a totally different early ontogeny, is common within the Rugosa. *Amplexus* Sowerby, 1814, apparently occurring from the Silurian to the late Permian and *Caninia* Michelin in Gervais, 1840, apparently known throughout the entire Carboniferous and Permian appeared to be 'waste baskets' when the early ontogeny of many amplexoid and/or caninoid taxa was studied. Only such expressions as 'amplexoid mature growth stage' and 'caninoid mature growth stage' are now applied to most species formerly included in those genera (see Fedorowski 2010 for more details). Why not differentiate between the bearers of a zaphrentoid and cryptophylloid ontogeny as a criterion adequate for the separate suborder identification of the corals under discussion?

In this place, the morphology of the calice in *Pentaphyllum armatum* (Fedorowski 2009b, fig. 2B, E) should be briefly characterised as being different from both *Cryptophyllum* and *Tachylasma*. In contrast to its name, six instead of five septa dominate in the calice. That character has been already recognised by some authors (e.g., Hinde 1890), but its taxonomic value has not been elevated. The counter septum, although long by comparison to the metasepta in the counter quadrants other than the counter-lateral septa, is slightly shorter than the latter. It is interpreted here as an elongation of the counter septum in the course of corallite growth similar to that established here in Gen. et sp. nov. (see below).

The above discussion concentrated mainly on the reasons preventing the acceptance of the suborder Tachylasmatina. The main reasons in favour of the independent status of the suborder are as follows: (i) the axial septum is not secreted within the corallite lumen, i.e., the earliest septogenesis did not follow any variant of the zaphrentoid brephic and early neanic growth stage; (ii) the counter septum is secreted independently from the cardinal septum and late in the ontogeny, following the cardinal, the alar and the counter-lateral septa in its occurrence; (iii) the counter septum either remains underdeveloped throughout corallite growth or increases in length in the course of corallite growth up to becoming equal to the remaining major septa; and (iv) there are two opposite trends in the development of the counter septum: in Plerophyllina it is derived from the axial septum, long in the early ontogeny, and may be step by step reduced in length during corallite growth in some genera (e.g., *Plerophyllum*, *Ufimia*). In Tachylasmatina it is as mentioned in points i–iii. The set of characters listed is adequate for accepting the independent suborder status of the Plerophyllina and Tachylasmatina. Parallel development of several mature characters in Plerophyllina and Tachylasmatina cannot prove the synonymy of those two as shown above.

The lower Carboniferous European representatives of the Family Pentaphyllidae discussed above constitute only part of taxa belonging to the suborder Tachylasmatina. Several may belong to the Family Tachylasmatidae Grabau, 1928, selected by Fedorowski (1973) as the nominal family for the suborder as having priority over the Pentaphyllidae. That selection was only in part unfortunate. *Tachylasma cha* is known from only a single transverse section of the mature growth stage of its holotype, but Grabau (1922, pl. 1, fig. 2a) illustrated that specimen as almost complete. Thus, there is a theoretical chance of its more complete study when/if it is found. Unfortunately, Grabau (1928, p. 37) noted the loss of the holotype label, reducing to zero the chance of finding the topotypes.

The stratigraphic position of *Tachylasma* is uncertain. Grabau (1922) considered *Tachylasma cha* as probably Carboniferous, but this cannot be proven. All the remaining species of *Tachylasma* introduced by him (Grabau 1922, 1928), are Permian in age. Schindewolf (1942, p. 175) considered the occurrence of *Tachylasma* as exclusively Permian: “*Tachylasma* dagegen is nach unserer derzeitigen Kenntnis aus das Perm beschrenkt.” Schindewolf (1952), followed by Weyer (1977), changed his previous opinion by introducing a new species name *Pentaphyllum* (*Tachylasma*) *silesiacum* Schindewolf, 1952 to the upper Serpukhovian specimens from the Upper Silesian Coal Basin (Poland and Czech Republic). However, a revision of the type collection of that species (Fedorowski 2012) documented its difference from the Permian *Tachylasma* which allowed its distinction as a new genus *Effigies* Fedorowski, 2012 of the Subfamily Commutinae Fedorowski, 1973. Thus, *Tachylasma* is absent from the European lower Carboniferous and stratigraphically younger strata of this part of Laurussia. However, it may occur in the Permian strata of the part of Laurussia comprising the recent Urals (Soshkina *et al*. 1941), Greenland (Flügel 1973) and the Canadian Arctic Archipelago (Fedorowski and Bamber 2001), if *Plerophyllum variabilis* Soshkina, Dobroljubova and Porfiriev, 1941 represents that genus. Fedorowski and Bamber (2001) moved *Plerophyllum variabilis* to *Tachylasma* but its morphology in both the immature and mature growth stage is atypical for *Tachylasma* in Grabau’s (1922, 1928) and Schindewolf’s (1942) meaning. Thus, the occurrence of *Tachylasma* in the areas other than the Palaeotethys Realm and in the strata other than Permian, is not reliably documented.

The latter statement has opened a question on the relationship, synonymy, or homeomorphy of the Families Pentaphyllidae and Tachylasmatidae as suggested by Hill (1981). That suggestion is not followed here. In the case of the Pentaphyllidae, both species of *Pentaphyllum* introduced by de Koninck (1872) occur in the upper Tournaisian strata of Belgium and *Cryptophyllum hibernicum* has been originally described from the Bundoran shale (i.e., Arundian–lower Viséan) of Donegal Bay, Ireland. The occurrences of 16 potential members of *Cryptophyllum*, originally bearing various generic names, and derived from various areas (Fedorowski 2009b, table 2), cover the time span from uppermost Famennian/lowermost Tournaisian to the Serpukhovian inclusively, with most being known from the Tournaisian and the Viséan (for further occurrences and comments see Fedorowski 2009b, pp. 569–573). Except for the ambiguous ‘*Cryptophyllum*’ *striatum* Rowett, 1969 from the post-Atokan of Alaska, the specimens described herein, identified as *Pentaphyllum* and Gen. nov. derived from the lower Bashkirian deposits of the Donets Basin, Ukraine, are the stratigraphically youngest European taxa comparable to either *Pentaphyllum armatum* or *P. caryophyllatum*. Thus, the family Pentaphyllidae is absent from Europe in the upper Carboniferous and Permian strata.

Species resembling *Pentaphyllum* were long ago recognised from the Permian of Asia, Australia and the Timor Island (e.g., Hinde 1890; Rothpletz 1892; Frech and Arthaber 1900; Gerth 1921; Koker 1924). Most of them were included in *Plerophyllum* Hinde, 1890, but the afore mentioned authors were aware about the close morphological similarity of their specimens to European taxa. Moreover, they were conscious about the upper Carboniferous gap in their occurrences, but the morphological similarities of those species to lower Carboniferous taxa were accepted by most of them as a close relationship irrespective of the differences in time and geographical occurrences. Only Frech and Arthaber (1900, p. 287) expressed some doubts of those relationships and considered the possibility of 'geological convergence'. This was the first suggestion known to me contesting the direct relationship of both European lower Carboniferous and Far East Permian corals. Schindewolf (1942, p. 175) did not accept the suggestion by Frech and Arthaber (1900), but pointed out the close similarity of both groups of corals in their ontogeny and the mature morphology, and concluded "…diese altersverschiedenen Formen systematisch mitainander zu vereinigen und mit dem Bestehen lang andauernden Entwicklungsreihen zu rechnen." The meaning of Schindewolf's (1942) words, expressed prior to the introduction of plate tectonics is understandable. However, Weyer and Ilina (1979), Ilina (1984) and Ezaki (1991) accepted morphological similarity as demonstrating the close relationship of the upper Permian corals from eastern Palaeotethys to Mississippian European taxa when the occurrence of the Pangea was obvious. I follow here my earlier opinion (see Fedorowski 2009b, p. 575) and reject the genus level relationship of the taxa from the lower Carboniferous of Europe and the Permian of the Far East.

An attempt by Ezaki (1991) to transfer variability in the early ontogeny, established by him in the upper Permian corals from Asia onto European taxa in order to document their close relationship is an obvious methodological error, as has been already pointed out (Fedorowski 2009b, p. 575). However, does the isolation in space and time of species passing through the cryptophylloid early ontogeny stage suggest their convergent evolution? The occurrence in both Europe and China of taxa similar in their early ontogeny and the mature morphology during Mississippian times (e.g., Fan *et al.* 2003; Wang *et al.* 2004) may indicate their common roots. The oceanic connection of both areas allowed for the possibility of a long distance movement of coral larvae. Many rugose coral species, unquestionably identified as common for Europe and Asia in the upper Viséan, adequately support that idea (e.g., Fedorowski 1981; Poty 1981; Rodríguez and Said 2009).

A gap in the occurrence of taxa comparable to *Cryptophyllum* or *Tachylasma* during most of the Pennsylvanian is a current problem, but to some extent I will agree with the statement of Schindewolf (1942, p. 175) "…daß *Tachylasma* sich von *Pentaphyllum* ableitet." The relationship is perhaps not so close as Schindewolf had suggested, and the relationship of *Tachylasma* to *Cryptophyllum*, with the counter septum permanently short, is closer than to *Pentaphyllum* with that septum elongated so as to almost reach the length of the counter-lateral septa, but the general idea can be considered as possible. Those commonly rooted Mississippian representatives of the Suborder Tachylasmatina became isolated by Pangea in their further phylogeny. Thus, a monophyletic phylogeny for both the European, and Far Eastern taxa with a cryptophylloid or tachylasmatid morphology can be suggested. The formation of Pangea may have resulted in the appearance of a separate lineage in the Palaeotethys Realm lasting there up to the late Permian, whereas the ancestral, European lineage terminated perhaps in the early Bashkirian or the Moscovian, if the Alaskan specimen described by Rowett (1969) is considered. The Palaeotethys lineage is not discussed here because my knowledge of Chinese literature is inadequate for well documented conclusions. This results in treating here the Palaeotethys lineage as either Lazarus taxa or to suspect the continuous development of the lineage through the Carboniferous and Permian. Irrespective of the option, the Palaeotethys lineage, i.e., the Family Tachylasmatidae, has common roots with the Pentaphyllidae. Thus, both the families Tachylasmatidae and Pentaphyllidae may be valid and both may belong to the Suborder Tachylasmatina.

Genus *Pentaphyllum* de Koninck, 1872

TYPE SPECIES: *Pentaphyllum armatum* de Koninck, 1872, designated by Schindewolf (1942, p. 180).

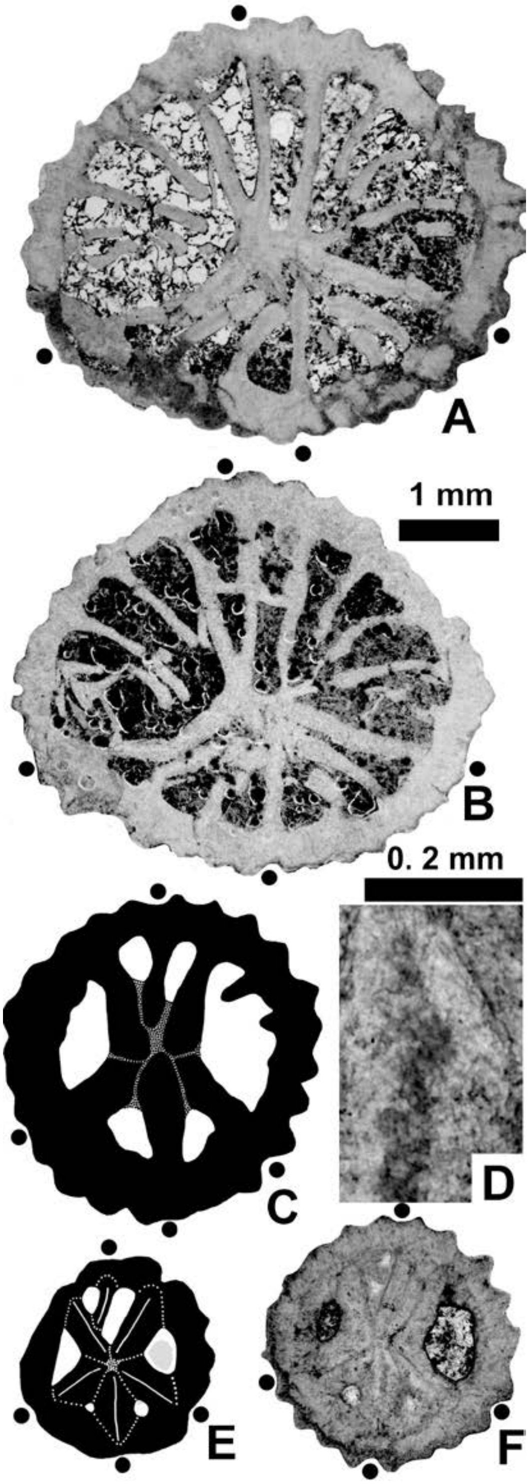
SPECIES ASSIGNED and DIAGNOSIS: Not established for the reasons pointed out in the discussion above.

REMARKS: The genus *Pentaphyllum* was revised quite recently (Fedorowski 2009a) and has not been discussed since. Thus, the reader is kindly referred to that paper and to the remarks on the family above. The taxonomic value of the amplexoid character of septa and the equalisation of all major septa in the mature growth stage are discussed below under the remarks to Gen. nov.

Only two corallites within the entire collection of more than 400 Bashkirian rugose corals from the Donets Basin described by Vassilyuk (1960, and in Aizenverg *et al.* 1983) and by me starting with Fedorowski (2009c) expose the characters of *Pentaphyllum*. The brephic growth stage is missing from both. The early neanic growth stage of one (Text-fig. 4E, F, C, respectively) is typically cryptophylloid, whereas that of the second one (Text-fig. 5B, D, E) is doubtful (see below). Also, their mature growth stages differ to the extent excluding a close relationship. Their early Bashkirian occurrence, however, later than all undoubtful *Pentaphyllum*-like and *Cryptophyllum*-like species known to me, makes them important in a phylogenetic aspect. Thus, they are described and fully illustrated, but left in open nomenclature.

Pentaphyllum sp. nov. 1
(Text-fig. 4)

DESCRIPTION: One almost complete corallite UAM-Tc.Don.1/377 with only the brephic growth stage missing. Lower part of deep calice preserved (Text-fig. 4A), but morphology of upper part destroyed by compaction. External wall up to 0.4 mm thick with deep septal furrows. In early neanic growth stage (Text-fig. 4E) with n:d value 6:1.8 mm; five septa, i.e., cardinal protoseptum, alar and counter-lateral major septa thick and long, meeting in corallite axis, but their middle dark lines (primary septa) separated. Counter protoseptum thinner than those five major septa, reaching approximately 1/2 of their length. It meets surface of left counter-lateral septum. Other septa absent from corallite lumen and their furrows, if originally present, not preserved. Numerous septal furrows recognisable within 0.7 mm corallite growth (n:d value 6:2.5 mm), but septal blades absent from corallite lumen and not recognised within thickness of external wall (Text-fig. 4F), possibly due to diagenetic alteration. Five major septa remain dominating. Counter protoseptum elongated to 2/3 length of the counter-lateral septum it meets. Next major septa appear in corallite lumen within 0.8 mm of further corallite growth (n:d value 11:3.0 mm); all in counter quadrants that strongly dominate in volume (Text-fig. 4C). Five major septa keep dominating, whereas counter protoseptum reaches 3/4 length of the counter-lateral septum it meets. In mature growth stage, approximately 2.6 mm of further



Text-fig. 4. *Pentaphyllum* sp. nov. 1. Specimen UAM-Tc.Don.1/377. Transverse thin sections. A – lower part of calice, mature growth stage, B – immediately below calice, mature growth stage, C – late neanic growth stage, D – remnants of trabeculae (enlarged from F), E, F – early neanic growth stage. For stratigraphic position see text. Scale bar between A and B corresponds to all images except D. Black dots correspond to protosepta and alar septa.

corallite growth, i.e., just below calice floor and in calice shortly above its floor (Text-fig. 4B, A, respectively) with n:d values 18:4.8 mm and 20:5.1 mm, all major septa only moderately thickened. Five dominating major septa remain connected in corallite lumen. Counter protoseptum almost as long as those dominating major septa, remain attached to lateral surface of left counter-lateral septum. Counter quadrants remain dominating over cardinal quadrants in both room and number of major septa. Most newly inserted major septa free-ended, approach short distance to corallite axis or adjacent dominating major septa. Rare minor septa appear as slight thickenings of external walls between some major septa.

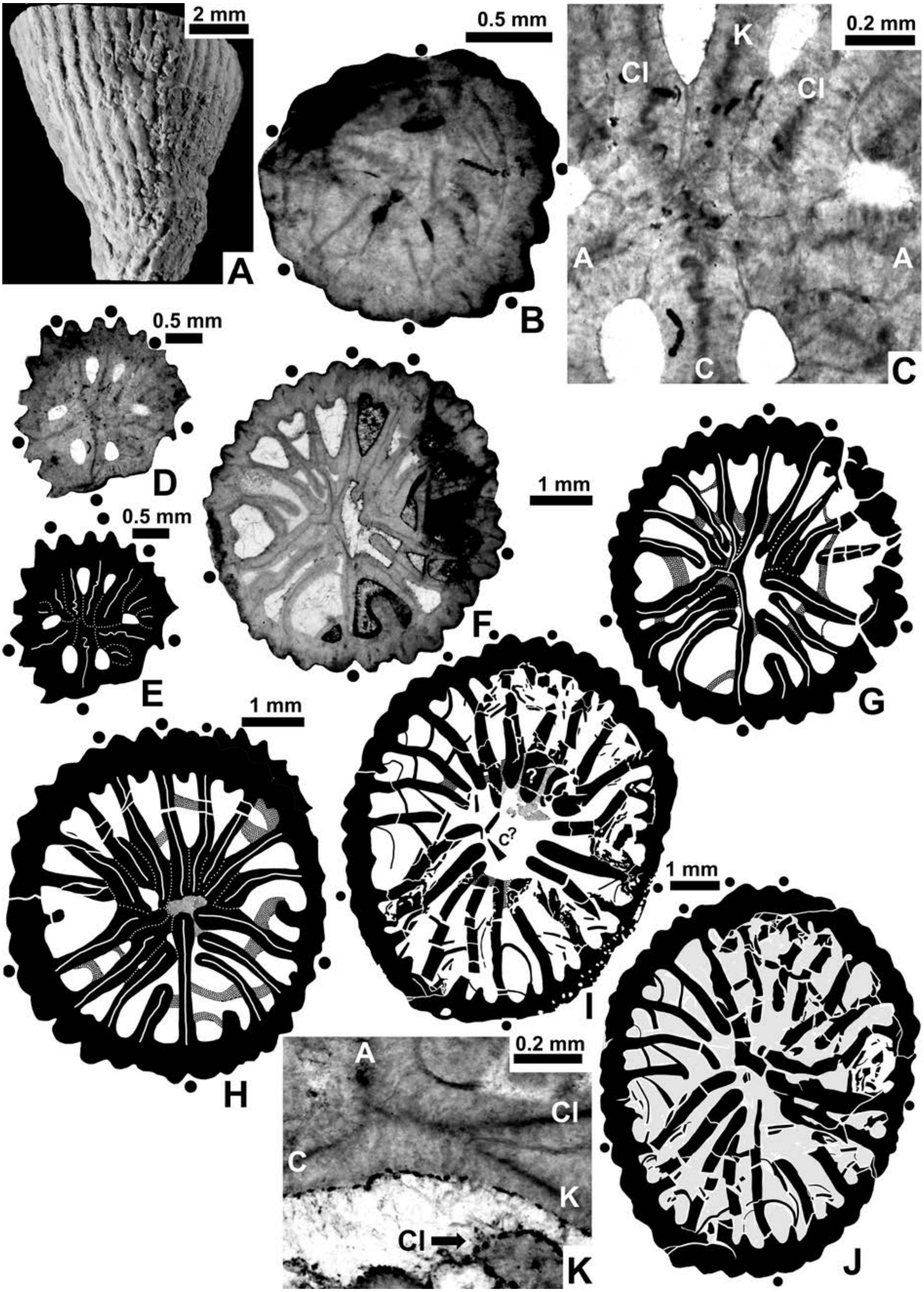
REMARKS: The character of the counter protoseptum, elongating step by step during corallite growth, is of special value in the context of the absence of the brephic growth stage. Such a progress is considered here as a proof of it being inserted separately and with some delay by comparison to other dominating major septa. Its elongation, up to almost reaching the length of the counter-lateral septa allows the identification of that specimen as closely related to the holotype of *Pentaphyllum armatum*. It differs from that holotype in having a smaller diameter and number of septa, in keeping all dominating major septa connected above the calice floor and in having the remaining major septa much longer.

OCCURRENCE: Kalmyus River Area, north of Voznesenka Village, Krutoy Yarok Balka (Ravine). Shales immediately above Limestone D_7^7. Upper Voznesenkian Horizon, Upper *Homoceras–Hudsonoceras* ammonoid Biozone, *Declinognathodus noduliferus* conodont Biozone or *Semistaffella minuscularia* foraminiferal Biozone. Lower Bashkirian.

?*Pentaphyllum* sp. nov. 2
(Text-fig. 5)

DESCRIPTION: One almost complete corallite UAM-Tc.Don.1/378. Its skeleton altered diagenetically, so that some details remain uncertain and interpretative. Calice flattened by pressure. Surface of 0.3–0.4 mm thick external wall bears deep septal furrows (Text-fig. 5A). Early brephic growth stage missing. Earliest neanic or late brephic growth stage, 1.8 mm in diameter (Text-fig. 5B) diagenetically altered. Five strongly thickened major septa, differentiated in shape and length fill corallite lumen almost completely. Small empty fragment present against septal furrow corresponding to counter protoseptum and absence of that protoseptum in corallite lumen may be interpreted either as being retarded in insertion or as diagenetic damage. Widely wedge-shaped cardinal protoseptum shorter than alar septa and not extending to corallite axis supports first option accepted here. Corallite morphology changes considerably within 1.1 mm of its further growth with n:d value 10:2.6×2.8 mm (Text-fig. 5D, E). Six major septa, i.e., both protosepta, alar and counter-lateral septa dominate and become almost equal in length and thickness. Protosepta located against one another meet in corallite axis, but their middle dark lines probably separated (Text-fig. 5C). Middle dark line of cardinal septum united with middle line of left counter-lateral septum same way as it does in a more advanced growth stage (Text-fig. 5K). Two new major septa inserted in the right counter quadrant; one in the left counter quadrant and one in the right cardinal quadrant make arrangement of septa asymmetrical. 4.1 mm of corallite growth not sectioned. Growth stage after that gap either late neanic or early mature with n:d value 20:5.1 mm. Major septa bilaterally arranged, long and variable in length (Text-fig. 5F, G). Middle lines of cardinal protoseptum, left alar and left counter-lateral major septa united (Text-fig. 5K). Counter protoseptum longer than right counter-lateral septum, but shorter from right counter-lateral septum to which it is attached. Their middle lines united. Bilateral symmetry in arrangement of major septa present till the end of a reasonably preserved part of corallite (Text-fig. 5H–J). Protosepta in that growth stage meet to form symmetry axis, but their middle dark lines probably separated. Counter protoseptum as long as counter-lateral septa. Alar septa longest of major metasepta in cardinal quadrants, but not truly dominating. Some minor septa appear in corallite lumen, most in counter quadrants. In mature growth stage with n:d value 22:8.1×6.5 mm (Text-fig. 5I, J) all major septa free-ended, slightly differentiated in length. In cardinal quadrants they shorten step by step towards long cardinal septum that approaches corallite axis. In counter quadrants that sequence is not followed. Counter septum slightly shortened, but longer that right counter-lateral septum. Temporary elongation of that septum (Text-fig. 5I) may be artificial. Minor septa present in almost all septal loculi, but remain as short, wedge-like bodies on external wall.

REMARKS: The variable, but generally long length of the counter protoseptum lasting up to the mature growth stage (Text-fig. 5J) is a character making the identification of the specimen described as


2 mm
A
0.5 mm
B
0.2 mm
K
Cl
Cl
A
A
C
C
0.5 mm
D
0.5 mm
E
F
1 mm
G
1 mm
H
?
C?
I
1 mm
J
A
0.2 mm
Cl
C
K
Cl
K

Pentaphyllum disputable. Diagenetic alterations increase these doubts precluding the indisputable recognition of the relationship of protosepta and length of the counter septum during the earliest corallite growth. The similarity of the early growth stages of ?*Pentaphyllum* sp. nov. 2 (Text-fig. 5B–H) to the early growth stages of the holotype of *Pentamplexus simulator* Schindewolf, 1940 (Schindewolf 1940, fig. 10a–c; Schindewolf 1942, fig. 89a–d, pl. 33, fig. 2a–d; Fedorowski 2009a, text-fig. 1A–H) increases those doubts. The early ontogeny of *P. simulator* documents its relationship to *Calophyllum* Dana, 1846 but not to *Pentaphyllum*. The early ontogeny of the specimen discussed here would be calophylloid, if: 1) the counter septum in the earliest growth stage studied (Text-fig. 5B) was long and its shortening apparent, resulting from diagenetic damage, but not underdeveloped as interpreted herein; 2) the middle dark lines of the protosepta, but not those of the cardinal protoseptum and the left counter-lateral septum are united. However, the middle dark line of the counter protoseptum closely approaches these two or even meets them (Text-fig. 5C); 3) the middle dark lines of the cardinal protoseptum and the right alar septum are united and are met by the middle dark line of the counter protoseptum and the left counter-lateral septum. The latter two join one another as equal (Text-fig. 5G, K), i.e., the counter septum cannot be indicated; 4) the counter protoseptum is temporarily shorter from the counter-lateral septa (Text-fig. 5I), but it is otherwise longer than one and shorter than the other counter-lateral septum (Text-fig. 5F, G, J). All those doubts result in the questionable identification of the specimen discussed. However, in general the differentiation in the length of its major septa is closer to that in *Pentaphyllum* rather than in *Calophyllum*. Thus, it is treated here as an extreme form of *Pentaphyllum*, clearly different from all species of that genus described so far.

OCCURRENCE: Kalmyus River Area, north of Voznesenka Village, Krutoy Yarok Balka (Ravine). Shales immediately above Limestone D_7^7. Voznesenkian Horizon, Upper *Homoceras*–*Hudsonoceras* ammonoid biozone, *Declinognathodus noduliferus* conodont biozone or *Semistaffella minuscularia* foraminiferal biozone. Lower Bashkirian.

Genus novum

TYPE SPECIES: Gen. et sp. nov. 1.

SPECIES ASSIGNED: By monotypy.

DIAGNOSIS: Solitary, nondissepimented rugose coral; early ontogeny pentaphylloid with protosepta inserted separately from one another; counter septum retarded in secretion and slightly shorter than counter-lateral septa, but six major septa, i.e., both protosepta, alar septa and counter-lateral septa dominate in the neanic growth stage; in mature growth stage major septa amplexoid, equal in length, leave axial corallite area free; cardinal fossula not developed; minor septa underdeveloped, appearing late in ontogeny; microstructure of septa trabecular.

REMARKS: This new genus was introduced with a formal name in the first draft of this paper, but this was contested by critical readers as being based on a single corallite. Thus, I leave it here in open nomenclature despite the almost complete preservation of the specimen, allowing the study of almost all growth stages, except for the early brephic stage and the calice damaged by compaction. Also, the microstructure of its septa, although destroyed in most corallite fragments, was preserved in some, thus allowing for that important character to be mentioned. The peculiar mature morphology, following the characteristic pentaphylloid morphology of the immature growth stage, leaves no doubts as to both its relationships and distinction.

The term 'pentaphylloid morphology' is used here to distinguish the early ontogeny of the corals apparently related to *Pentaphyllum armatum* from the corals of *P. caryophyllatum* and taxa related to that species. *Pentaphyllum armatum* is the type species for the genus *Pentaphyllum*, whereas *P. caryophyllatum* belongs to *Cryptophyllum* as suggested already by Hudson (1936a) and Fedorowski (2009b) and accepted here (see remarks to the family). The early ontogeny of the latter is known as cryptophylloid (Fedorowski 2009b, text-fig. 1A, B). The counter septum in both lineages was inserted in the disconnection from the cardinal septum. However, it remains highly underdeveloped during the entire ontogeny

← Text-fig. 5. ?*Pentaphyllum* sp. nov. 2. Specimen UAM-Tc.Don.1/378. Transverse thin sections, except A. A – corallite side view, B – early neanic growth stage, C – middle dark lines (primary septa) in corallite axis (enlarged from D), D, E – neanic growth stage (E – drawing of D), F–H – early mature growth stage (G – drawing of F), I, J – mature growth stage, K – middle dark lines (primary septa) in corallite axis (enlarged from H). For stratigraphic position see text. Scale bars between two adjacent images corresponds to both, those right of image corresponds only to that image. Black dots correspond to protosepta and alar septa. Abbreviations: A – alar septum, C – cardinal protoseptum, Cl – counter-lateral septum, K – counter protoseptum.

in corallites of the cryptophylloid lineage, whereas in corallites of the pentaphylloid lineage, the counter septum increases its growth in the course of the ontogeny, up to becoming almost equal to the counter-lateral major septa, as exemplified by the holotype of *P. armatum* (Fedorowski 2009b, text-fig. 2B, E) or equal to them as observed in Gen. et sp. nov. 1.

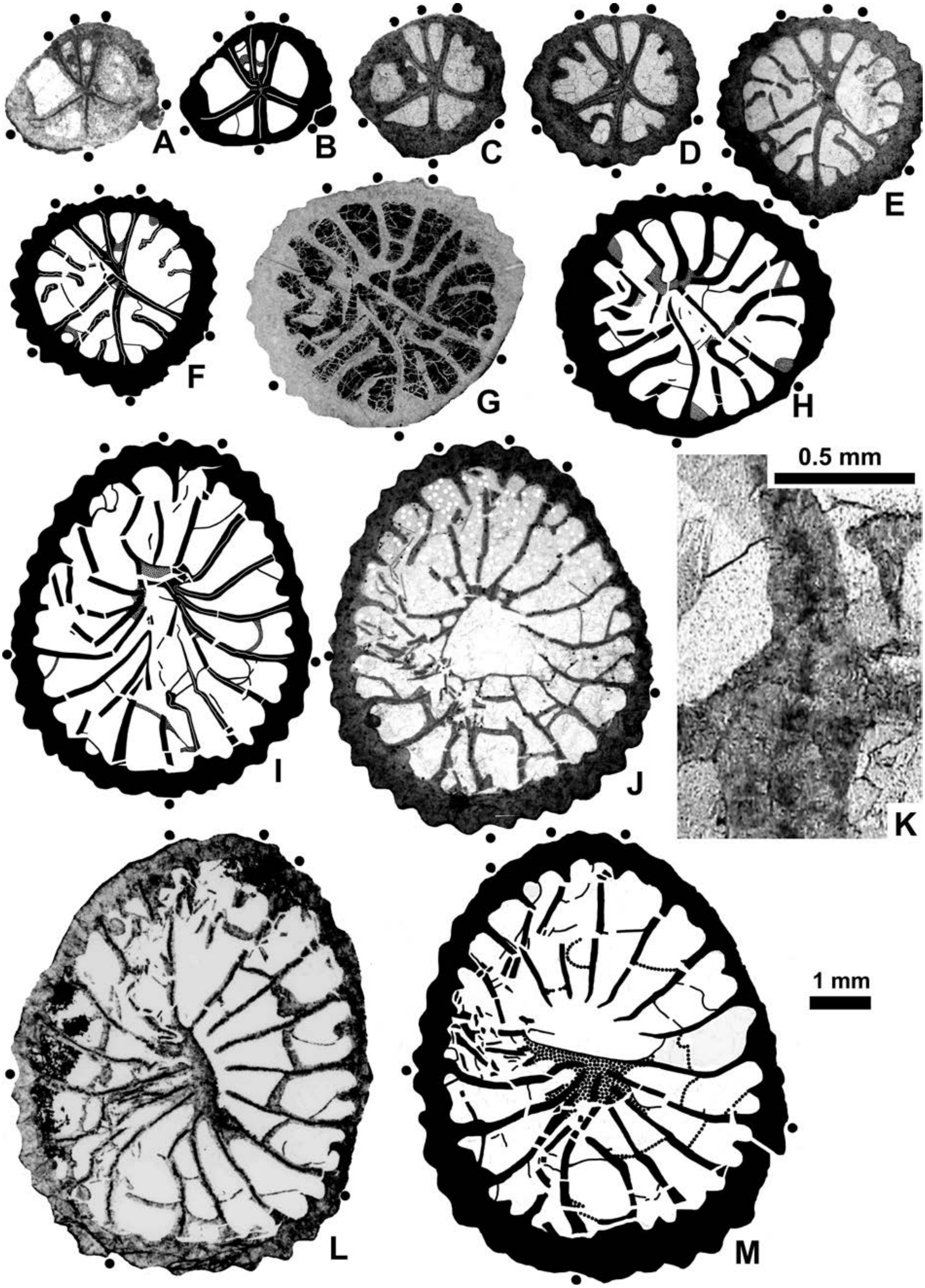
My opinion concerning the value of the early ontogeny is discussed above with remarks to the Family Pentaphyllidae and in my papers mentioned with those remarks. Thus, only *Pentamplexus* Schindewolf, 1940 and *Pseudocryptophyllum* Easton, 1944 are briefly discussed herein as exposing some similarities in the early ontogeny (both genera) and shortening of major septa (the former).

Pentamplexus, revised by Weyer and Ilina (1979) and Fedorowski (2009a), was included by Ezaki (1991) in the synonymy with *Pentaphyllum* together with *Pleramplexus* Schindewolf, 1940. Ezaki (1991, p. 62) mentioned the paper by Weyer and Ilina (1979) but disregarded their opinion concerning those ampleximorph genera. He considered the shortening of major septa as taxonomically insignificant and explained it as an alteration of a short and long septal corallite growth. However, an apparent alteration illustrated by Ezaki (1991, pl. 1, fig. 1i–k; pl. 7, fig. 1h–k) resulted from the amplexoid character of the major septa. Differences in their length depend upon the position of the transverse sections just above the tabula (long septa) or below it (short septa). Thus, the amplexoid character of the major septa, but not their alteration in length was demonstrated by Ezaki (1991) and his idea cannot be accepted. Also, I reject Ezaki's (1991) idea of a restricted taxonomic value of the derivation and development of the counter septum (see above). In addition to the latter questions and domination of six, rather than five major septa in the type species contrary to its generic name, one more issue, i.e., the geographic and stratigraphic positions of the species described by de Koninck (1872) *vs* those described by Schindewolf (1940, 1942), Ilina (1965, 1984), Flügel (1968, 1972, 1991, 1997); Weyer and Ilina (1979), and Ezaki (1991) should be raised in this part of the discussion. Remarks dealing with the question of the relationship at family level of the taxa from two distant areas, i.e., Europe on the one hand and the Timor Island, Armenia, Iran and the Far East on the other hand, are discussed in remarks to the family (see above). I accept the relationship at family level of the taxa from both areas, but I cannot accept the common generic position of the Asian upper Permian and European Mississippian species described as *Pentaphyllum*. Thus, not only the enormous difference in time of their occurrence, i.e., approximately 80–100 Ma, but also the formation of Pangea and the complete isolation of European and Asian sites by that supercontinent must be considered. My restudy of *Pentamplexus simulator* Schindewolf, 1940 (Fedorowski 2009a), documenting its position within the Family Polycoeliidae de Fromentel, 1861, supports at least in part this suggestion. The question of relationship *vs* homeomorphy in rugose corals, including some pentaphylloid *vs* plerophylloid taxa has been discussed in one of my previous papers (Fedorowski 2010) and is not repeated here.

The mature morphology of the corallite described herein (Text-fig. 6L, M) combines the amplexoid character of the major septa, including the protosepta, equalisation in length of all major septa and their moderate shortening. That set of characters allows its comparison to the species illustrated by Ezaki (1991) in the amplexoid aspect and to *Pentamplexus* in the shortening of the major septa. However, these characters cannot be treated as proof of the relationship to the specimens from Asia and the Timor Island for the reasons discussed above. They clearly document the distinction of its bearer from *Pentaphyllum armatum* at genus level.

Pseudocryptophyllum (Easton 1944, pl. 4, figs 8–11, pl. 16, fig. 31) from the Chouteau Limestone (Tournaisian) of Missouri, USA, bears some resemblance in its morphology to *Pentaphyllum*. Unfortunately, neither its description nor illustrations can serve as a rigid basis for the discussion of its relationship. Five major septa dominate in its earliest ontogenetic growth stage and its counter septum which is only slightly shorter than the counter-lateral septa may suggest its relationship to *Pentaphyllum*, whereas an aulos-like structure present in maturity may document its generic distinction when/if confirmed. Isolation of the Mississippi Valley Province from the remaining parts of the early Carboniferous seas, made most of its rugose coral fauna endemic. Thus, a relationship of any taxon from that province to the European taxa requires much stronger

Text-fig. 6. Gen. et sp. nov. 1. Specimen UAM-Tc.Don.1/379. Transverse thin sections. A–D – early neanic growth stage (B – drawing of A), E, F – late neanic growth stage (F – drawing of E), G–I – late neanic early mature growth stage (G – peel, H, I – drawings of peel images), J, L, M – mature growth stage (M – drawing of peel image), K – remnants of tabulae in septum (enlarged from E). For stratigraphic position see text. Scale bar corresponds to all images except for K. Black dots correspond to protosepta, alar and counter-lateral septa. →


A
B
C
D
E
F
G
H
I
J
0.5 mm
K
L
M
1 mm

evidence than that available from the description of *Pseudocryptophyllum* by Easton (1944).

Gen. et sp. nov. 1
(Text-fig. 6)

MATERIAL: Specimen UAM-Tc.Don.1/379 only. Corallite ceratoid, only slightly curved with attachment scars weak. Thick external walls bear deep septal furrows that appeared early in ontogeny. Early brephic growth stage missing. Late brephic or early neanic to mature growth stage well preserved. Calice crushed. Five thin sections and ten peels were available for the study.

DIAGNOSIS: Specimen with mean n:d value in maturity 20:6.8 mm; external wall thick with distinct septal furrows; major septa in mature growth stage thin, amplexoid, beneath tabula 3/4 corallite radius long.

DESCRIPTION: Corallite with n:d value of earliest growth stage preserved 6:2.2×1.6 mm. Cardinal, alar and counter-lateral septa meet in corallite axis. Counter septum only slightly reduced in length, attached to left counter-lateral septum. Middle dark lines of these septa isolated by sclerenchymal thickening of counter-lateral septum (Text-fig. 6A, B). First major septa other than mentioned above appeared in corallite lumen within 0.7 mm of its growth and n:d value 10:2.6×2.4 mm (Text-fig. 6C). Minor septa absent from this growth stage and during approximately 3.5 mm of further corallite growth although their furrows are recognisable. Counter quadrants dominate in volume from earliest growth stage observed, but domination of these quadrants in number of septa begin clearly with n:d value 12:2.7×2.5 mm. In addition to counter-lateral septa, two short minor septa occur in each counter quadrant and one major septum accompanies alar septum in each cardinal quadrant (Text-fig. 6D). Bilateral symmetry in arrangement of septa accentuated with n:d value 17:3.2×2.9 mm, 0.8 mm above the previous growth stage (Text-fig. 6E). That short-lasting morphology terminates the classic pentaphylloid arrangement of major septa with five septa dominating, counter septum only slightly shorter than counter-lateral septa and remaining major septa well developed, reduced successively in length towards cardinal septum and alar septa.

The transition from the neanic to mature growth stage begins with n:d value 18:4.5×4.1 mm, an almost total rearrangement of major septa and equalisation in length of most of them except long cardinal septum and right alar septum (Text-fig. 6G, H). In early mature to mature growth stage (Text-fig. 6I–M) with n:d value 18:6.1×5.1 mm to 20:7.1×5.5 mm, six major septa dominating in early ontogeny became equal to remaining major septa and underwent similar changes in length and arrangement, resulting from the amplexoid character and position of given transverse section on the surface of tabula or beneath tabula. Only cardinal septum recognisable by underdevelopment of last pair of major septa inserted in cardinal quadrants. Microstructure diagenetically altered in most septa. In rare instances (Text-fig. 6K) remnants of comparatively large trabeculae can be established. It is difficult to judge whether their diameter, approximately 0.05 mm, is original or they were diagenetically enlarged by overgrowth of inorganic crystals.

OCCURRENCE: Kalmyus River Area, north of Voznesenka Village, Glubokiy Yarok Balka (Ravine). Shales immediately above Limestone D_7^7. Voznesenkian Horizon, upper *Homoceras–Hudsonoceras* ammonoid biozone, *Declinognathodus noduliferus* conodont biozone or *Semistaffella minuscularia* foraminiferal biozone. Lower Bashkirian.

CONCLUDING REMARKS

Pentaphylloid or cryptophylloid early ontogeny has not been documented either in *Pentaphyllum armatum* or in *Tachylasma cha*, i.e., the type species of the genera eponymous for the families. However, there are many taxa, differentiated in their mature morphology, but strikingly similar in their early ontogeny that are characterised by retardation of the counter protoseptum in appearance and development. The lineage with the zaphrentoid early ontogeny occurs parallel to this lineage of corals. Mature morphology of those taxa is differentiated as well, with some variants closely resembling the taxa which develop pentaphylloid or cryptophylloid early ontogeny. Schindewolf (1942) was the first to recognise that fundamental difference and attributed the subfamily level to that character. Fedorowski (1973) elevated that character to the suborder level and introduced the suborder Tachylasmatina, not accepted by most scientists.

The non-cognate rugose corals commonly utilised similar skeletal constructions in the mature growth stage (e.g., amplexoid or caninoid growth stage) that follow a completely different early ontogeny. Thus, only the latter character, but not the mature morphology, must be taken into account in phylogenetic reconstructions. A typical zaphrentoid early septogenesis begins with secretion of the axial septum, divided soon after into the cardinal and the counter septa, variously modifying in length during further corallite growth. The alar and the counter-lateral septa are inserted next. Shortening of the counter septum in the course of corallite growth, such as that observed in *Plerophyllum*, is one of the variants. In contrast, the counter septum in the pentaphylloid or cryptophylloid ontogeny is inserted only when the cardinal, the alar and the counter-lateral septa already occur in the corallite lumen. Also, it either stays underdeveloped to a variable extent, or becomes elongated in the course of corallite growth up to becoming unrecognisable from other major septa. Such completely different trends in development, lasting at least during the Carboniferous and Permian and observed in many genera, cannot be ignored. Thus, I maintain the existence of the Suborder Tachylasmatina as an independent taxon, parallel to the Suborder Plerophyllina.

The occurrence of species with a pentaphylloid or cryptophylloid ontogeny in the Mississippian both in Europe and in the Far East suggests their direct relationship. However, the barrier of Pangea, impassable for rugose corals, resulted perhaps in the independent development of the phylogenetic lineage in the Palaeotethys Realm. Thus, the validity and relationship of both families: Tachylasmatidae and Pentaphyllidae is suggested with the former being restricted to the Palaeotethys Realm and mostly comprising Permian taxa, whereas the latter, being ancestral to the Tachylasmatidae, was perhaps restricted in occurrence to the Mississippian and the earliest Pennsylvanian times.

The taxa described herein, although represented by only three specimens, document the passing of pentaphyllid taxa through the Serpukhovian mass extinction, i.e., the most severe period in the phylogeny of the Carboniferous rugose corals. Also they expose a potential to create skeletons with characters unknown from their ancestors. The role of the Bashkirian Rugosa from the Donets Basin for the phylogeny of the Pennsylvanian and Permian rugose coral taxa in general is widely discussed in the concluding paper that follows (Fedorowski in preparation).

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