

Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 12. Concluding considerations

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ABSTRACT:

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A detailed analysis of the upper Viséan, Serpukhovian and Bashkirian Rugosa of the Donets Basin confirms their Mississippian/Pennsylvanian turnover during the *Eumorphoceras* / *Homalophyllites*–*Hudsonoceras* Zone, as postulated earlier (Fedorowski 1981a). The deterioration of rugose corals, globally diverse in time and space in the late Viséan and Serpukhovian, has resulted in the patchy distribution of survivors and newcomers, present in the Bashkirian. Difficulties in inter-basinal communication and the isolation of some sites have resulted in a different content of Bashkirian Rugosa in particular patches, with only rare genera in common. New data has made it possible to document the appearance of the first late Carboniferous genera in the Donets Basin as early as the lower Voznessenian Horizon (= lower Chokierian Substage), i.e., close to the beginning of the Bashkirian Stage. The two stages of diversification, established in the Bashkirian rugose corals of the Donets Basin, cannot find their counterparts elsewhere. A palaeogeographic overview of the most important sites of diversified rugose corals documents the need to re-examine many taxa, which should be based on complete specimen studies. This and the precise placement of taxa in the modern stratigraphy must be done in order to make rugose corals globally comparable. Simple repetitions of names, commonly used in general summaries, is strongly misleading in both stratigraphic and palaeogeographic reconstructions.

Key words: Rugosa; Global overview; Serpukhovian/Bashkirian crisis; Lowermost Bashkirian recovery.

INTRODUCTION

The late Serpukhovian–early Bashkirian was the period of most important turnover in the evolution of late Palaeozoic rugose corals. Hill (1948, 1973, 1981), Vassilyuk *et al.* (1970) and Vassilyuk (1974, 1975) directly or indirectly pointed to this turnover. Vassilyuk (1974, p. 3) wrote: “...between Namurian A and Namurian B there was a turnover in coral development from the early Carboniferous to the late Paleozoic phase” (translated from Russian). Although this statement does not correspond exactly to more recent data, its general idea is clear. Unfortunately, the theory of plate tectonics was not applied in the

papers mentioned by Hill (1981, pp. F59–F62). Thus, this fundamental base of palaeobiogeographic reconstructions was ignored by their authors, including Hill (1981). Fedorowski (1978a, 1981a) summarised earlier data, applied plate tectonics to palaeobiogeographic reconstructions, and suggested a single cycle of evolution of Carboniferous and Permian rugose corals. He divided this cycle into three phases, two of which occurred in the Carboniferous: the early Carboniferous (Mississippian) phase that began with the end of the Famennian/Tournaisian faunal turnover and ended with a deep crisis in the evolution of rugose corals at the end of the Arnsbergian Substage or Zapaltyubian Horizon in Ukrainian nomenclature;

and the middle or late Carboniferous (Pennsylvanian) phase that began in the Chokierian Substage, or Voznessenian Horizon in Ukrainian nomenclature, and lasted until the end of the Carboniferous. This general division is still valid today, although many papers have been published since that summary. Most of these new data concern the Viséan Rugosa, important for this stage but of little value for the topic discussed here. Nevertheless, a limited number of papers on Viséan Rugosa are mentioned elsewhere in this paper. The exceptions to this are the upper Viséan (Asbian and Brigantian Substages or Donetzian and Mezhivian Horizons) Rugosa from the Donets Basin. These and the Serpukhovian species from this basin, described mainly by Vassilyuk (1959, 1960, 1964) and Vassilyuk and Zhizhina (1978, 1979) are tabulated (Text-fig. 1) and discussed to demonstrate the Mississippian / Pennsylvanian turnover of the rugose corals in the Donets Basin as a kind of global model.

Papers on Serpukhovian taxa are considered here for two reasons: firstly, studies of Serpukhovian Rugosa have increased considerably in comparison to those mentioned in my earlier summary (Fedorowski 1981a) documenting a geographical dispersion and taxonomic diversity of rugose corals more broadly than previously thought. Secondly, Serpukhovian taxa are important as they commonly hide roots for the Bashkirian rugose corals, allowing a more precise commentary on the latter fauna at both regional and global scales. The number of papers dealing with the Viséan and Serpukhovian Rugosa is too numerous to cite in this introduction. Their citations are scattered throughout the text below, where appropriate. Older and new literature confirms the particular value for the Carboniferous–Permian evolutionary cycle of the early and middle Bashkirian rugose corals. Two groups can be distinguished in this fauna: survivors and newcomers. Therefore, a brief overview of data from the world literature is introduced. An analysis of the succession of rugose corals in specific areas is overlaid on the stratigraphy based on studies of conodonts, foraminifera and ammonoids wherever possible (see citations below).

In order to clearly show the turnover of the Carboniferous rugose coral fauna in the Donets Basin, not only taxa from the Viséan–Serpukhovian interval (Text-fig. 1), but also taxa from the middle and upper Bashkirian described by Fomichev (1953)

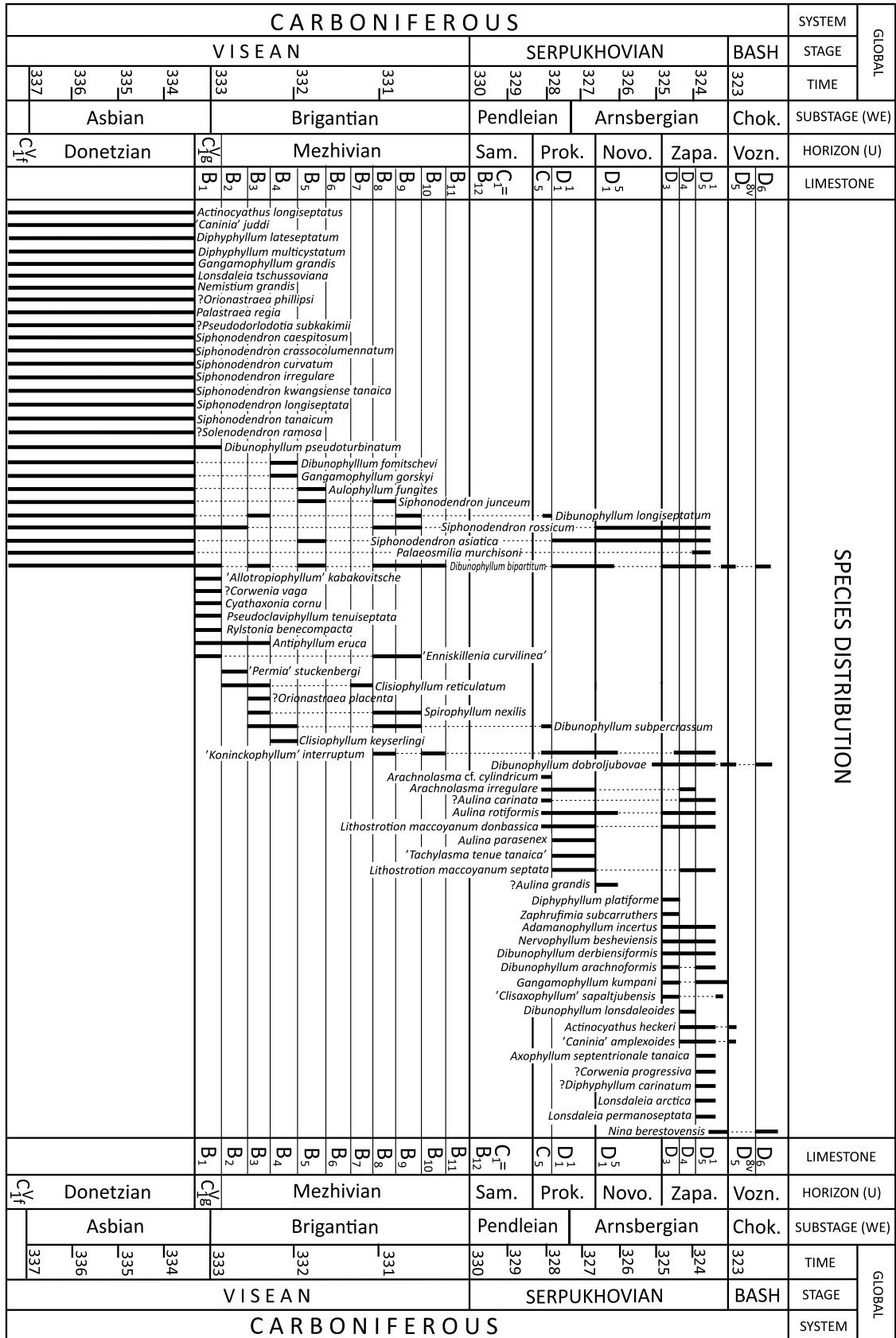
are cited in Text-fig. 2 and in the Discussion. The absence of these previously obtained data will result in a false idea of the development and sequence of rugose corals in the Donets Basin.

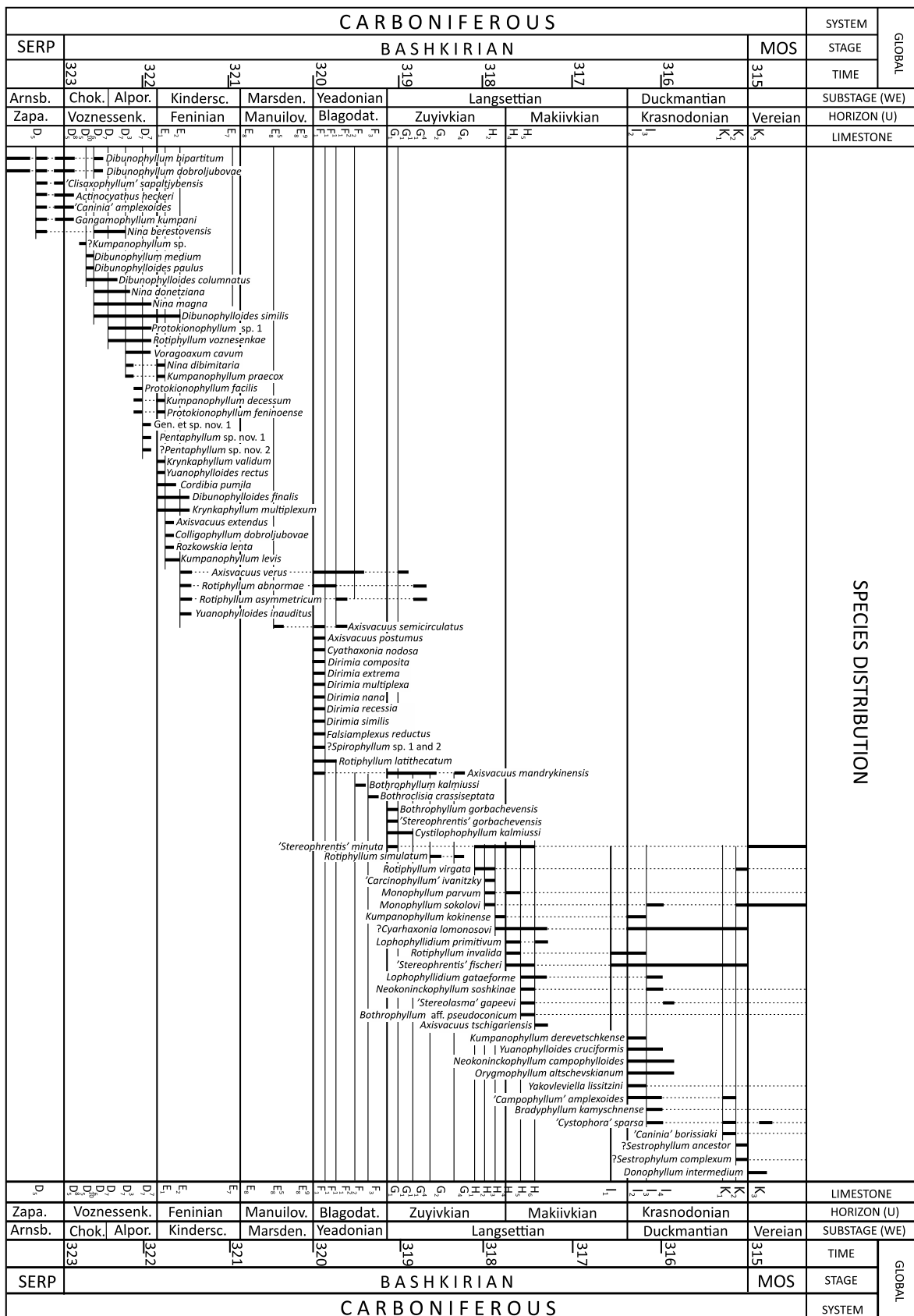
The Donets Basin is one of the few areas in the world where there is a relatively abundant collection of rugose coral specimens from all substages (or horizons in Ukrainian nomenclature) of the upper Viséan, Serpukhovian and Bashkirian strata (Text-figs 1 and 2). All these horizons are well-documented with ammonoid, foraminiferal and conodont markers (see papers cited below). This paper concludes a series of twelve papers on Bashkirian rugose corals from the Donets Basin (Fedorowski and Vassilyuk 2001, 2011; Fedorowski 2009b, c, 2017a, b, 2019a, b, 2021a, b; Fedorowski and Ogar 2013; Fedorowski and Ohar 2019). All these papers together form a monograph on the lower and middle Bashkirian Rugosa of this basin. Detailed taxonomic data can be found in these papers. A brief history of the Bashkirian stage and the history of its lower boundary, which was not permanently established for a long time, are presented by Fedorowski (2009b). The main characters of the geological succession in the Donets Basin during early and middle Bashkirian time are briefly commented on by Fedorowski (2009b, 2017a, 2019c). Drastic changes and/or the disappearance of some important type sites are mentioned by Fedorowski and Ogar (2013) and Fedorowski and Ohar (2019).

To establish the stratigraphic position of the described species, extensive summaries of the entire Carboniferous succession in the Donets Basin have been used, including the history of the investigations of individual horizons and their summarised profiles of the type sections (Poletaev *et al.* 2011) and a further summary by Gozhyk (Ed., 2013). The Pennsylvanian conodont succession established by Nemyrovskaya (1999, 2017) and the sequence stratigraphy (Eros *et al.* 2012) supplement the summaries. These papers allow me to reduce the geological setting of the Donets Basin to a few key details in this study. For geological details of the sites discussed in the Palaeogeographic Overview, the reader is referred to the papers cited in that overview.

Only a few taxa of rugose corals were known from the early and middle Bashkirian of the Donets Basin before the publication of my series of papers listed above. Fomichev (1953) described four

Text-fig. 1. Succession of upper Viséan and Serpukhovian rugose coral species in the Donets Basin (after Vassilyuk 1960, 1964; Vassilyuk and Zhizhina 1978, 1979). The ranges of the Asbian, Brigantian and Serpukhovian stages are represented disproportionately and their duration is corrected by proper annotation. Abbreviations: Bash. – Bashkirian, Chok. – Chokierian, Novo. – Novolyubivkian, Prok. – Prokhorivkian, Sam. – Samarian, Vozn. – Voznessenian, Zapa. – Zapalyubian; Horizon (U) – horizons in Ukraine, Substage (WE) – substages in Western Europe. →





species from the Limestone F Group (upper lower Bashkirian). He left one of them in open nomenclature. Vassilyuk (1960) described five Serpukhovian species, extending their occurrence to the basal Bashkirian (Limestone D₅^{8 upper}). Two of them re-appeared in Limestone D₆ (Text-figs 1 and 2). In addition, she introduced three new Bashkirian taxa: *Bothrophyllum berestovensis*, *Dibunophyllum finalis* and *Lytvophyllum dobroljubovae* redescribed, re-illustrated and re-named in my papers (Fedorowski 2017a, 2021a). Vassilyuk (1975; in Aizenverg *et al.* 1987; in Poletaev *et al.* 1990) mentioned a few but did not illustrate Bashkirian rugose corals. Such mentions are not considered in this summary. However, the taxa named and illustrated by Vassilyuk (in Aizenverg *et al.* 1983) are considered as valid despite the lack of description (see Fedorowski 2017a). Fedorowski and Vassilyuk (2001, fig. 1) have already attempted to summarise the sequences in the occurrence of Bashkirian taxa from the Donets Basin. They showed a poverty of the lower Bashkirian rugose coral fauna compared to the fauna from the older and younger strata. This poverty was only apparent, resulting from the incompleteness of coral studies at the time of their summary. It turns out to be much less drastic when one considers the 52 named species and 25 species left in open nomenclature, described in the series of papers summarised herein.

MATERIAL AND METHODS

The entire collection of Bashkirian Rugosa from the Donets Basin (Ukraine), consists of more than 400 specimens, of which 380 (acronym UAM-Tc. Don.1), stored at the Institute of Geology, Adam Mickiewicz University in Poznań, are preserved well enough to be identified at least to the genus level. Most of these specimens were collected by the late Dr. Nina Pavlovna Vassilyuk, former professor at the Donetsk Polytechnic. All these specimens were donated to me for study and repository. Most of the specimens studied in collaboration with Professor Victor V. Ohar from the National Taras Shevchenko University of Kyiv, Ukraine (Fedorowski and Ogar 2013; Fedorowski and Ohar 2019) were collected by him. Part of this collection is housed at the Institute

of Geology, Adam Mickiewicz University in Poznań together with Professor Vassilyuk's collection and bears the same acronym as mentioned above. Other specimens from this collection are housed in the National Taras Shevchenko University of Kyiv, Ukraine, acronym TSNUK.

The taxonomic variability of the rugose corals studied is so great that the number of specimens is sometimes insufficient to accurately represent and describe the species. As a result, 25 species are left in open nomenclature. All of them are most probably new species, some represent unknown genera. Fairly well-preserved specimens were classified into eight families (one new) with seven subfamilies (three new), 17 genera (seven new) and 52 named species (31 new). Some of the named species introduced by Fomichev (1953), especially these from strata younger than the middle Bashkirian, have only been commented on and illustrated in order to define these species and genera more precisely. These corrections were necessary to facilitate discussion and comparisons of new species. All these corrections and additions were based on peels taken from the collection of Fomichev (1953), located in the VSEGEI Museum in St. Petersburg (Russia), re-examined by me in 1968.

Both the older and, unfortunately, some of the more recent literature data are either insufficiently complete for indisputable generic identifications or I cannot agree with these identifications. Besides, I belong to the camp of splitters when it comes to the characterization of rugose corals and their evolution. Thus, an explanation of the obstacles I have encountered in using the literature data and my approach to taxonomy must be explained here as the methods used. The following obstacles and requirements are important: 1) The extinction of the Rugosa 252 my ago without any surviving offspring, and their exoskeletons, devoid of any organic remains, made these skeletons the only source of the taxonomic data thus requiring a complete investigation of all growth stages; 2) The number of skeletal structures possible for these primitive animals is limited. This has resulted in frequent repetition of identical skeletal structures found in phylogenetically distant taxa. Therefore, homeomorphy should be accepted as common and should be considered in all coral studies; 3) The different morphology of immature skeletons may

← Text-fig. 2. Succession of Bashkirian rugose coral species in the Donets Basin (after Fomichev 1939, 1953; Fedorowski 2009b, c, 2017a, b, 2019a, b, 2021a, b; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013; Fedorowski and Ohar 2019). Abbreviations: Alpor. – Alportian, Arnsb. – Arnsbergian, Blagodat. – Blagodatnian, Chok. – Chokierian, Kindersc. – Kinderscoutian, Manuilov. – Manuilovian, Marsden. – Marsdenian, Mos. – Moscovian, Serp. – Serpukhovian, Voznessenk. – Voznessenkian, Zapa. – Zapalyubian; Horizon (U) – horizons in Ukraine, Substage (WE) – substages in Western Europe.

end in an almost identical morphology of mature, taxonomically distant species and genera. Thus, describing and illustrating individual specimens solely on the basis of their mature skeletons, and failing to illustrate neanic growth stages in addition to mature ones, makes such identifications unacceptable and of limited value for comparative taxonomic and geographical practice; 4) Blastogeny is an important, but often overlooked tool in the generic identification of colonial taxa (Różkowska 1960; Fedorowski and Jull 1976; Fedorowski 1978b, 1981b). Like early ontogeny in solitary taxa, blastogeny should be considered crucial for the identifications and comparisons of colonial taxa; 5) Data on the microstructure of septa and intercorallite walls of massive colonial species are missing from almost all old descriptions of rugose corals and are commonly omitted from recent work, whereas their taxonomic value is shown to be crucial for the Scleractinia, i.e., the Rugosa's closest relatives and may be of a similar value for the Rugosa when not recrystallized deeply; 6) Rugose corals, like all sessile marine invertebrates, are dependent in their species distribution both on the larval swimming period and on geographical barriers, in particular on the directions of sea currents. Therefore, palaeogeography must be thoroughly analysed as an important factor in the identification of species and genera.

Many existing taxa do not meet some or all of the criteria listed, making their identifications at least questionable. The genus level is adopted here as the most appropriate for interregional comparisons. Species occurring in different areas are rarely compared in the following analysis. Their step by step comparisons are beyond the scope of this paper and my capabilities. However, the compared generic names should meet the common identification criteria mentioned above, or indicate the level of uncertainty in their identification. This has resulted in a different treatment of the literature data in this analysis: 1) Generic names introduced by the authors' data and raising little or no doubt have been included without change in the lists from individual areas and/or formations; 2) Alternative names are proposed in brackets when I disagree with the original generic designation, but published illustrations and descriptions are sufficient to introduce such alternative names; 3) I place original names in lists with a question mark or in inverted commas when the taxon in question is described and illustrated in a way that precludes acceptance or modification. In the interest of saving space, reasons for introducing alternative names are rarely given.

Chinese rugose corals, both in terms of range and diversity, are treated only superficially in this over-

view, because I feel incompetent in this matter. Only a few taxa are reviewed here based on the original collections studied by me. These are discussed in detail. Language, although important, cannot be decisive if the taxa are documented with comprehensive illustrations. Unfortunately, these are rarely sufficient for confident taxonomic identifications. Also, age determination is commonly restricted to formations with varying, usually long extents compared to chronostratigraphy. This severely limits the comparison of the first appearances of Chinese representatives of given taxa with their appearances from other regions of the world, making it impossible to recapitulate both the source areas of the taxa and the directions of their migrations. Therefore, the part of the discussion concerning Chinese genera should be treated only as examples (see subsection China below).

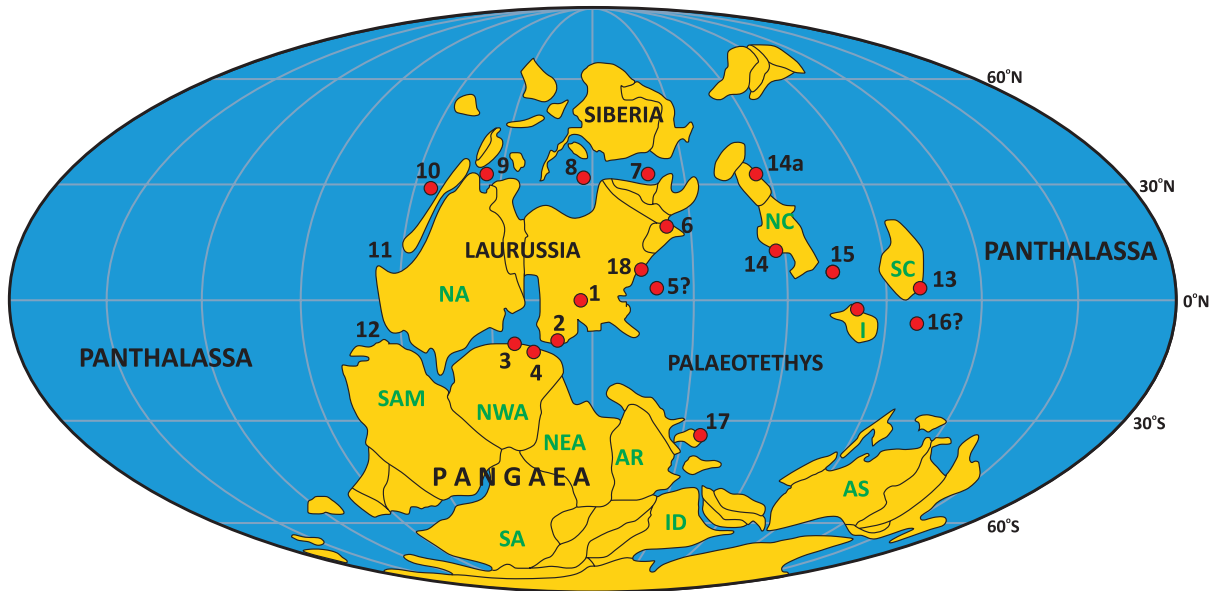
PALAEOGEOGRAPHIC OVERVIEW

(Text-fig. 3)

The late Viséan, Serpukhovian and Bashkirian were ages of expanded Variscan orogenic deformation, varying locally in time and intensity. All of them together caused dramatic changes in the palaeogeography of the world, ultimately leading to the formation of the Pangea Supercontinent. General ideas about these events and their ultimate outcome have become axioms, but the details of individual orogenies and the geographical changes they caused vary. For example, the late Serpukhovian (E₂ Genozone) and the early Bashkirian (H-R Genozones) were regressive periods in many areas of the world, but only the former applies to the Donets Basin, while the transgressive phase began there with the Bashkirian (Izart *et al.* 2002). In contrast, short-lived environmental conditions available to corals appeared in the E₂ Genozone in the Upper Silesian Coal Basin of Poland and the Czech Republic (Schwarzbach 1937; Schindewolf 1952; Weyer 1974, 1977; Fedorowski and Machłajewska 2014). These diverse local conditions and glaciation in the southern hemisphere, also recognised in the northern hemisphere (e.g., Stephenson *et al.* 2010), resulted in a geographically dispersed and patchy occurrence of the upper Serpukhovian and Bashkirian rugose coral fauna.

North-western and Central Europe

The history of rugose corals in this part of the Laurussia may serve as a model for their rapid and almost complete disappearance at the end of the



Text-fig. 3. Occurrence of Bashkirian rugose coral faunas on a palaeogeographic map (from Torsvik and Cocks 2017, simplified and slightly modified after Wang *et al.* 2021). Abbreviations: AR – Arabia, AS – Australia, I – Indochina, ID – India, NA – North America, NC – North China, NEA – North-Eastern Africa, NWA – North-Western Africa, SA – South Africa, SAM – South America, SC – South China. Numbers: 1 – Western and Central Europe, 2 – Spain, 3 – Morocco, 4 – Algeria, 5 – Voronezh Anteclise, 6 – Moscow Basin, 7 – Ural and Timan Mountains, 8 – Novaya Zemlya, 9 – Alaskan Province, 10 – Pacific Coast Province, 11 – Western Interior Province, 12 – Southeastern Province, 13 – South China, 14 and 14a – North China, 15 – Northern Japan, 16 – Akiyoshi Terrane, 17 – Northern Iran, 18 – Donets Basin.

Brigantian (late Viséan). Rugose corals occurred in this area during most of the Mississippian, and were studied for over three centuries by many dozens of researchers. Late Viséan (Asbian and Brigantian) Rugosa were particularly abundant and widely distributed, as summarised by Fedorowski (1981a). That summary can be supplemented by many subsequent contributions dealing with the systematics of rugose corals and/or clarifying their stratigraphic positions (e.g., Poty 1975, 1981, 1983, 1993; Nudds 1977, 1981, 1999; Weyer 1982, 1983, 1993, 1994; Mitchell and Mitchell 1983; Somerville and Strank 1984; Somerville *et al.* 1986; Nudds and Somerville 1987; Mitchell and Somerville 1988; Mitchell 1989; Poty and Hannay 1994; Somerville 1997; Poty *et al.* 2001, 2006; Poty and Hecker 2003). According to early works summarised by Hill (1938–1941), several Brigantian (late Viséan) rugose corals were still found in the E₁ and E₂ Genozones (Serpukhovian) in southern Scotland and northern England. Recent papers by Cózar and Somerville (2014, 2020) documented the accumulation of foraminifera-yielding marine deposits in southern Scotland and northern England up to the upper Arnsbergian Substage (Zapaltyubian Horizon) (Cózar and Somerville 2014, fig. 2), but the corals were not listed as accompanying

the foraminifera. Also foraminifera-bearing marine deposits were developed in parts of Ireland up to the upper Serpukhovian. Professor Ian D. Somerville has confirmed the occurrence of rare rugose corals in these deposits. In his e-mail of 26 November 2020, he wrote: “The only genus I know of is *Orionastraea*.”

The very rich upper Viséan rugose coral fauna flourishing during the Brigantian age (late Viséan) in the Świętokrzyskie (= Holy Cross) Mountains and Sudetes in Poland disappeared before the end of this stage and never returned there (Fedorowski 1971, 1981a). Since Schwarzbach’s (1937) study, however, relatively rich and diverse Rugosa have been known from the Upper Silesian Coal Basin of Poland and the Czech Republic. Many specimens have been tentatively identified by Schwarzbach (1937) and described in detail by Schindewolf (1952), who introduced several new species and one new genus *Antiphyllum*. Matl (1971) and Řehoř and Řehořova (1972) followed Schindewolf’s (1952) identifications in their descriptions of specimens from this basin. Weyer (1974, 1977) made a first revision of earlier studies. Fedorowski (2010a, 2012a, b) studied several new collections and re-examined all specimens previously studied by the above-mentioned authors. Fedorowski and Machłajewska (2014) described a collection newly

acquired by Machłajewska. Identifications of species and genera published in earlier papers and these by Fedorowski (2010a, 2012a, b), Fedorowski and Machłajewska (2014) differ significantly. Therefore, Fedorowski and Machłajewska (2014, table 3) tabulated all these names to demonstrate these differences. Most of the taxa included in this table originated from the middle Arnsbergian, i.e., the E₂b Genozone. Only two poorly represented species, left in open nomenclature, i.e., *?Antiphyllum* sp. nov. 1 (represented by one incomplete specimen) and *Zaphrufimia* sp. nov. 1 (represented by two incomplete specimens), came from the upper E₁ Genozone (upper Pendleian). Most genera and species described from the Upper Silesian Coal Basin are so far restricted to this basin. The widely distributed *Zaphrentites* Hudson, 1941, *Zaphrufimia disjuncta* (= *Zaphrentis disjuncta* Carruthers, 1910 from the E₂ Genozone in southern Scotland) and *Ostravaia* Fedorowski, 2010a, recognised in the Lublin Basin, eastern Poland (Fedorowski 2015), are species suggesting the possibility of a limited marine connection of the Upper Silesian Coal Basin and its coral fauna with other areas. This link with the Lublin area is easy to accept, but that with Scotland is puzzling to me for now. The following genera have been identified from the Upper Silesian Coal Basin: *Antiphyllum* (+ subgenus *Antiphyllites* Fedorowski 2012b); *Ostravaia*; *Variaxon* Fedorowski, 2010a; *Zaphrufimia* Fedorowski, 2012a; *Effigies* Fedorowski 2012b; and *Triadufimia* Fedorowski in Fedorowski and Machłajewska, 2014.

The Lublin Basin was very rich in rugose corals in the late Viséan (Fedorowski 1968; Khoa 1977). Some of these taxa continued to occur in the lower Serpukhovian. Rare specimens of the latter were described by Khoa (1977), and a relatively rich collection was studied by Fedorowski (2015). This entire fauna is restricted to the lower part of the E₁ Genozone (lower Pendleian) and disappeared in younger strata, despite the common presence of marine intercalations within the terrigenous deposits (Musiał and Zdanowski in Fedorowski 2015, fig. 2). Three of the taxa identified by Fedorowski (2015), i.e., *Dibunophyllum bipartitum* (McCoy, 1849), *Siphonodendron strzelcense* Khoa, 1977 and *Cyathaxonia* aff. *cornu* Michelin, 1847 continued directly from the Viséan. *Rotiphyllum plumeum* Fedorowski, 2015, *Zaphrentites rotiphylloides* Fedorowski, 2015 and *Nervophyllum lukoviensis* Fedorowski, 2015 are directly related to the Viséan species of these genera; *Ostravaia* aff. *silesiaca* Fedorowski, 2010b and *Zaphrufimia anceps* Fedorowski, 2015 can be regarded as ancestors (?) for the taxa of the Upper Silesian Coal Basin; whereas

Axisvacuus tenerus Fedorowski, 2015 and *Cordibia* sp. may be considered as precursors of the Bashkirian representatives of these genera. In addition, a group of new genera, unknown from outside the Lublin Basin, was identified. These are: *Chelmia*, *Birkenmajerites*, *Occulogermen*, all of Fedorowski (2015) and, possibly the peculiar *?Sochkineophyllum symmetricum* Fedorowski, 2015, which may belong to a new genus. The coral fauna discussed here is thus typical of a transitional period development, being a mixture of old taxa and newcomers. This composition may suggest partial isolation of the Lublin Basin coral fauna, as indicated by ephemeral, endemic new genera, while the widely distributed species and genera document its association with other coral-bearing areas.

Rugose corals made two more invasions into Western and Central Europe. A single specimen, described by Smith (1931) as *Zaphrentis* sp. nov. was found in the marine band of the *Cancelloceras cancellatum* Zone (middle Yeadonian) in Wales. Judging from the illustration it may belong in the long-lived genus *Ufimia* Stuckenbergh, 1895.

The second marine ingression in Wales occurred in the *Donetzoceras aegiranum* Genozone. It left several specimens of rugose and tabulate corals described by Smith (1931) as *Cyathaxonia* cf. *rushiana* Vaughan, *?Caninia cornucopiae* Michelin, *Zaphrentis postuma* Smith and the unillustrated *Emmonsia parasitica* (Phillips) (dates not given by Smith 1931). I have not reviewed the specimens described and illustrated by Smith (1931, pl. 1, figs 1–10). However, the original illustrations and descriptions made it possible to synonymise Smith's *?Caninia cornucopiae* with *Zaphrentis postuma* Smith, 1931, to recognise this species as present in the *Bilinguites–Cancelloceras* Genozone of the Donets Basin, and to include it in *Axisvacuus* Fedorowski, 2009c.

The marine ingression in the *Donetzoceras aegiranum* Biozone spread into Belgium, from where *Zaphrentis* aff. *postuma* was described by Demanet (1943). My unpublished revision of two specimens by Demanet (1943) documents features typical of the genus *Bradyphyllum* Grabau, 1928, into which they were provisionally included. Several undescribed non-dissepimented corals from the Lublin Coal Basin, possibly representing the same marine ingression, are in my possession.

In summary: 1) The Sudetic Orogeny uplifted much of Western and Central Europe towards the end of the Brigantian (late Viséan), rendering it sterile of marine environments suitable for corals. Such suitable environmental conditions were prolonged only in northern England and southern Scotland in the

Eumorphoceras Genozone (Serpukhovian), hosting mainly an impoverished Brigantian coral fauna. 2) Marine platform sedimentation in parts of Britain and perhaps Belgium continued up to and including the Arnsbergian, but corals are absent from these platforms except for one genus. 3) Serpukhovian rugose corals have been recorded from two sites in Central Europe: (i) as Viséan relicts with an admixture of newcomers developed in the Lublin Coal Basin up to and including the lower E₁ Genozone; (ii) as an ephemeral but diverse fauna of rugose corals that appeared in the late Pendleian and flourished in the middle Arnsbergian (E₂b) Biozone of the Upper Silesian Coal Basin in Poland and the Czech Republic. The number of new taxa allowed this small-sized site to be considered a creative faunal area. 4) Two short-lived marine ingressions, bringing highly depleted non-dissepimented corals, were the only evidence of Bashkirian corals in this part of Europe.

Southern Europe

The history of Carboniferous rugose corals in this part of Europe (Spain and southern France) is very different from that of Western and Central Europe, discussed above. The few studies on Serpukhovian and younger strata from this area, published before 1980 are discussed in my earlier summary (Fedorowski 1981a, pp. 122, 128). New data on the taxonomy of Serpukhovian and/or Bashkirian rugose coral taxa of southern France are not known to me.

In the case of Spain, the Carboniferous history of rugose corals is diverse. The sequence in faunal occurrence based on tectonic units in northern Spain (Cantabrian Mountains) has been summarised by Sanchez de Posada *et al.* (1996) in a sedimentological and palaeontological context. This area was supposed to represent deep-water basinal or cephalopod facies from the Late Devonian to the early Serpukhovian. The Carboniferous Genicera Formation extends from the middle or upper Tournaisian to the lower Serpukhovian, and possibly even to the Arnsbergian (Sanchez de Posada *et al.* 1996, p. 83). Rare, non-dissepimented rugose corals are derived from these deep-water strata. Kullmann (1966, 1968) described part of this fauna and assigned his taxa a lower Namurian age (*Eumorphoceras* Genozone). The generic names used by him are not cited here as they are misleading. Most of them need a revision and should be renamed. Fedorowski and Kullmann (2013) introduced a new genus *Voinimitor*, represented by a single species, i.e., *V. projectus* Fedorowski and Kullmann, 2013 from the Alba Formation that may

be either late Viséan or early Serpukhovian in age. The Valdeteja Formation is defined by foraminifera derived from the type section as upper Bashkirian, with only the upper strata belonging to the lowermost Moscovian (Vereian) (Villa *et al.* 2001). A detailed stratigraphic position of rugose corals from the other formations is also somewhat questionable. The entire rich fauna is tentatively treated as probably occurring in the middle and/or late Bashkirian, and reaching the peak of its development in the Moscovian.

These deep-water deposits, transitioned into the distinctly different, shallow-water Barcaliente Formation, were restricted to the early Namurian A (Pendleian) in Palencia, but in most areas developed up to the early Namurian B (Kinderscoutian) (Rodríguez *et al.* 1986, fig. 2; Sanchez de Posada *et al.* 1996, fig. 2). The change in depositional conditions between the Genicera and Barcaliente formations was perhaps due to the rotation of Gondwana caused by the different phases of the Hercynian Orogeny. The early phase of rotation, manifested by drastic facies changes in the northern areas, raised the seafloor in northern Spain from a deep basin to shallow-water marginal facies without pushing the area beyond its equatorial position. This position, already proposed by Fedorowski (1981a), was adopted by Rodríguez *et al.* (1986) and has not been questioned since.

The two most important studies of Pennsylvanian rugose corals from northern Spain are the work of de Groot (1963), revised by Fedorowski (2004) with a few changes, and the opus of Rodríguez (1984a). Unfortunately, de Groot's (1963) paper is mainly devoted to the uppermost Bashkirian and younger taxa. Thus, its main part, which is important for a general overview of the phylogeny of rugose corals and their geographical distribution, is beyond the scope of the present paper.

The opus of Rodríguez (1984a), complemented by his short summaries (Rodríguez 1984b, 1985) and the analysis of Rodríguez *et al.* (1986) remain the most important achievements in the study of Bashkirian rugose corals of the Cantabrian Mountains in the context of the present paper. The study of Boll (1985), dealing with a collection from the southern Cantabrian Mountains would have been an important addition to these studies if it had been well-documented. Unfortunately, the poor representation of many taxa and the inadequate illustrations reduce the cognitive value of this paper. Several of the identifications of Boll (1985) have already been corrected by Rodríguez *et al.* (1986), but I do not always agree with these corrections. Also several ideas of Boll (1985), such as his approach to the genera *Caninia* Michelin

in Gervais, 1840 and *Kionophyllum* Chi, 1931, are not acceptable to me. I have therefore decided to omit this paper from consideration rather than attempt to correct the names used by him. Such corrections, based on his poor illustrations, inadequate for careful analysis, can only multiply nomenclatorial chaos.

Rodríguez (1984a) described several genera of corals from the Cosgaya Formation, assigned by him to the ‘last Serpukhovian’. However, Rodríguez *et al.* (1986, fig. 2) extended the range of this formation to the lower Namurian B, i.e., the Kinderscoutian Substage (Bashkirian). Also, the upper part of Namurian A (Alportian and Chokierian Substages) corresponds to the lowermost Bashkirian. Thus, corals from the Cosgaya Formation should be considered Bashkirian, as confirmed by Coronado and Rodríguez (2009). However, it is important to keep in mind the doubts regarding the Serpukhovian/Bashkirian boundary discussed by Sanz-López *et al.* (2006).

The number of genera mentioned as occurring in ‘Namurian A’, roughly correlated either with the Zapaltyubian or the Voznessenkian Horizon in the Donets Basin (see above), varies from source to source. Rodríguez (1984b, p. 434) lists *Caninostrotion* Easton, 1943b; *Dibunophyllum* Thomson and Nicholson, 1876; *Fomichevella* Fedorowski, 1975; *Kionophyllum*; *Kizilia* Degtyarev, 1965; ‘*Nemistium*’ and *Semenophyllum* of Rodríguez, 1984a, while Rodríguez *et al.* (1986, fig. 3) list thirteen genera. In addition to the genera listed above (with the exception of *Fomichevella* transferred by them to ‘Namurian B’), these are: *Actinocyathus* d’Orbigny, 1849; *Amandophyllum* Heritsch, 1941; *?Axophyllum* Milne Edwards and Haime, 1850; *Diphyphyllum*; *Gangamophyllum* Gorsky, 1938; *Lonsdaleia* McCoy, 1849; *Lytvophyllum* Dobrolyubova in Soshkina *et al.*, 1941; *Siphonodendron* McCoy, 1849 and *Ufimia*. The taxa listed are a mixture of Viséan relicts and genera representing Fedorowski’s (1981a) ‘second phase’ in the phylogeny of rugose corals. This phase began with the Chokierian (Voznessenkian) coral fauna. *Fomichevella*, *Kionophyllum*, ‘*Lytvophyllum*’ (possibly = *Colligophyllum* Fedorowski, 2021a) and taxa of doubt to Rodríguez *et al.* (1986) belong to this phase. Rodríguez (1984a, b) pointed out the direct relationship of the mentioned rugose corals from the Cantabrian Basin to the fauna of Western and Eastern Europe and North America. I fully agree with the first part of that suggestion, but I do not see a close relationship between the Spanish and North American coral faunas. I also agree with most of the identifications, which are adequately supported by

illustrations, except for two, i.e., *Amandophyllum* and ‘*Lytvophyllum*’, both discussed earlier (Fedorowski 2017a and 2021a, respectively).

The fauna of rugose corals from the Cantabrian Mountains discussed above differs in diversity and content from both the older (i.e., the Genicera Formation; see above) and younger (Bashkirian) fauna from this area. The latter fauna must be divided into two groups. The older fauna, i.e., from the Vejo Formation (approximately middle part of Namurian C), corresponding perhaps to the upper lower Bashkirian Blagodatnian (Limestones F₁–F₂) in the Donets Basin, is very limited in number and occurrence. Rodríguez (1984b) listed only *Allotropiophyllum* Grabau, 1928 and *Kionophyllum* as occurring in the middle part of the Vejo Formation in the Liébana Valley. Rodríguez *et al.* (1986) added *Fomichevella* and *?Tschussoskenia* Dobrolyubova, 1936 to this list as occurring in ‘Namurian B, C’ (= Kinderscoutian to Yeadonian inclusive, i.e., lower Bashkirian).

The paucity of Bashkirian corals mentioned ended with the appearance of an abundant fauna in the Perapertú, Carmen, Cucayo and Valdeteja formations. Unfortunately, the chronostratigraphic position of these formations and their fauna mentioned in various publications differ. Rodríguez (1984b, p. 434) clarified the biostratigraphic position of the lithostratigraphic units used by de Groot (1963), i.e., the Santa Maria Limestone and the Perapertú Formation. Both are “the same as the Dobres Limestone, i.e. late Bashkirian to earliest Vereyan.” This statement contradicts the position of the Perapertú Formation outlined by Rodríguez *et al.* (1986, fig. 2) as uppermost Namurian C and lowermost Westphalian A (= uppermost Blagodatnian and Zuyevian in the Donets Basin). The Valdeteja Formation is defined by foraminifera derived from the type section as upper Bashkirian, with only the upper strata belonging to the lowest Moscovian (Vereian) (Villa *et al.* 2001). The detailed stratigraphic position of rugose corals from the other mentioned formations is also somewhat questionable. The entire rich fauna is tentatively treated as probably occurring in the middle and/or late Bashkirian, but reached the peak of its development in the Moscovian.

Only taxa from Fedorowski’s (1981a) ‘phase 2’ occur in that youngest Bashkirian rugose corals fauna, if not counting genera such as *Amplexus* Sowerby, 1814; *Pseudozaphrentoides* Stuckenbergh, 1904 and *Spirophyllum* Fedorowski, 1970. *Amplexus* and *Spirophyllum* are most likely homeomorphs of the Mississippian types, whereas the name

Pseudozaphrentoides should be applied only to specimens with an amplexoid early ontogeny and an elongated cardinal septum at maturity, i.e., bearing the characters of the holotype of *P. jerofoevi* Stuckenber, 1904 revised by Fedorowski (1975, fig. 1a, b). These characters are not illustrated by Rodríguez (1984a, fig. 162). The taxonomic position of *Duplophyllum* Koker, 1924; *Koninckocarinia* Dobrolyubova, 1937; *Stylastraea* Lonsdale, 1845 and *Stylostrotion* Chi, 1935, listed by Rodríguez *et al.* (1986, fig. 3) as occurring in the Cantabrian Mountains of Spain are uncertain. My earlier opinions on *Duplophyllum*, *Stylostrotion* and *Koninckocarinia* are discussed in Fedorowski (1986b, p. 209; 1991a, pp. 90, 91; 2021b, p. 62). The holotype of *Stylastraea inconfertata* Lonsdale, 1845 is discussed and illustrated in Fedorowski *et al.* (2007, pp. 199–201). Some others, such as *Axolithophyllum* Fomichev, 1953 and *Petalaxis* Milne Edwards and Haime, 1852 are widely distributed, while *Asturiphyllum* Rodríguez, 1984a is a new genus. Fedorowski (2004) revised most of the taxa described by de Groot (1963) and made several changes in their identifications. The most important of these are: 1) The recognition of two wall types in the taxa classified by de Groot (1963) as *Petalaxis*. Those with a dividing wall were left within *Petalaxis*, while a new subgenus *Degrootia* Fedorowski, 2004 was introduced for those with a partition. 2) de Groot's (1963) specimens assigned to *Lithostrotion reticulatum* (Fomichev, 1939) were transferred to *Calyxcorallia* Fedorowski, 1991 and *Lithostrotion trimorphum* de Groot, 1963 was transferred to *Arctocorallium* Fedorowski, 2004 and placed also in *Calyxcorallia*. Rare taxa of the fauna discussed above (e.g., *Axolithophyllum*, *Petalaxis*) have reappeared in the Moscovian with a facies-induced hiatus in their occurrence in Westphalian B, i.e., upper Bashkirian (Rodríguez *et al.* 1986, figs 2, 3). However, most Moscovian taxa are new to the Cantabrian Mountains. Their analysis is beyond the scope of the present paper.

Summing up the discussion on the sequence in the rugose coral occurrences in northern Spain the following should be pointed out: 1) Only rare non-dissepimented rugose corals of uncertain affinities occurred in northern Spain during the pre-Serpukhovian Carboniferous time; 2) It cannot be established whether the dissepimented solitary and colonial rugose corals arrived to northern Spain from North-Western and/or Eastern Europe or from southern Spain where a rich and diversified rugose coral fauna flourished in the Viséan and up to the Serpukhovian inclusively (see below). A detailed spe-

cies by species analysis, required for such a conclusion, is behind the scope of the present paper. The Cantabrian Mountains area was geographically intermediate between these two possible source areas and may have served as a refugium for both; 3) Lower Bashkirian faunas are rare and scattered, whereas the age of those from the Perapertú, Carmen, Cucayo and Valdeteja formations are uncertain. They are perhaps of middle to late Bashkirian and early Moscovian age; 4) The truly diversified and rich coral fauna reached its peak in the Moscovian, which is beyond the scope of this paper.

Although Viséan rugose coral faunas are generally omitted from consideration herein, the one thriving in southern Spain, i.e., on the southern edge of Laurussia, is briefly mentioned as an exception, since it was almost completely unknown until the publication of the papers cited below as examples. This fauna represents a kind of bridge between the fauna of northern Africa and Central and Western Europe, being thus important for palaeogeography. Rodríguez and Falces (1992, 1994), Rodríguez *et al.* (2001a, b, 2002, 2004, 2006, 2016), Gómez-Herguedas and Rodríguez (2005, 2009), and Rodríguez and Said (2009) have documented that this fauna is rich and diverse. It mainly includes genera and species known from Central and Western Europe, such as *Aulophyllum fungites* (Fleming, 1828), *Dibunophyllum bipartitum*, *Koninckophyllum interruptum* Thomson and Nicholson, 1876, *Siphonophyllia samsonensis* (Salée, 1913), *Solenodendron furcatum* (Smith, 1925) and several *Lithostrotion* Fleming, 1828 and *Siphonodendron* species. However, *Axoclisia cuspidiforma*, *Caninophyllum becharense*, *Haplolasma lamelliferum*, and *Siphonophyllia siblyi*, all of Semenov-Tian-Chansky (1974) and described from North Africa first, and *Dibunophyllum aff. lonsdaleoides* Vassilyuk, 1960 from the Donets Basin, point to these two areas as also communicating with southern Spain.

Gómez-Herguedas and Rodríguez (2005) described the southern Spanish rugose coral fauna from the lower Serpukhovian in the Córdoba area. The state of preservation of the specimens does not allow for full identification and description of several taxa, which were left in open nomenclature or characterised as unidentified but are most likely new. The fauna is diverse, but in general can be described as a relic of the Viséan enriched by several new and possibly endemic taxa, as mentioned by the authors. *Dibunophyllum dobrolyubovae* Vassilyuk, 1960, *Lithostrotion maccoyanum* Milne Edwards and Haime, 1851, *Diphyphyllum fasciculatum* (Fleming, 1828), and *Diphyphyllum gracile*

McCoy, 1851 document a direct connection to Central/Western and Eastern Europe, while *Amygdalophyllum cornudensis* Gómez-Herguedas and Rodríguez, 2005 and *Guadiatia* Gómez-Herguedas and Rodríguez, 2005 are possibly endemic. Younger specimens than the rugose corals discussed here from southern Spain are unknown to me.

North Africa

The analysis of North African Rugosa is generalised here and restricted mainly to Algeria and Morocco, as most of the Viséan to Bashkirian coral fauna has been described from these areas (see citations below). In order to establish the stratigraphic frames for the Rugosa, conodonts (e.g., Weyant 1982, 1986), ammonoids (e.g., Lemosquet and Pareyn 1985; Lemosquet *et al.* 1985) and foraminifera (Sebbar 2006) were taken into account. The latter, with some limitations, due to minor differences between his statements and the study by Kulagina *et al.* (2001, 2009, 2013), Kulagina and Pazukhin (2002), and Kulagina and Sinitsyna (2003), and due to the summary by Cózar *et al.* (2015). Unfortunately, the first appearances and extensions of individual index taxa are commonly not rigid and/or are interpreted differently by different authors. For example, the appearance of *Declinognathodus noduliferus* (Ellison and Graves, 1941), widely regarded as a marker of the lowest Bashkirian (Voznessenian in the Donets Basin, confirmed by Nemyrowska 2017) allowed Weyant (1986, p. 365) to place the Tagnana Formation from the Béchar Basin close to the Serpukhovian/Bashkirian boundary. Lemosquet *et al.* (1985, p. 368) recorded the first appearance of *Homoceras* sp. and *Isohomoceras* sp. in the lower part of this formation, i.e., at about the level of the first appearance of *D. noduliferus*, but added: “the ammonoid assemblage could represent a part of the Kinderscoutian Stage.” This appearance was subsequently accepted by Legrand-Blain (1989). On the other hand, Atif and Legrand-Blain (2011, fig. 2), who analysed brachiopods, placed the lower part of the Tagnana Formation (i.e., Member 1, levels A–D) in the upper Serpukhovian (E₂b, c Genozone). Also in the foraminifera column the Serpukhovian / Bashkirian boundary is marked with a dashed line, with *Eostaffella chomatifera* Kireeva in Rauzer-Chernousova *et al.*, 1951 as the lowest Bashkirian marker, and the conodont column is left undivided with *D. noduliferus* corresponding to level E of Member 1 of the Tagnana Formation (Atif and Legrand-Blain 2011, fig. 2). In turn, Lys (1979, 1985) placed the entire Member 1 in the *Homoceras*–

Hudsonoceras Genozone and suggested a possible assignment of the upper part of the Djenien Formation to this geozone. Cózar *et al.* (2015, p. 8) confirmed the latter suggestion by finding *Plectostaffella varvariensis* (Brazhnikova and Potievskaya, 1948) in the upper part of this formation. Kulagina and Sinitzina (2003) authenticated the position of Cózar *et al.* (2015) by placing that species at the bottom of the Bashkirian Stage. However, this suggestion contrasts with the positions of ammonoids and conodonts. Both the *Homoceras*–*Hudsonoceras* and *D. noduliferus* genozones appear higher in the Béchar Basin, in level E of Member 1 of the Tagnana Formation, as mentioned above. Cózar *et al.* (2015, p. 8) explained their position as follows: “The shallow-water facies in those formations suggest a more reliable record is gained using the foraminifers, and that the base of the Bashkirian should be repositioned at a level within the middle part of the Djenien Fm (Fig. 3).” This statement draws attention to the environment as an influential factor that can affect indications of index fossils. However, it creates a stratigraphic dilemma regarding the stratigraphic positions of some rugose coral taxa from North Africa.

To sum up: The differing interpretations of the stratigraphic ranges of conodonts, ammonoids and foraminifers make it difficult to place data from old collections in modern biostratigraphic schemes. This is particularly important with regard to the Serpukhovian/Bashkirian boundary. Several species may be considered either Serpukhovian or Bashkirian, depending on the author’s choice of the index fossil in question.

In my earlier paper (Fedorowski 1981a), taxa of European and North African rugose corals were included in a common Western European Province. Indeed, many genera and species of rugose corals described from north-west Africa were first described from Western and Central Europe, and some from Eastern Europe, i.e., from Western Palaeotethys. Two periods can be distinguished in the study of North African rugose corals. The older of these includes papers by Menchikoff and Hsu (1935), Termier and Termier (1950), Fabre (1955), Semenoff-Tian-Chansky (1974, 1985), Semenoff-Tian-Chansky and Sutherland (1982) and Semenoff-Tian-Chansky in Legrand-Blain (1989). These early data on Mississippian and Lower Pennsylvanian strata and fossils, including rugose corals, have been greatly supplemented in the new study period (e.g., Said and Rodríguez 2007, 2008; Said *et al.* 2007, 2010, 2011, 2012; Cózar *et al.* 2008, 2011, 2014a, b, c, 2015, 2019; Aretz 2010, 2011; Aretz and Herbig 2010; Rodríguez

et al. 2012, 2013a, b, 2016; Somerville *et al.* 2012, 2013). Those papers have precisely defined the stratigraphic occurrences, palaeogeography and palaeoecology of rugose corals, but have repeated many taxa described in earlier papers. Both old and new achievements confirm the co-occurrence in Europe and North Africa of species from the Viséan and many species from the Serpukhovian (see Tables 1 and 2), regardless of the presence of the Rheic Ocean that separated these areas. This common co-occur-

rence allowed the formation of a common palaeozoological province, the Western European Province (Fedorowski 1981a) for the Viséan corals of both areas, which can be extended to the Serpukhovian. The following lists include taxa from the upper Viséan and Serpukhovian described in North Africa regardless of the basin from which they are described, as the main purpose of these lists is to confirm the existence of a province common to Western Europe and North Africa. There are, however, several taxa from

Dissepimented solitary Rugosa	Colonial Rugosa
<i>Arachnolasma cylindrica</i> Yu, 1933	<i>Actinocyathus floriformis</i> (Martin, 1809)
<i>Arachnolasma sinense</i> Yu, 1933	<i>Aulina</i> (<i>Pseudoaulina</i>) <i>botanica</i> Nudds, 1977
<i>Aulophyllum fungites</i> (Fleming, 1828)	<i>Aulokoninckophyllum carinatum</i> (Carruthers, 1909)
<i>Axophyllum densum</i> (Ryder, 1930)	<i>Diphyphyllum fasciculatum</i> (Fleming, 1828)
<i>Axophyllum kirsopianum</i> (Thomson, 1880)	<i>Diphyphyllum furcatum</i> Thomson, 1883
<i>Clisiphyllum garwoodi</i> (Salée, 1913)	<i>Diphyphyllum lateseptatum</i> McCoy, 1849
<i>Clisiphyllum keyserlingi</i> McCoy, 1849	<i>Espiella columellata</i> Rodríguez and Hernando, 2005
<i>Dibunophyllum arachnoforme</i> Vassilyuk, 1960	<i>Lithostrotion araneum</i> (McCoy, 1844)
<i>Dibunophyllum bipartitum</i> s.l. (McCoy, 1849)	<i>Lithostrotion decipiens</i> (McCoy, 1849)
<i>Dibunophyllum linnense</i> Hill, 1940	<i>Lithostrotion maccoyanum</i> Milne Edwards and Haime, 1851
<i>Haplolasma densum</i> (Lewis, 1930)	<i>Lithostrotion vorticale</i> (Parkinson, 1809)
<i>Koninckophyllum interruptum</i> Thompson and Nicholson, 1876	<i>Palatraea regia</i> (Phillips, 1836)
<i>Koninckophyllum magnificum</i> Thompson and Nicholson, 1876	<i>Siphonodendron intermedium</i> Poty, 1981
<i>Palaeosmilia munchisoni</i> Milne Edwards and Haime, 1848	<i>Siphonodendron irregulare</i> (Phillips, 1836)
<i>Siphonophyllia samsonensis</i> (Salée, 1913)	<i>Siphonodendron junceum</i> (Fleming, 1828)
	<i>Siphonodendron martini</i> Milne Edwards and Haime, 1851
	<i>Siphonodendron pauciradiale</i> (McCoy, 1844)
	<i>Siphonodendron scaleberense</i> Nudds and Somerville, 1987
	<i>Siphonodendron sociale</i> (Phillips, 1836)

Table 1. Upper Viséan and Serpukhovian dissepimented solitary and colonial rugose coral taxa of North Africa.

Viséan taxa	Serpukhovian taxa
<i>Amygdalophyllum asselense</i> Semenoff-Tian-Chansky, 1974	<i>Arachnolasma djihaniense</i> Semenoff-Tian-Chansky, 1974
<i>Amygdalophyllum pachyphylloides</i> Semenoff-Tian-Chansky, 1974	<i>Axophyllum pseudokirsopianum</i> Semenoff-Tian-Chansky, 1974
<i>Amygdalophyllum turbophylloides</i> Semenoff-Tian-Chansky, 1974	<i>Bothrophyllum proteum</i> Semenoff-Tian-Chansky, 1974
<i>Axoclisia cuspidata</i> Semenoff-Tian-Chansky, 1974	<i>Carcinophyllum coronatum</i> Fabre, 1955
<i>Axophyllum dibunophylloides</i> Semenoff-Tian-Chansky, 1974	<i>Clisiphyllum benziregense</i> Semenoff-Tian-Chansky, 1974
<i>Caninia matea</i> Semenoff-Tian-Chansky, 1974	<i>Clisiphyllum keyserlingi crassiseptatum</i> Semenoff-Tian-Chansky, 1974
<i>Caninophyllum archiaci</i> (Milne Edwards and Haime, 1852)	<i>Diaschophyllum chevalieri</i> Semenoff-Tian-Chansky, 1974
<i>Carruthersella menchikovi</i> Semenoff-Tian-Chansky, 1974	<i>Dibunophyllum pruvosti</i> Semenoff-Tian-Chansky, 1974
<i>Clisiphyllum macrocolumellatum</i> Said and Rodríguez, 2008	<i>Koninckophyllum complexum</i> Semenoff-Tian-Chansky, 1974
<i>Dibunophyllum akachense</i> Semenoff-Tian-Chansky, 1974	<i>Koninckophyllum destitutum</i> Semenoff-Tian-Chansky, 1974
<i>Haplolasma arciferum</i> Semenoff-Tian-Chansky, 1974	<i>Koninckophyllum variabile</i> Semenoff-Tian-Chansky, 1974
<i>Haplolasma lamelliferum</i> Semenoff-Tian-Chansky, 1974	<i>Palaeosmilia multiseptata</i> Semenoff-Tian-Chansky, 1974
<i>Haplolasma parvicarinatum</i> Semenoff-Tian-Chansky, 1974	<i>Palaeosmilia resotti</i> Menchikov and Hsu, 1935
<i>Haplolasma paraarciferum</i> Aretz, 2011	
<i>Koninckophyllum distans</i> Semenoff-Tian-Chansky, 1974	
<i>Pareynia gangamophylloides</i> Semenoff-Tian-Chansky, 1974	
<i>Pareynia splendens</i> Semenoff-Tian-Chansky, 1974	
<i>Pseudozaphrentoides alloiteaui</i> Semenoff-Tian-Chansky, 1974	
<i>Siphonophyllia siblyi</i> Semenoff-Tian-Chansky, 1974	
<i>Tizraia berkhlii</i> Said and Rodríguez, 2007	

Table 2. Viséan and Serpukhovian rugose coral taxa of North Africa. New genera created by Semenoff-Tian-Chansky (1974) are in bold.

the upper Viséan and Serpukhovian that were either described in North Africa first or are so far endemic to the area. Those taxa are listed separately.

Non-disseminated Rugosa are very rare in the upper Viséan and Serpukhovian of North Africa and most of them either remain in open nomenclature or their taxonomic position is uncertain (e.g., *Saharaphrentis* Aretz, 2011). Therefore, only *Cyathaxonia cornu* Michelin, 1847 is listed here as a non-disseminated species, certainly occurring in North Africa.

Disseminated solitary and colonial Rugosa of the upper Viséan and Serpukhovian of North Africa include 15 and 19 species, respectively (Table 1).

New Viséan and Serpukhovian taxa were first introduced from North Africa mainly by Semenoff-Tian-Chansky (1974). Prior to that study, only Menchikoff and Hsu (1935) and Fabre (1955) introduced one new species each. Taxa believed by Semenoff-Tian-Chansky (1974) to be Viséan and Viséan taxa introduced by other authors are listed in Table 2. Those considered by him to be lower Namurian (= Serpukhovian in the 1985 paper = perhaps lower Bashkirian; see below) were mostly from the Béchar Basin. Also, the exact stratigraphic position of only the latter are given by Semenoff-Tian-Chansky (1985, his table 9). New North African Serpukhovian taxa (perhaps lower Bashkirian; see below) are listed in Table 2.

Lists of taxa co-occurring in Europe and North Africa and taxa endemic to or first described from North Africa (Tables 1 and 2) are compiled to point to: (i) the range and divergence of the North African rugose coral fauna, (ii) North Africa as a refugial area, and (iii) their similarity on the one hand and difference on the other with respect to the European fauna. However, detailed analysis of the North African rugose corals from the Viséan and Serpukhovian is omitted as being beyond the scope of this paper. Only brief remarks are given below, mainly concerning my doubts related to the identification of some taxa important for palaeobiogeography or phylogeny.

Semenoff-Tian-Chansky and Sutherland (1982) published a review of the main distribution areas of Bashkirian rugose corals (excluding China). I cannot agree with their suggestion: “The Bashkirian fauna of the Donets Basin is dominated by solitary corals without disseminations...”, while the suggestion “The Bashkirian [in the Donets Basin] is also characterised by the appearance of new solitary genera with disseminations... of truly Middle Carboniferous type” (Semenoff-Tian-Chansky and Sutherland 1982, p. 134) is fully confirmed by my research (Fedorowski 2009c, 2017a, b, 2019a, b, 2021a, b; Fedorowski and Ogar

2013; Fedorowski and Ohar 2019). Also, one can agree to some extent (e.g., Kossovaya 2009; Fedorowski 2021a) with their statements (p. 137) “Bashkirian coral fauna of the Urals have almost nothing in common with those of the Donets Basin, except for the occurrence of *Lytvophyllum antiquum* Gorsky, probably identical to *L. dobroljubovae* Vassilyuk.” However, the occurrence of *Colligophyllum*, *Cystolonsdaleia* Fomichev, 1953, *Kumpanophyllum* Fomichev, 1953, *Orygmophyllum* Fomichev, 1953, *Petalaxis* and *Yuanophylloides* Fomichev, 1953, and possibly *Dibunophylloides* Fomichev, 1953 and *Donophyllum* Fomichev, 1953 (see comments on Ural below), in both areas makes a direct connection between them more possible. Semenoff-Tian-Chansky (1985, table 9) listed *Siphonodendron* cf. *dutroi* Armstrong, 1972a as occurring in the upper Djenien Formation of the Béchar Basin. He repeated that information in Legrand-Blain *et al.* (1989, p. 9) and suggested a faunal exchange between North Africa and North America. He also wrote: “*Siphonodendron* allied to *S. pauciradiale* spread in Tindouf and Taoudenni basins, constituting a conspicuous biostrome.” Based on more recent studies (e.g., Rodríguez *et al.* 2012, 2013b), this last statement by Semenoff-Tian-Chansky (in Legrand-Blain *et al.* 1989) is confirmed, but not his conclusion, based on *Siphonodendron* cf. *dutroi*. The Meramecian North American specimen (Armstrong 1972a, p. 414, pl. 3, figs 1–7; pl. 4, figs 1, 3–5) differs so much from that of North Africa (Semenoff-Tian-Chansky 1985, pl. 10, figs 5a, b) that I reject any affinity between these specimens.

Semenoff-Tian-Chansky (1985, table 9) marked (with dashed lines) the Serpukhovian/Bashkirian boundary in the middle part of Member 2 of the Tagnana Formation. This recognition disagrees with his earlier suggestion (Semenoff-Tian-Chansky 1974, p. 288). He correlated the Tagnana Formation with strata from Chokierian to Marsdenian inclusive. This later position disagrees with both the earlier recognition of this boundary on the basis of ammonoids and conodonts (see above) and that suggested by Lys (1979) and confirmed by Cózar *et al.* (2015) on the basis on foraminifera, which lowered this boundary to the middle of the Djenien Formation. This may mean that not only the species listed by Semenoff-Tian-Chansky (1974) in his table 9 as originating from the Tagnana Formation, but also these from the upper Djenien Formation are already lower Bashkirian.

Not entirely convincing are the new data on rugose corals from northwest Africa (Aretz 2011; Atif *et al.* 2016). My doubts about these papers start with inadequate illustrations of the taxa. In my experience,

most solitary rugose corals cannot be unambiguously identified from a single transverse section taken from a random part of the specimen. Unfortunately, most of the species described by Aretz (2011) are illustrated by one transverse section at a time, while there are no illustrations of longitudinal sections, particularly important for dissepimented solitary corals. Illustrations of early ontogeny are absent in all species described by Aretz (2011), making several of his data uncertain. I therefore have several concerns about the identifications of species in this paper, some raised already (Fedorowski 2015) and some specified here. The first concerns the unnecessary multiplication of taxa. The specimens identified by Aretz (2011) as *?Amplexizaphrentis* Vaughan, 1906, *Zaphrentites*, *Zaphrentoides* Stuckeberg, 1895 and *Saharaphrentis* may in fact all belong to the same genus and closely related species when their entire ontogeny and septal microstructure are carefully studied. They show the following common features: the counter septum elongated, the cardinal septum shortened and located in a parallel-walled cardinal fossula that reaches the corallite axis or extends behind it, and the counter-lateral septa shortened to varying degrees, in some strongly.

My second doubt, based on three examples, concerns palaeobiogeography. 1) *Lophophyllidium* sp. The dark upper part of the photograph (Aretz 2011, fig. 5K) illustrates a cross-section made over the floor of the calyx, but does not illustrate the counter fossula (Aretz 2011, p. 594). The cardinal septum appears to contact the pseudocolumella, instead of being shortened as in *Lophophyllidium* Grabau, 1928. The counter septum, described as shortened, would eliminate this specimen from the genus if/when confirmed. With all these doubts I will not include the species described in *Lophophyllidium*, and the single transverse section presented does not allow the suggestion of an alternative taxon. Given the ?early Viséan stratigraphic position of this specimen (Aretz 2011, p. 592), it would be the oldest known *Lophophyllidium* coral. The migration would therefore be towards North America, but not *vice versa*, if Aretz's (2011) identification is confirmed. The oldest North American lophophyllidia known to date are those described by Webb (1984) and Webb and Sutherland (1993) from the Imo Formation, the last Mississippian (i.e., upper Serpukhovian) of Northern Arkansas. 2) *Dibunophyllum arachnoforme* Vassilyuk, 1960 of Aretz (2011). The North African specimen differs from the type specimen in several important details. Being directly familiar with the Ukrainian collection, I do not place the

North African specimen in the Donets Basin species. 3) *Turbinatocaninia* sp. of Aretz (2011, fig. 8F). The absence of a longitudinal section in early growth, documenting the occurrence of a pseudocolumella, makes Aretz's identification unfounded. Dobroljubova (1970) emphasised the occurrence of a pseudocolumella (Russian: *osevaya plastinka*) in the early ontogeny as the most important feature of her new genus *Turbinatocaninia*.

Given the above, Aretz's (2011) conclusion regarding the origin of North African Pennsylvanian corals cannot be accepted as proven, and his statements "...new genera, possibly immigrating from the Donets Basin appeared" and "... but at least in the Pennsylvanian [the studied fauna] gets input from the western United States and the Donets Basin" (Aretz 2011, p. 617) are unsupported by facts. The Pennsylvanian coral fauna from North Africa (e.g., Semenoff-Tian-Chansky 1974, 1985; Rodríguez *et al.* 2013a, b, 2016; Cózar *et al.* 2014a) shows European relationships *sensu lato*, but has little in common with the new species and genera from the Donets Basin (Vassilyuk 1960, 1964 and in Aizenverg *et al.* 1983; Fedorowski 2009b, c, 2017a, b, 2019a, b, 2021a, b; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013; Fedorowski and Ohar 2019). Also, a connection to North American rugose coral fauna is unsupported by unambiguous facts. Despite the above criticisms, the work of Aretz (2011) is important for the virtually unknown Viséan and Serpukhovian rugose coral fauna of eastern Algeria (Illizi Basin).

As in the neighbouring Algeria, many upper Viséan European species occur in the Moroccan basins. These are listed above and will not be repeated. Many of these species in the Tindouf Basin, Adarouch area and Jerada Basin continued into the early and early late Serpukhovian (Rodríguez *et al.* 2012, 2013a). Also Rodríguez *et al.* (2016, fig. 2) listed a rich fauna of Viséan taxa from the lower and lower upper Serpukhovian in the Idmarrah and Tirlhela sections of the Ardauch area. Moreover, three of these species, i.e., *Aulophyllum fungites*, *Dibunophyllum bipartitum* and *Diphyphyllum fasciculatum*, continued their existence up to the upper lower Bashkirian, where they co-occur with the Mississippian *Solenodendron furcatum*, *Siphonodendron tindoufense* Rodríguez, Sommerville, Said and Cózar, 2013 and four species left in open nomenclature, all belonging to European genera.

One of the richest lower Bashkirian rugose corals fauna described to date is that from the Tindouf Basin biostrome (Rodríguez *et al.* 2013b). Other rich faunas are those described by Semenoff-Tian-

Chansky (1974, 1985) from the upper Djenien and lower Tagnana formations. Ten genera were described in total, nine of which, except *Axoclisia* Semenoff-Tian-Chansky, 1974, are of European origin. Two out of the 14 species included in these genera are left in open nomenclature (*Arachnolasma* sp. and *Gangamophyllum* sp.) and one was identified as cf., i.e., *Axoclisia* cf. *coronata* (Fabre, 1955). Five named species, i.e., *Actinocyathus sarytschevae* Dobrolyubova, 1958, *Dibunophyllum bipartitum*, *Diphyphyllum maximum* Poty, 1981, *Palaeosmilia murchisoni* and *Palastraea regia* (Phillips, 1836) are of European origin, while six named species (five new) remain unknown outside North Africa. These are: *Axoclisia sahariense* Rodríguez, Sommerville, Said and Cózar, 2013b, *Axophyllum moroccoense* Rodríguez, Sommerville, Said and Cózar, 2013b, *Actinocyathus mariae* Rodríguez, Sommerville, Said and Cózar, 2013b, *Palaeosmilia resotti* Menchikoff and Hsu, 1935, *Siphonodendron ouarkizense* Rodríguez, Sommerville, Said and Cózar, 2013b and *S. tindoufense*. The composition of the taxa from the Tindouf Basin biostrome, the Adarouch Region (Rodríguez *et al.* 2016) and the Béchar Basin (Semenoff-Tian-Chansky 1974, 1985) allows the assessment of these basins as refugia for the Viséan rugose coral fauna during the Serpukhovian and Bashkirian stages, as already aptly recognised by Cózar *et al.* (2014a).

To sum up: 1) In spite of many old and new studies, some doubts remain about the Serpukhovian/Bashkirian rugose corals turnover; 2) The Serpukhovian and Bashkirian fauna of the North African basins remains conservative, making faunal fluctuations rather mild and masked by many Viséan genera whose occurrence extends down to the lower part of the upper Bashkirian. This is due to the persistence of environmental conditions acceptable for rugose corals.

Voronezh Anteclise

The rugose corals of this area are mainly known from the works of Dobrolyubova (1958), Kozyreva (1973, 1974a, b, 1976, 1978a, b, c, 1980, 1984a, b), and Vassilyuk and Kozyreva (1974). Most of them were described and illustrated from the southern flank of the anteclise. The upper Viséan and Serpukhovian Rugosa of that area are similar to those from the Donets and Moscow basins. In contrast, the Bashkirian Rugosa of the Voronezh Anteclise differs in their generic content from those of the Donets Basin and several other sites in the world. This may have resulted from their development on the oceanic carbonate platform (Text-fig. 3) as suggested both by

continuous limestone sedimentation and the character of the rugose corals fauna.

Unfortunately, the stratigraphic positions and ranges of individual rugose coral taxa from the Voronezh Anteclise are difficult to compare with the modern stratigraphic scale and correlation scheme. This is particularly important and difficult for the probable counterparts of the upper *Eumorphoceras* (E₂) and *Homoceras* (H_{1,2}) Genozones. These zones were correlated by Kozyreva (1978c, table 2) with the Protvinian Regional Substage (her V coral assemblage), expanded by her up to the Krasnopolyanian Regional Substage (= Feninian Horizon in the Donets Basin). Such a broad understanding of the Protvinian has made the faunal turnover in the Voronezh Anteclise difficult to compare with that of other regions. Kossovaya (1996, 1997b, 1998, 2002) attempted to apply modern correlation standards to the marine Carboniferous strata and corals in the western part of Russia (including the Voronezh Anteclise) and Ukraine. Unfortunately, these correlations leave many uncertainties, as discussed in the subsection on the Ural and Timan Mountains.

Only an approximate succession of rugose coral faunas in the Voronezh Anteclise can be determined. This succession is at least partly related to environmental conditions, as demonstrated by Kozyreva (1978c). Besides, credit should be given to the identifications of taxa by T.A. Kozyreva, accepting most of the non-illustrated taxa used by her for general analyses. Almost all solitary (15) and five colonial taxa out of the 30 analysed by Kozyreva (1978c, 1984a) remain as lists, but not in illustrated taxonomic publications. My doubts concern the following taxa: 1) *Lonsdaleoides* Heritsch, 1936 originally described as colonial may be a solitary gregarious form (Bamber *et al.* 2017). 2) The identification of a corallite as *Nemistium* Smith, 1928 cannot be accepted as long as its axial offsetting is documented along the lines of the type species for the genus *N. edmondsi* Smith, 1928. The same applies to *Diphyphyllum* Lonsdale, 1845. 3) *Copia* Vassilyuk and Kozyreva, 1974 is perhaps an older synonym of the solitary, gregaria-forming *Koninckinaotum* Fedorowski, 1971. This recognition extends its range to the Brigantian (upper Viséan). 4) *Palaeosmilia* Milne Edwards and Haime, 1848, described by Kozyreva (1978c, p. 84) as colonial, should be regarded as *Palastraea* McCoy, 1851.

Kozyreva's (1978c) analysis points to the Tarussian and Steshevian Regional Substages, i.e., the approximate equivalents of the lower *Eumorphoceras* (E₁) Genozone (Pendleian) as the time when the lower Carboniferous rugose coral fauna of the Voronezh

Anteclise achieved its peak of development. She also indicated many taxa occurring in the lower part of the Novopskovian Regional Substage, probably corresponding to both the Protvinian and Zapaltyubian Regional Substages in the modern scheme, i.e., to the Arnsbergian or upper *Eumorphoceras* (E_2) Genozone in the Western European scheme, or longer. Kozyreva (1978c, p. 85; 1984a, p. 103) suggested a drastic decrease in the number of species and an almost complete elimination of Viséan taxa before the beginning of the Streltsovskian Horizon. According to the Stratigraficheskiy Slovar SSSR (1977, p. 355), the Streltsovskian Horizon corresponds to Limestones E_1 to E_8 , i.e. the Feninian Horizon in the Donets Basin (= Kinderscoutian Substage in Western Europe). Thus, relict Viséan taxa may have continued to exist in the Voronezh seas at a time corresponding to most of the Voznessenkian Horizon in the Donets Basin or the *Homoceras*–*Hudsonoceras* Genozone. The possible association of the Voronezh coral fauna with the rich upper Serpukhovian and Bashkirian coral faunas of the North African basins, postulated by Semenoff-Tian-Chansky (1985), may to some extent confirm such a long occurrence of that fauna in the Voronezh Anteclise as suggested.

Re-establishment of a rugose coral fauna on the southern flank of the Voronezh Anteclise occurred in the Streltsovskian Horizon (b_1), considered by Kozyreva (1984a) to be earliest Bashkirian in age (= perhaps equivalent to the Feninian Horizon in the Donets Basin). The composition of this rich fauna is unique in terms of the presence of exclusively colonial taxa of rugose corals, accompanied by Tabulata and Chaetetida (Kozyreva 1984a). Besides, morphologically complex representatives of the cerioid genus *Petalaxis* dominate, accompanied by the plocoid or thamnasterioid Viséan relict *Aulina* Smith, 1917, the newcomer '*Lytvophyllum*' *dobroljubovae* and '*Thysanophyllum* ex. gr. *pseudovermiculare* McCoy' of uncertain provenance (see Fedorowski 2021a for comments). The lack of suitable illustrations precludes firm identification of some or all specimens of '*L.*' *dobroljubovae* from the Voronezh Anteclise as co-specific with the type from the Donets Basin, included in the genus *Colligophyllum*. '*Lytvophyllum*' *dobroljubovae* occurs up to and including the Belovodskian (b_5) Horizon (= Limestones H_4 to I_2 or the Mekeivian Horizon in the Donets Basin = Upper Langsettian in Western Europe).

In addition to the Streltsovian, four other coral-yielding horizons (b_2 – b_5), consisting mainly of limestones, were distinguished by Kozyreva (1984b) in the Voronezh Anteclise. These are: Belikotskian

(not mentioned in the Stratigraphicheskiy Slovar SSSR 1977, but possibly corresponding to the Manuilivian Horizon in the Donets Basin and the Marsdenian Substage in Western Europe); Bondarevskian, according to the Stratigraphicheskiy Slovar SSSR (1977) corresponding to Limestones F_1 to G_1 = Blagodatsnean Horizon in the Donets Basin or Yeadonian Substage in Western Europe; Dontzovskian corresponding to Limestones G_1 to H_4 = Zuyivkian Horizon in the Donets Basin or Lower Langsettian in Western Europe; and Belovodskian Horizon characterised above. Several new species of *Petalaxis* distinguished by Kozyreva (1974, 1984a) dominate in horizons b_2 – b_4 . They are accompanied by several tabulates and chaetetids in all these horizons and by species and genera of rugose corals either continuing from older horizons, or newcomers such as *Cystolonsdaleia* and *Protodurhamina* Kozyreva, 1978 which appeared in Horizon b_2 . The latter occur up to Horizon b_3 , when *Pseudodorlodotia* Minato, 1955 and *Lonsdaleia* appear, and extend to the Dontzovskian Horizon (b_4). The latter horizon contains the richest and most diverse assemblage of rugose coral fauna in the Voronezh Anteclise. In addition to the genera mentioned, there are five new species of *Petalaxis*, '*Lytvophyllum*' *dobroljubovae*, *Opiphyllum* Kozyreva, 1973 and '*Thysanophyllum*'. The fauna of rugose corals of the Voronezh Anteclise was strongly reduced in the Belovodskian Horizon (b_5) when the solitary dissepimented coral *Bothrophyllum conicum* (Fischer von Waldheim, 1830) appeared, and '*L.*' *dobroljubovae* and *Pseudodorlodotia aizenvergi* Kozyreva, 1984b prolonged their occurrence (Kozyreva 1984b, p. 103). This fauna disappeared at the end of this horizon and does not occur in the Dubovetzkian (b_6) Horizon, i.e., in the Krasnodonian Horizon in the Donets Basin or Duckmantian Substage in Western Europe.

To summarise the sequence and content of the coral fauna in the different horizons of the Voronezh Anteclise, the following should be stated: 1) Despite some uncertainties about the exact stratigraphic positions of the corals and uncertain correlations with the fauna of other sites, the upper Viséan coral fauna was present in the area perhaps longer than in other European sites, being comparable in a very general sense with the fauna of North Africa. 2) Composed exclusively of colonial taxa in the period equivalents of the horizons of the Donets Basin from Feninian to Zuyivkian inclusive, the Voronezh Anteclise fauna differs significantly from the fauna of the Donets Basin and the fauna of all other sites in the world. 3) The increase in the development of the rugose

coral fauna of the Voronezh Anteclise (Dontzovian = Zuyivkian = lower Langsettian) corresponds to the slight decline in coral development in the Donets Basin (Text-fig. 2) and the timing of the long-term low rate differentiation in the Cantabrian Mountains. In contrast, the coral fauna of the North American Midcontinent from about the same period is rich and diverse, but these two rich faunas differ in 100% of taxa. 4) The disappearance of coral fauna from the Voronezh Anteclise slightly preceded the enrichment of coral fauna in the Donets Basin, the developmental boom of corals in the Cantabrian Mountains, and the continued richness of corals in the North American Midcontinent Province, and perhaps in southern China.

Moscow Basin

This area, which was very rich in corals during the Viséan and Serpukhovian, was uplifted at the end of the Zapaltyubian Regional Substage or Horizon in the Donets Basin. Izart *et al.* (2002, p. 145) described this time interval as follows: "...emersion occurring during the major part of Bashkirian and alternation of marine limestone and claystone during late Bashkirian..." Corals have not yet been found in the Bashkirian part of the succession. They re-invaded the area during Vereian time and soon became rich and diversified. This subject is beyond the scope of the present paper.

Ural Mountains, Timan Mountains and Novaya Zemlya

This large area is discussed together because its geological history, resulting from easy faunal communication, can be unified. The Bashkirian was a globally regressive period resulting from glaciation in the southern hemisphere. However, local tectonic movements demonstrated by Izart *et al.* (2002) must also be taken into account when considering the distribution and sequence of the rugose coral fauna discussed in this section. The area of the Ural Mountains was characterised by Izart *et al.* (2002) as 'low transgression'. The same can be applied to the Timan Mountains and Novaya Zemlya.

Carboniferous corals from different parts of the discussed area have been documented by many scientists, such as Lonsdale (1845), Eichwald (1861; revised by Fedorowski in Fedorowski and Goryanov 1973), Stuckenber (1895), Carruthers (1909), Perna (1923), Gorsky (1932, 1935, 1938, 1941, 1951, 1978), Dobrolyubova (1936), Degtyarev (1965, 1973a, b,

1975, 1979), Rakshin (1965), Kachanov (1971, 1973), Sayutina (1973), and Gorsky *et al.* (1975). The rugose coral genera described in these papers, whose names are mostly not mentioned herein, were included in the Viséan to Bashkirian parts of my earlier summary (Fedorowski 1981a). Despite the passage of more than 40 years, the basic data published in those papers have not been supplemented substantially, while the approach to taxonomy and global stratigraphy, including stage boundaries, have changed considerably. This means that many taxa published in those papers require a careful revision based on type collections provided by topotypes, if the former are insufficient for a complete study. Some of my taxonomic suggestions (see below) should in no way be regarded as revision. Furthermore, "...the exact position of the corals in particular sections is insufficient" (Kossovaya 2009, p. 69). These two inaccuracies together significantly reduce the cognitive value of the important fauna of the region in question.

More recent studies have not clarified the doubts mentioned. Ogar (1990) published an unillustrated list of Bashkirian corals from the Southern Urals (Gornaya Bashkiria), i.e., from the eponymous area for the Bashkirian Stage, introduced by Semikhatova (1934). This list, reproduced below, was checked and corrected at my request by its author, Professor V.V. Ohar (Kyiv University) who wrote (e-mail of 1.11.2021): "In conclusion, I would like to emphasize that my answers to your questions are preliminary and my ideas may change in the process of a more in-depth study of my Ural collection." In his e-mail of 24. 11. 2021 he added: "*Darwasophyllum* and *Protokionophyllum*: Now I doubt that these are correct definitions". Therefore, most of his identifications are treated here as provisional. Kossovaya (1996, fig. 10) repeated the generic names from Ogar's (1990) paper without comments. Kossovaya (1996, 1997, 2001, 2007, 2009 and in Ponomarieva *et al.* 2015) corrected some generic names of earlier authors and attempted to correct the stratigraphic positions of several taxa. Unfortunately, the lack of appropriate illustrations in her papers makes verification of her corrections impossible. Also, the general interpretation of the Mississippian/Pennsylvanian rugose coral turnover of Kossovaya (1996) is not followed here (see below). Nonetheless, the lists of Serpukhovian and Bashkirian rugose coral genera from Novaya Zemlya (Kossovaya 1996, figs 3, 4) help to define the stratigraphy of the taxa described by Gorsky (1935, 1938, 1951) from the archipelago. Kossovaya (1996) listed 14 Viséan relict genera as the only rugose corals in the upper Serpukhovian. The non-disseminated

Cyathaxonia Michelin, 1847 and *Sychnoelasma* Lang, Smith and Thomas, 1940 that she listed are accepted, but *Zaphrentites* is doubtful. The solitary dissepimented *Dibunophyllum*, *Gangamophyllum* and *Palaeosmia* are accepted, but *Arachnolasma* Grabau, 1922 and *Siphonophyllia* Scouler (MS) in McCoy, 1844 are doubtful, while the name *Axophyllum* takes precedence over *Carcinophyllum* Thomson and Nicholson, 1876 (Hill 1981, p. F398). The colonial genera *Actinocyathus*, *Lonsdaleia*, *Siphonodendron* and *Tschernowiphyllum* Dobrolyubova, 1958 are accepted, while *Corwenia* Smith and Ryder, 1926 is questionable. Only *Palaeosmia* and *Carcinophyllum* (= *Axophyllum*) are extended to occur in the lowermost Bashkirian *Plectostaffella bogdanovkensis* Biozone. Other Serpukhovian genera were eliminated and middle Carboniferous corals have not yet appeared, making this biozone almost barren of rugose corals. This poverty corresponds to the statements of Degtyarev (1973a; see below).

Kossovaya's (1996, figs 3, 4) data on subsequent Bashkirian biozones are inconsistent. She included seven zones in her fig. 3, whereas in fig. 4 she illustrated only five zones, i.e., up to and including the *Pseudostaffella peregorsky–Profusulinella staffelleformis* Biozone (= Yeadonian Substage). The first two zones are discussed above. From the following three zones she listed only solitary dissepimented and colonial corals: *Bothrophyllum* Trautschold, 1879 and *Protodurhamina* in the *Eostaffella pseudostruvei–E. postmosquensis* Biozone; a continuous occurrence of two genera listed above and *Profischerina* Cotton, 1973 (= *Heintzella* Fedorowski, 1967), *Pseudokoninckophyllum* Vassilyuk and Polyakova, 1986 (= *Yuanophylloides*, see Fedorowski 2019a), *Donophyllum* (doubtful; only blastogeny can confirm its taxonomic position) and *Lytvophyllum* (perhaps = partly *Colligophyllum*) in the *Pseudostaffella antiqua* Biozone; and *Donophyllum* and the newcomers '*Caninia*' (almost certainly a genus other than the Tournaisian Western European *Caninia*), *Cystolonsdaleia*, *Fomichevella* and *Petalaxis* in the *Pseudostaffella peregorsky–Profusulinella staffelleformis* Biozone. Three genera, i.e., *Donophyllum*, *Colligophyllum* and *Yuanophylloides*, if their identifications are confirmed, may suggest some connection with the fauna of the Donets Basin. *Donophyllum*, reported from strata much older in Novaya Zemlya than in the Donets Basin, may suggest its ancestral position if firmly documented.

The distribution of some corals in the Timan Mountains (Kossovaya 1996, fig. 5) differs from that in Novaya Zemlya, if my understanding of the quoted

figure is correct. The Viséan genera *Dibunophyllum*, *Lonsdaleia* and *Actinocyathus* occurred in Northern Timan up to and including the *Plectostaffella bogdanovkensis* Biozone (lower Bashkirian, Voznessenkian Horizon). The genera occurring in the younger biozones are mostly the same as in Novaya Zemlya and need no further comment. The occurrence of *Diphyphyllum lateseptatum* will be treated as questionable till the axial offsetting and lack of axial structure in these specimens is documented.

Ogar (1990) identified the following Bashkirian genera and species from the Southern Urals: *Darwasophyllum irregulare* Pyzhanov, 1964 (see note on North America below) from the Bogdanovkian Horizon (included by Kossovaya 2009, fig. 1 in the Sjurianian Horizon); *Dibunophyllum bipartitum*, *Diphyphyllum lateseptatum* (see notes on the Timan Mountains), *Fomichevella*, *Lytvophyllum antiquum* Gorski, 1978 (= perhaps a new genus with lost structures: V.V. Ohar, in e-mail of 1.11.2021, related to *Colligophyllum*), *Protokionophyllum vassilyukae* Ogar, 1990 (seems to be more similar to *Krynkaophyllum* Fedorowski, 2021a: V.V. Ohar, in e-mail of 1.11.2021; see also comment above), *Profischerina* (= *Heintzella*), *Protodurhamina peculiare* (Gorski, MS in Degtyarev, 1979) in the Sjurianian Horizon; *Darwasophyllum* Pyzhanov, 1964, *Fomichevella*, '*Lytvophyllum*', '*Protodurhamina*', '*Profischerina*' and *Protokionophyllum* Vassilyuk, 1983 (see above) represented by the same species as in older horizons, *Bradyphyllum*, *Stereolasma* Simpson, 1900 (this is a Middle Devonian endemic genus from the eastern USA, lacking from the Urals; the specimens from the Urals resemble *Rotiphyllum* Hudson, 1942) and *Koninckophylloides* aff. *juresanensis* Gorski, 1978 and *K. notatum* Ogar, 1990 as newcomers in the Akavaskian Horizon; representatives of *Darwasophyllum*, *Fomichevella*, '*Lytvophyllum*', '*Protodurhamina peculiare*', '*Profischerina*' and *Koninckophylloides* aff. *juresanensis* and two species of *Corwenia*, i.e., *C. toulai* Gorski, 1951 and *C. karanelgensis* Gorski, 1975, both assigned to *Protodurhamina* by Ogar (1990), in the Askynbashian Horizon. The latter of these species may belong to *Corwenia* if it has a weak axial column as Gorski's (1975) specimen does (see below).

My brief analysis based on Gorski's (1978) illustrations and descriptions should start with the remarks of Professor V.V. Ohar (e-mail of 24.11. 2021) who wrote: "Thus, zone C₂¹ by Gorski has a younger age, covering the upper part of the Bashkirian and the lower part of the Moscovian ages (no upper Serpukhovian and no lower Bashkirian). This is indi-

rectly confirmed by my data on the Bashkirian Urals. Unit C_2^2 with frequent '*Lytvophyllum antiquum*' apparently corresponds to the Akavasian Horizon. It is compared with C_2^b of Bashkirian Urals. Units C_2^3 and C_2^c are even higher horizons of the Bashkirian and Moscovian Stage. It is possible that corals from the Sjuranian Substage (Bogdanovskian and Kamennogorian horizons of Kulagina *et al.* (2001, 2009) from the Kizelovsko-Chusovsky area are absent from the collection of I.I. Gorsky." The comments cited resulted in my making changes to the distribution of corals as described by Gorsky (1978) from the Urals. The following species described by him as derived from Zone C_2^1 should be accepted as younger, possibly upper Bashkirian: *Hapsiphyllum usvense* Gorsky, 1978 (= *Sychnoelasma*); *Caninia minuta* Gorsky, 1978, *C. macula* Gorsky, 1978 and *C. irinae* Gorsky, 1978 belong perhaps to *Arctophyllum* Fedorowski, 1975. The positions of *Caninia tchus-sowensis* Gorsky, 1978, *C. ivanovi* Gorsky, 1978, *C. microcystosa* Gorsky, 1978 and *Pseudotimania irregularis* Gorsky, 1978 cannot be determined from the published illustrations. However, none of the species identified as *Caninia* belong to this Tournaisian genus. *Lophophyllum lukiense* Gorsky, 1978 morphologically resembles *Paraheritschioides* Sando, 1985b, but is solitary. *Lophophyllum* (*Koninckophyllum*) *kosvense* Gorsky, 1978 perhaps belongs to *Orygmo-phyllum* and may be the stratigraphically oldest species of this genus. The true *Koninckophyllum* Nicholson and Thomson, 1876 does not occur in the Serpukhovian and younger strata of the Urals.

Bashkirian (Akavasian Horizon) taxa listed in Gorsky (1978) include: *Arachnolasma singulare* Gorsky, 1978 (resembles *Dibunophylloides* and may belong to this genus); *Bothrophyllum tolstikinae* Gorsky, 1978; *B. pseudoconicum crassa* (perhaps = *Arctophyllum* Fedorowski, 1975); *Campophyllum* aff. *uralicum* Dobrolyubova, 1936 (= *Fomichevella*); *Caninia irinae regularis* Gorsky, 1978 (perhaps = *Bothrophyllum*); *Corwenia karanelgensis* Gorsky, 1978 possibly belongs to *Corwenia*, as indicated by the narrow and incomplete axial column; it represents a morphologically modified Viséan relict genus; *Fischerina stuckenbergi* Dobrolyubova, 1936 (= *Heintzella*); *Koninckophylloides* Gorsky, 1978 is accepted as an independent genus; offsetting is not documented and it may be solitary gregarious; *Lithostrotion karanelgense* Gorsky, 1978 and *L. ineptum* Gorsky, 1978 (= *Kumpanophyllum*); *Lithostrotionella stylaxis uralica* Gorsky, 1978 and *L. flexuosa* (Trautschold, 1879) (= *Petalaxis*); *Lophophyllidium uralense* Gorsky, 1978 (accord-

ing to Kossovaya in Ponomarieva *et al.* 2015 = *Amygdalophylloides* Dobrolyubova and Kabakovich, 1948); *Lophophyllidium zilimi* Gorsky, 1978 (dissepimentarium excludes it from this genus; taxonomic position cannot be suggested); *Lophophyllum* (*Koninckophyllum*) *ripheicum* Gorsky, 1978 and *L. (K.) vesiculosa* Gorsky, 1978 belonging perhaps to the Family Bothrophyllidae Fomichev, 1953; and *Lytvophyllum antiquum* Gorsky, 1978 which includes Bashkirian, Moscovian and possibly Gshelian specimens. The holotype (Gorsky 1978, pl. 21, figs 12, 12a) and some paratypes (pl. 21, figs 11, 14–17; pl. 22, figs 1, 2, 5, text-figs 36, 37 = pl. 22, figs 4, 7) are Moscovian. The specimens illustrated by Soshkina (1925) are either upper Moscovian or lower Gshelian (Gorsky 1978, pl. 21, figs 1, 1a, 2, 2a). The remaining specimens (Gorsky 1978, pl. 21, figs 7, 18) are of uncertain stratigraphic position as mentioned above. Most specimens represent either *Colligophyllum* or a new genus (possibly genera) related to it. Kossovaya (2009) transferred most of the specimens included by Gorsky (1978) in *Lytvophyllum antiquum* to her new species ?*Pseudolytvophyllum askynensis* (see Fedorowski 2019b). The two specimens illustrated by Gorsky (1978, pl. 22, figs 5, 7; text-figs 36, 37) most probably belong to *Heintzella*. The group of species discussed represents perhaps the most common Bashkirian taxa in the area. Their careful re-examination may therefore lead to the establishment of precise and easily comparable biozones. A single transverse thin section of *Dibunophyllum* sp. indet., perhaps from C_2^c , i.e., upper Bashkirian or Moscovian deposits of Bashkiria, exposes the main typical features of this genus, flourishing in the Viséan, but present up to the middle Bashkirian in the Donets Basin, North Africa and the Sverdrup Basin in the Canadian Arctic Archipelago. This would be the stratigraphically youngest occurrence of *Dibunophyllum* if confirmed.

Degtyarev (1979) supplemented Gorsky's (1978) descriptions of the Bashkirian and Moscovian Rugosa from Bashkiria. Unfortunately, incomplete illustrations and the poor state of preservation of several species he described make it impossible to confirm some of his identifications. I do not comment on his Moscovian coral taxa, although I do not accept any of his species identifications as *Caninia* or *Caninophyllum* Lewis, 1929. Nor will I follow his identifications of *Cyathaxonia*, *Bradyphyllum*, *Hapsiphyllum* Simpson, 1900 and *Monophyllum* Fomichev, 1953 (see Fedorowski 2009b). None of the species described from Bashkirian strata as '*Koninckophyllum*' belong to this genus. Degtyarev

(1979) was of a similar opinion, putting these names in inverted commas. The colonial ‘K.’ *kosvense* perhaps belongs to *Opiphyllum*. The other species of ‘*Koninckophyllum*’ were also considered colonial. This is suggested by the phrase ‘*oblomki*’ (Russian for fragments) used in the descriptions, although the word ‘colony’ was used only for ‘K.’ *ripheicum*. Documentation of most of these species is insufficient to suggest alternative names. Only one specimen of ‘K.’ *ripheicum* (Degtyarev 1979, pl. 47, fig. 2a, b) can be classified as a probable *Heintzella*, if it is indeed colonial, while a specimen of ‘K.’ aff. *singulare* (Degtyarev 1979, pl. 48, fig. 4) may belong to *Dibunophylloides* if it is solitary. ‘*Fischerina stuckenbergi*’ with a continuous axial column should perhaps be renamed *Corwenia*, while species identified as ‘*Corwenia*’ but lacking axial columns may belong either to *Heintzella* or to *Dibunophylloides*. Two colonies were illustrated by Degtyarev (1979) under the name ‘*Lithostrotion peculiare*’ (Gorsky in MS, Degtyarev, 1979). One of these colonies (Degtyarev 1979, pl. 51, fig. 1) may belong to *Heintzella*, as indicated by the weak, interrupted axial structure and shortened cardinal septum. The second (Degtyarev 1979, pl. 51, fig. 2) closely resembles *Protodurhamina strelzovskensis* Kozyreva, 1978 (her pl. 1, fig. 1) with a continuous pseudocolumella and elevated tabulae in the longitudinal section. Comments on *Campophyllum* Milne Edwards and Haime, 1850, *Darwasophyllum* and *Lytvophyllum* are presented above. It is unfortunate that Degtyarev (1979), having expressed so many doubts in the identification of the taxa, did not attempt to revise them and propose correct names.

The use of an insufficiently identified genera to correlate Ural strata with strata of distant rugose corals sites should be regarded as causing errors rather than helping correlation. As an example, consider Kossovaya’s (1997, table 3) attempt to correlate the *Protodurhamina* Zone, which includes three older substages of the Bashkirian in the Urals, Timan Mountains and Novaya Zemlya with northern Spain and North America. The occurrence of *Protodurhamina* in these substages is not documented by irrefutable data, while Kossovaya (1997, p. 87) writes: “The lower limit of the *Protodurhamina* Zone is traced in the base of Namurian B of Cantabrian Mountains (Rodríguez *et al.* 1986) and coincided with the elimination of the most Lower Carboniferous genera”. In reality, *Protodurhamina* is absent from Spain and North America. Also, the rugose coral faunas from the Cosgaya, Valdeteja and Veja formations, considered by Rodríguez (1984a, b,

1985) and Rodríguez *et al.* (1986) to be Bashkirian, are very rare and differ distinctly from the Rugosa of the Urals, Timan Mountains and Novaya Zemlya (see above). Thus, both the application of the name *Protodurhamina* and the correlation of the areas discussed using the zonal name *Protodurhamina* is misleading.

With so many doubts about both the taxonomy and the ranges of the various genera, I give up at this point an attempt to propose a succession of rugose coral genera in the area under discussion. I also do not wish to add to the nomenclatural chaos by publishing here a list of the genera initially revised above. They should be treated as no more than introductory suggestions. Only a thorough revision will clarify the taxonomic content of Bashkirian Rugosa in Novaya Zemlya, the Timan Mountains and the Urals. Only genus names applied to specimens from this area, but in my opinion in reality absent, are listed. Moreover, some taxa have already been discussed in my previous papers (Fedorowski 2004, 2009b, c, 2015, 2017b, 2019a, 2021a), to which the reader is referred. Taxa either absent from the Serpukhovian and Bashkirian strata of the area under discussion, or not studied in detail adequate for their approval, or with pre-occupied names include: *Amplexus*, *Campophyllum*, *Caninia*, *Caninophyllum*, *Clinophyllum* Grove, 1935, *Cystophora* Yabe and Hayasaka, 1916, *Eostrotion* Vaughan, 1915, *Fischerina* Stuckenbergh, 1895, *Hapsiphyllum*, *Homalophyllites* Easton, 1944, *Koninckophyllum*, *Leonardiphyllum* Moore and Jeffords, 1941 (should perhaps be *Leonardophyllum*), *Lithostrotion*, *Lonsdaleiastraea* Gerth, 1921, *Lophophyllum* Milne Edwards and Haime, 1850, *Lytvophyllum*, *Nemistium*, *Stereolasma*, *Zaphrentis* Rafinesque and Clifford, 1820 and *Zaphriphyllum* Sutherland, 1954.

Contrary to all the doubts mentioned above, the fluctuation in the presence of rugose corals in Novaya Zemlya, the Timan Mountains and the Urals took place in a time interval spanning the upper Serpukhovian and lower Bashkirian strata, although it cannot be indicated as precisely as for the Donets Basin (see below). Also, it is not as sharp worldwide as suggested by Kossovaya (1996). Degtyarev’s (1973a) priority in establishing this turnover should also be pointed out. He suggested a strong depletion of rugose coral fauna in the Urals (Degtyarev 1973a, p. 218): “Coral fauna, especially lower Namurian (Ust’-Sarbaiskiy Horizon) is extremely poor, occurring very seldom, commonly sporadic...”. According to the Stratigraficheskyy Slovar SSSR. Karbon, Perm (1977), this part of the stratigraphic column, characterised by *Eostaffella postmosquen-*

sis Kireeva, 1951 (In: Rauser-Chernousova *et al.*, 1951), *Cravenoceras* spp., *Hudsonoceras* spp. and *Homoceras* spp., corresponds to the Namurian A in Western Europe and the Voznessenkian Horizon in the Donets Basin. Thus, either the faunal crisis in the area in question occurred later than in many parts of the world, or the stratigraphic schemes at the disposal of Degtyarev (1973a, b) were not precise enough. According to Kossovaya (1996, fig. 2), the crisis took place in the *Plectostaffella bogdanovkensis* Zone. Comparing the coral fauna from the middle Carboniferous (i.e., Bashkirian and Moscovian) to that of the lower (including the Serpukhovian) and the upper Carboniferous, Degtyarev (1973a, p. 220) wrote: "...one can speak of their sharp separation from the coral complexes of the Lower and Upper Carboniferous." In the same paper he suggested that: "*Lytvophyllum antiquum* (Gorsky) was the most characteristic and widespread species [‘forma’ as he wrote] for the Bashkirian" (all citations translated from Russian). He conceded that several lower Carboniferous names applied by the authors to the Bashkirian Rugosa were incorrect and should be replaced by new generic names.

I have several reservations about Kossovaya’s (1996) concept of the Serpukhovian/Bashkirian turnover of rugose corals. The extinction is not sharp worldwide, but varied in time and intensity, leading to a patchy distribution of corals, as discussed extensively in the Palaeogeographic Overview above and in the Discussion and Summary below. New data from the Donets Basin and North Africa were not available for her. However, data from several areas were available which contradicted her concept. Examples include the Akiyoshi Terrane fauna, flourishing at the time of the crisis, the faunal succession in North Africa established by Semenoff-Tian-Chansky (1974, 1985), the abundant Morrowan fauna in the North American Midcontinent Province, and the rich Chinese fauna corresponding roughly to the upper Serpukhovian/lower Bashkirian. New data, especially those from North Africa, suggest that this extinction period was extended in time in some areas.

The base of the *Homoceras* Genozone is not a global ‘extinction event’ as postulated by Kossovaya (1996). On the contrary, it includes both survivors and newcomers, as documented by studies from the Donets Basin and on the North African and North American corals. Thus, the *Homoceras*–*Hudsonoceras* Genozone is the beginning of a ‘recovery event’ mixed with a ‘survival event’ in these areas. Concrete data available to date do not allow for this recognition to be extended onto other regions

of the world, although it seems very likely in China. The appearance of Mississippian taxa in the middle (or upper) Bashkirian in such an isolated site as the Sverdrup Basin (Canadian Arctic Archipelago) should also be considered. This fauna must have survived in a hitherto unknown refugium.

Kossovaya’s (1996) concept of ‘post-crisis ontogenetic changes’ should also be discussed, as it can imply important, but in my opinion false, consequences. Any change in the ontogeny is equivalent to a genetic mutation and should be treated as diversification of the phylogenetic lineage. The taxonomic value of such diversification depends on the depth of these changes. Since only exoskeletons, which are the source of all information provided by a corallite or colony, are available for rugose corals, only very careful investigations on well-preserved specimens from a clearly defined stratigraphic succession can form the basis for the concept mentioned above. Kossovaya (1996) did not adhere to this basic condition. It suffices to point to ‘the *Caninia* lineage’ as an example. *Caninia cornucopiae* Michelin in Gervais, 1840, the type species for the genus, is a Western European Tournaisian species. Its complete ontogeny was documented by Carruthers (1908). Only a Tournaisian specimen with identical ontogeny and septal microstructure found in the Urals and a series of younger specimens from a series of well-documented younger deposits of the same area can support Kossovaya’s (1996) suggestion. Unfortunately, no such data is available in the existing literature. On the contrary, the Bashkirian specimens from the Urals described as ‘*Caninia*’ are not only distant in time and space from the Western European type species of *Caninia*, but their complete early ontogeny remains unknown. Nor has the complete ontogeny of a specimen indisputably belonging to *Caninia* from the Urals, the Timan Mountains or Novaya Zemlya ever been described. Hence Kossovaya’s (1996, p. 190) statement relating true *Caninia* and Bashkirian ‘*Caninia*’ that “The earlier ontogenetic stages remain the same”, is unfounded. Kossovaya (1996, p. 190) tried to support her concept with microstructure by writing: “At the same time, the fine structure of the descendant species *Caninia* has become stable compared to its ancestor (Kossovaya and Kropacheva 1993).” However, the poor and inadequately enlarged illustrations (Kossovaya and Kropacheva 1993, pl. 1, figs 1–8) showing both the primary septa and their secondary sclerenchymal cover, most likely diagenetically altered, cannot serve as reliable documentation. Moreover, these illustrations do not show the microstructure of *Caninia cornucopiae*, and there is no reference to the microstructure of the latter species in

the cited paper. Thus, this microstructural ‘support’ is here also judged to be unfounded. Kossovaya’s (1996, p. 197) concluding sentence: “Thus, the preadaptation of some rugose corals at mid-Carboniferous event is connected with early ontogenetic changes (coenogenesis)...” lacks documentation and her idea is rejected.

In conclusion: 1) Despite long-term studies of rugose corals, the succession of Serpukhovian and Bashkirian Rugosa cannot be established step by step for Novaya Zemlya, the Timan and the Ural Mountains. This is due to two factors: (i) uncertain taxonomy, making the various generic names ambiguous, (ii) the uncertain stratigraphic position of taxa described by previous authors. 2) Although several of the generic names applied to Bashkirian corals from this area are questionable, making direct comparison with genera from other areas difficult, the conclusion of the rugose coral faunal turnover suggested by Degtyarev (1973a), Fedorowski (1978a, 1981a), Rodríguez *et al.* (1986) and Kossovaya (1996) is documented by the appearance of new genera the Bashkirian strata. 3) Only the study of a faunal succession comparable to that of the Donets Basin will indicate the precise boundary of the rugose coral faunal turnover in this important area.

North American part of Laurussia

Although the two-stage sub-division of the North American Carboniferous has been in use for decades, the first presumably continuous succession across the Mississippian–Pennsylvanian boundary has only recently been established (Brenckle *et al.* 1997) in Arrow Canyon, Nevada. Moreover, the first find of *Isohomoceras* at a test site in Nevada was made by Titus *et al.* (1997). These results, further studies on the ammonoids of the North American Middle Carboniferous (Titus and Manger 2001), and the occurrence of the conodont *Declinognathodus noduliferus* almost contemporaneously with *Isohomoceras*, have made the lower boundary of the North American Pennsylvanian, i.e., the beginning of the Morrowan, closely comparable to the beginning of the Bashkirian Stage in Europe, North Africa and East Asia. However, a hiatus near the boundary beds in the Arrow Canyon stratotype section was pointed out by Aretz *et al.* (2020, p. 819). Also, Menning *et al.* (2006, fig. 3) pointed to a hiatus corresponding to the Voznessenkian Substage (= Chokierian and Alportian Substages) in Arkansas and Oklahoma. Thus, they correlated the lower boundary of the Hale Formation and the Wapanucka Limestone with the lower boundary of the Feninian Horizon in the Donets

Basin (= Krasnopolyian Horizon = Kinderscoutian Substage). Numerous Morrowan, i.e., Bashkirian corals have been described from the Hale Formation and the Wapanucka Limestone (Jeffords 1942; Moore and Jeffords 1945; Rowett and Sutherland 1964). These taxa, as well as most Serpukhovian rugose corals from other areas of the USA (see below), were published long before the modern Serpukhovian/Bashkirian boundary was established, which creates some difficulty in determining the sequence of their first occurrences.

Sando *et al.* (1975, 1977) distinguished five provinces in the Mississippian of North America, supplemented by Bamber *et al.* (2017, pp. 2, 3; these supplements are included here in brackets): Alaskan (including the British Mountains in the Yukon Territory and the Brooks Range of northern Alaska), Pacific Coast (including the Alexander and northern Stikine Terrane of south-eastern Alaska and north-western British Columbia and allochthonous carbonates of the Coffee Creek Formation in Central Oregon, USA), Western Interior (including the Rocky Mountains and Plains of western Canada and USA), Southeastern (including the Mississippi Valley Region of east-central and southeastern USA), and Maritime (including several areas of Atlantic Canada).

Only four of these provinces were discussed by Rodríguez *et al.* (1986; Text-fig. 1). They did not include the Alaskan Province because Serpukhovian corals are poorly known from that area (e.g., Armstrong 1970, 1972a, b, 1975). Bamber *et al.* (2017, p. 6) confirmed this information.

Five Serpukhovian coral genera, all typically recorded in Europe, were listed by Rodríguez *et al.* (1986; Text-fig. 1) from the Pacific Coast Province, but only European *Siphonodendron* from Peratrovich Island in southern Alaska (Armstrong 1970) was confirmed by Bamber *et al.* (2017, p. 6) as belonging to this genus. In contrast, a rugose coral fauna was provisionally identified by Fedorowski and Bamber (in Gunning *et al.* 2006, p. 64) from the upper Serpukhovian and lower Bashkirian (foraminiferal zones 18 and 20 of Mamet and Skipp 1970) of the Stikine Terrane (see also Gunning *et al.* 2007 for details on the Arctic Lake Formation). The following Serpukhovian genera were identified: *Lophophyllidium* and *Rotiphyllum* (solitary, non-dissepimented); *Dibunophyllum*, *Palaeosmilia* (solitary, dissepimented); *Lonsdaleoides* (perhaps solitary gregarious); *Cystolonsdaleia*, *Eastonastraea* Stevens and Rycerski, 1989, *Heintzella* and *Nemistium* (colonial). Some of these names, especially *Lonsdaleoides* and *Eastonastraea* may be replaced by new generic names.

Fedorowski *et al.* (2014a) revised *Heritschioides* Yabe, 1950 and its type species *Waagenophyllum columbicum* Smith, 1935 from the Blind Creek Limestone, southern British Columbia. The limestone was documented by Danner (1997) as late Serpukhovian or early Bashkirian in age. Thus, *Heritschioides* should be added to the list of Serpukhovian genera occurring in the Coastal Province.

Rodríguez *et al.* (1986; Text-fig. 1) listed several genera from the Serpukhovian of the Southeastern Province, based on previous data (e.g., Easton 1943a, b, 1944, 1945, 1951; Nelson 1960; Armstrong 1962; Frauenfelder 1965, 1970; Fagerstrom and Eisele 1966; Weyer 1965), summarised by Sando and Bamber (1985). Only the rugose coral papers by Webb (1984, 1987; Webb and Sutherland 1993) can be added to this list. The taxa described by the latter authors are the most completely studied and their identifications are fully accepted here. From the list of Rodríguez *et al.* (1986; Text-fig. 1) only the occurrence of *Amplexus* and *Koninckophyllum* can be questioned, while *Bradyphyllum* described by Webb and Sutherland (1993) should be added. Rodríguez and Kopaska-Merkel (2014) added *Lublinophyllum* Khoa, 1977, *Palaeostraea*, *Siphonodendron* and *Zaphrentites*. These European genera, the European species *Siphonodendron martini* Milne Edwards and Haime, 1851 from the Chesterian, and *Arachnolasma* and *Actinocyathus floriformis* d'Orbigny, 1852, both from Meramecian, suggest a closer relationship of this province to Europe than previously thought.

Only five Serpukhovian genera were listed by Rodríguez *et al.* (1986; Text-fig. 1) from the Western Interior Province based on papers by Sando (1963, 1965, 1969, 1975, 1976, 1984, 1985a, b, 1989), and Sando and Bamber (1985). The occurrence of *Amplexus* in this list is disputed here. Only species possessing the earliest brephic growth stage with six very short major septa, i.e., the morphology established in the type species for the genus – *Amplexus coraloides* Sowerby, 1814 (see Fedorowski 2003, fig. 1:6) can be qualified as belonging to this genus from the lower Mississippian of the British Isles. The above list was completed by Bamber *et al.* (2017) with *Lublinophyllum* and *Schoenophyllum* Simpson, 1900 from foraminiferal zones 16 and 17 (upper Brigantian–lower Pendleian), *Cystolonsdaleia* from foraminiferal zones 17 and 18 (Pendleian–lower Arnsbergian), and *Bifossularia* Dobrolyubova in Dobrolyubova and Kabakovich, 1966 and *Caninostrotion* from foraminiferal Zone 18 (lower Arnsbergian).

The Maritime Province with the rugose coral fauna included by Fedorowski (1981a) in the

Western European Province (a suggestion confirmed by Bamber *et al.* 2017, p. 11) includes mainly upper Viséan taxa with a few extensions to the lower Serpukhovian. Its first description by Bell (1929) was completed by Lewis (1935), listed by Fedorowski (1981a) and summarised by Poty (2002).

Bashkirian rugose coral faunas have been mentioned by Rodríguez *et al.* (1986; Text-fig. 2) in only two North American provinces, i.e., the Midcontinent and Western Interior. New data (see below) allow for the accepting of an extension to the Bashkirian Provinces of the Pacific Coast and Alaska. The Maritime Rugose Corals Province disappeared at the end of the Viséan as did the Western European Province, confirming the inclusion of the former into the latter as suggested by Fedorowski (1981). The level of investigation of the coral faunas listed by Rodríguez *et al.* (1986) from the Midcontinent and Western Interior provinces is different. Illustrated papers on Morrowan (lower Bashkirian) corals have been published for the Midcontinent Province (Jeffords 1942, 1948; Moore and Jeffords 1945; Rowett and Sutherland 1964), while papers on the Western Interior Province are based mainly on lists published by Sando (1984, 1985a). Several of the generic names listed by Sando (1984, 1985a, 1989) and Rodríguez *et al.* (1986) from the North American Bashkirian need revision or have already been found to be incorrect (Fedorowski 2017a, 2019a).

My personal familiarity with several of the collections of North American Pennsylvanian Rugosa described so far allows for preliminary corrections and/or taxonomic remarks (see below), but these should by no means be considered conclusive. Furthermore, some new data (Gunning *et al.* 2006; Fedorowski and Bamber 2012; Fedorowski *et al.* 2012, 2014a, b, 2019, 2021; Kawamura and Stevens 2012; Stevens *et al.* 2012; Fedorowski and Stevens 2014) document an extension of the Coastal and Alaskan Provinces into the Bashkirian and Moscovian (Fedorowski *et al.* 2014b).

Sando's (1985, p. 345) suggestion of a provisional identification of the North American *Dibunophyllum* and *Neokoninckophyllum* Fomichev, 1939 as *Amandophyllum* is misleading (Fedorowski 2017a, 2019a). *Amandophyllum* was first described by Heritsch (1936) from the Carnic Alps as *Clisiophyllum* and later renamed *Amandophyllum* (Heritsch 1941) to distinguish the lower Permian specimens from the Carnic Alps from the Viséan genus from Europe. Given the closure of the Rheic Ocean and the formation of Pangea, his concept is fully supported by drastic changes in palaeobiogeography. Thus, I do not currently accept the presence of this genus in

the upper Viséan in Poland (Fedorowski 1971, p. 111) and deny the ancestral role that was suggested for it by Fedorowski (1986a, p. 261) and by Garcia-Bellido and Rodríguez (2005, p. 326) for some upper Carboniferous taxa. The Polish ‘*Amandophyllum*’ represents only the *Amandophyllum* morphotype (Fedorowski 2019a).

The same is true for the North American *Dibunophyllum*, suggested by Sando (1985) for the name *Amandophyllum*. Species classified as *Dibunophyllum* by various North American authors are known to occur from the lower Morrowan (Moore and Jeffords 1945) to the lower Permian (Ross and Ross 1962). Their mature morphology in transverse section resembles that of both *Dibunophyllum* proper and *Amandophyllum*, whereas the longitudinal section of the latter is unknown (Heritsch 1936, pl. 18, figs 23–28). The absence of an axial column in longitudinal section in *Amandophyllum* can only be predicted, whereas the absence of this structure in North American dibunophylla is documented (e.g., Newell 1935; Moore and Jeffords 1945; Rowett and Sutherland 1964; Cocks 1970). This important morphological difference clearly distinguishes the North American ‘*Dibunophyllum*’ from the European *Dibunophyllum* proper. Morphology in early ontogeny is another important feature to consider. This feature is not known from *A. carnicum*, whereas it was documented by Cocks (1970) in the American ‘dibunophylla’. Thus, the North American ‘dibunophylla’ would be theoretically related to *Amandophyllum carnicum* only if: (i) the early ontogenies of the two lineages were strictly comparable, (ii) the axial column was missing in the species from the Carnic Alps, and (iii) the palaeogeography would permit. The first two preconditions may be postponed for the time being, making the third one decisive. The North American dibunophylla were long living (lower Bashkirian to lower Permian). Moreover, the Rheic Ocean, replaced by the Iberia Midcontinent Pathway between Panthalassa and Palaeotethys (Garcia-Bellido and Rodríguez 2005, fig. 2), existing perhaps up to the Moscovian inclusively, allowed for a connection between eastern and western shelves of Euramerica. However, indisputable *Amandophyllum* is absent from the Serpukhovian, also from the entire Pennsylvanian of the eastern shelves of Euramerica and the far Asiatic sites. It appeared in the lower Permian of the eastern shelves of Pangea, i.e., at least 10 Ma after the closing of that pathway. Thus the long-lived American ‘*Dibunophyllum*’ cannot be considered a parent of *Amandophyllum*. I therefore reject the concept of Sando (1985), supported by Garcia-Bellido and Rodríguez (2005). I also maintain the position of

convergent occurrence of several characters in the Rugosa, which resulted in the homeomorphy of many taxa (Fedorowski 1981a, 2010b; Webb 1993). Not only *Dibunophyllum* but also *Neokoninckophyllum*, characterised by Sando (1985, p. 346) as common in the Morrowan and *Pseudozaphrentoides*, commented by him as the “most abundant and widespread” (Sando 1985, p. 346) are probably absent from North America (Fedorowski 2017a, 2019a). In the case of North America, the latter two names perhaps cover several different genera.

The Morrowan deposits of the Midcontinent Province, USA, yield abundant and diverse non-dissepimented rugose coral genera, accompanied by dissepimented solitary corals. Colonial corals are probably absent. The specimen illustrated by Rowett and Sutherland (1964, pl. 9, fig. 5) may either represent a very weak fasciculate colony or is proto-colonial (Fedorowski 2019a). The specimens listed by Garcia-Bellido and Rodríguez (2005, p. 326) as colonial and transferred by them to *Dibunophylloides* are proto-colonial in growth form (Fedorowski and Ogar 2013) and cannot be included in the solitary *Dibunophylloides* (Fedorowski 2017a).

The following non-dissepimented taxa can be listed from the Midcontinent Province:

- *Lophophyllidium* was the most common and diverse upper Carboniferous non-dissepimented rugose coral genus in North America, occurring from the Upper Mississippian (upper Serpukhovian) Imo Formation (Webb 1984) and extending into the lower Permian (Fedorowski 1987).
- the long-lived *Bradyphyllum* (with some *Hapsiphyllum* specimens of Moore and Jeffords, 1945, and *Fasciculiamplexus* Easton, 1962 as its probable synonyms).
- *Barytichisma* Moore and Jeffords, 1945 (including *Paracaninia sana* Moore and Jeffords, 1945, *Thecophyllum* Fomichev, 1953 and *Amplexizaphrentis* of Sando, 1984 as synonyms).
- *Leonardophyllum* Moore and Jeffords, 1941 and *Lophotichium* Moore and Jeffords, 1945, which only appeared in this stratigraphic interval but persisted until the lower Permian (Fedorowski 1987).
- *Falsiamplexus* Fedorowski, 1987 (= *Amplexus corrugatus* Mather, 1915 = *Amplexocarinia corrugata* Mather, 1915 of Moore and Jeffords 1945 and Rowett and Sutherland 1964 = *Amplexocarinia* of Sando 1984), *Stereocorypha* Moore and Jeffords, 1945 and *Empodesma* Moore and Jeffords, 1945; some of these genera are present in the Western Interior Province (Sando 1984, 1985; Rodríguez *et al.* 1986).

The dissepimented solitary rugose corals flourished in the Midcontinent Province through the Pennsylvanian (Newell 1935; Jeffords 1942, 1948; Cocke 1969, 1970; Cocke and Cocke 1969; Cocke and Haynes 1973; Cocke and Molinary 1973; Sando 1984) into the lower Permian (Ross and Ross 1962, 1963), forming a major part of the rugose coral fauna in the area. Most of these corals were originally included in the lower Carboniferous European genera such as *Dibunophyllum*, *Rhodophyllum* Thomson, 1875 *Koninckophyllum*, *Pseudozaphrentoides*, and the middle to upper Carboniferous *Neokoninckophyllum*, and should be re-named (see above). Only two genera are common both to the Donets Basin and the Midcontinent area: 1) *Barytichisma*, described from the Donets Basin as *Thecophyllum* (see Fedorowski and Vassilyuk 2011); and 2) *Yuanophylloides* identified by Moore and Jeffords (1945) as *Dibunophyllum* and *Neokoninckophyllum*, by Rowett and Sutherland (1964) as *Koninckophyllum*, and by Cocke (1970) as *Neokoninckophyllum* (see Fedorowski 2019a).

Rare colonial corals were reported by Sando (1984) from the Western Interior Province. The protocolonial and/or weakly colonial *Craterophyllum verticillatum* Barbour, 1911 (= *Crataniophyllum* Lang and Thomas, 1957) and three truly colonial taxa occur in this province: the opportunistic and cosmopolitan fasciculate *Heintzella*, first found in the lower Permian (Fedorowski 1967), but known to occur in either the Bashkirian or possibly the upper Viséan (Fedorowski *et al.* 2007, p. 90); the opportunistic *Fomichevella* first described from the upper Carboniferous, but known perhaps from the upper Viséan to lower Permian (Fedorowski *et al.* 2007, p. 84); the cosmopolitan *Petalaxis* probably appeared in the upper Viséan (Sando 1983), but continued to flourish to the lower Permian (Bamber and Fedorowski 1998; Fedorowski *et al.* 2007).

Solitary, non-dissepimented and dissepimented corals are common in the Western Interior Province (Sando 1984, 1985, 1989; Rodríguez *et al.* 1986), but most of them are only listed, which precludes comments on the correctness of their inclusion in European genera.

Data from Rowett (1969) and Armstrong (1972, partially revised by Fedorowski and Stevens 2014) and new data (Fedorowski and Bamber 2012; Fedorowski *et al.* 2012, 2019, 2021) allow the suggestion of an extension of the Alaska Province into the late Bashkirian. Fedorowski and Bamber (2012) and Fedorowski *et al.* (2012) discuss the Bashkirian corals of the Sverdrup Basin, whose palaeogeographic position Dr. E.W. Bamber (letter of April 12,

2021) characterised as follows: “we have incomplete knowledge of the northern fauna, but it appears that the south-western part of the Sverdrup Basin overlaps with the Alaska coral province. We cannot be sure of this because of large areas that have been affected by the Ellesmerian orogeny and sub-Permian erosion.”

Two new species, *Nemistium liardense* and *Heritschioides simplex* both of Fedorowski, Bamber and Richards, 2019 from the Mattson Formation, Liard Basin, Yukon Territory, Canada are perhaps the oldest Bashkirian taxa in the Alaska Province. The age of the upper member of the Mattson Formation yielding these corals was suggested by Fedorowski *et al.* (2019) as early Bashkirian. In turn, it was considered Viséan or Serpukhovian by earlier authors (see Fedorowski *et al.* 2019, pp. 852–856).

Other occurrences are younger. Rowett (1969) described from Alaska the new species *Cryptophyllum striatum* of ‘postMorrowan – preMissourian age’, i.e., late Bashkirian or early Moscovian. Fedorowski (2009a, p. 571) characterised this species as “perhaps the stratigraphically youngest representative of the *Cryptophyllum*-like lineage.” Armstrong (1972b) described two new species *Corwenia jagoensis* and *Lithostrotionella wahooensis* from the Wahoo Limestone in the Brooks Range, Alaska, considered by him to be Atokan, i.e., late Bashkirian and early Moscovian in age. Fedorowski and Stevens (2014) revised these coral type collections, transferred the holotype of *C. jagoensis* to *Paraheritschioides* and introduced the new species *Heritschioides separatus* and *Paraheritschioides compositus*, based on the paratypes of *C. jagoensis*. In addition, they transferred *Lithostrotionella wahooensis* to the new genus *Arctistrotion* Fedorowski and Stevens, 2014 established on the basis of a colony from the Crinoidal Limestone (upper Bashkirian) of Kuiu Island, Alexander Terrane, Alaska, included here in the Pacific Coastal Province.

A peculiar fauna of rugose corals from the lower upper Bashkirian in the Sverdrup Basin, Arctic Canada (Fedorowski and Bamber 2012; Fedorowski *et al.* 2012) completes the list of papers on possible corals from the Alaska Province (see above). Three taxa, i.e., *Dibunophyllum bipartitum craigianum* (Thompson, 1874), *Palaeosmilia purchisoni* and *Lonsdaleia duplicata* (Martin, 1809) are known from the European and North African Viséan and Serpukhovian. The specimen described as *Tizraia?* sp. aff. ‘*Diphyphyllum*’ *carinatum* Gorsky, 1951 perhaps belongs to a new species closely related to the Brigantian and/or Serpukhovian taxa from Novaya Zemlya and North Africa. *Paraheritschioides* sp.

may be one of the oldest species of this genus so far known from North America (for a more comprehensive discussion see Fedorowski and Bamber 2012; Fedorowski *et al.* 2012).

Continuation into the Bashkirian and Moscovian of the Pacific Coast Province was documented by Gunning *et al.* (2006, 2007), Fedorowski *et al.* (2007, discussion only), Kawamura and Stevens (2012), Stevens (2012), Stevens *et al.* (2012), Fedorowski and Stevens (2014), and Fedorowski *et al.* (2014a). Stratigraphically, the oldest Bashkirian coral fauna of the province was collected from the Arctic Lake Formation in the Stikine Terrane (Gunning *et al.* 2006, fig. 4; 2007, p. 32, figs 5, 7), corresponding to the lower part of Zone 20 of Mamet and Skip (1970) and Mamet *et al.* (1993). Two dissepimented solitary genera: *Bifossularia* and *Pseudotimania* Dobrolyubova and Kabakovich, 1948, and five fasciculate colonial genera: *Fedorowskiella* Stevens and Rycerski, 1989, *Fomichevella*, *Heintzella*, *Nemistium* and *Paraheritschioides* were tentatively identified by Fedorowski and Bamber (in Gunning *et al.* 2006, p. 64). These genera form a mixture of Viséan–Serpukhovian taxa (*Bifossularia*, *Nemistium*), opportunistic, widely distributed and long-lived taxa (*Fomichevella*, *Heintzella*), the typical Pennsylvanian newcomer *Paraheritschioides*, present in the upper Carboniferous and lower Permian (Fedorowski *et al.* 2007, p. 96), and the endemic *Fedorowskiella*, first described from the lower Permian deposits of the Stikine Terrane (Stevens and Rycerski 1989). The occurrence of the latter genus in the lower Bashkirian requires more comprehensive study.

There is a gap in the record extending from Zone 20 characterised above to the lower Atokan (= Duckmantian Substage in Western Europe = Krasnodonian Horizon in the Donets Basin). Kawamura and Stevens (2012) recorded several solitary, possibly solitary and colonial taxa from the lower Atokan of the Klamath Terrane. The specimens they described as ‘type 1’ of *Corwenia? jagoensis* (Kawamura and Stevens 2012, fig. 2: 10, 11, 14) bear all the morphological features of *Dibunophylloides* and would perhaps be included in this genus if they were solitary. However, the specimens resemble also the morphology of the holotype of *C. jagoensis* transferred to *Paraheritschioides* by Fedorowski and Stevens (2014) and would belong to that genus if they were colonial. Unfortunately, the fragmentary state of preservation of Kawamura and Stevens’s (2012) specimen, as well as several other species described by the latter authors makes their growth form unclear. ‘Type 2’ of *C.? jagoensis* (Kawamura and Stevens

2012, fig. 2:1, 2, 4–7) with a rather complex axial structure in transverse sections and fragments of the axial column in longitudinal sections closely resembles *Paraheritschioides compositus* Fedorowski and Stevens, 2014 and probably belongs to this species. Thus, *Corwenia* is absent from the Klamath Terrane and Coastal Province, just as it is absent from the Brooks Range (Armstrong 1972) and the Alaska Province (Fedorowski and Stevens 2014). The solitary, *Bothrophyllum*-like species (Stevens *et al.* 2012) perhaps belongs to a new genus. The colonial growth form of *Heritschioides armstrongi* Kawamura and Stevens, 2012 is confirmed by an offsetting corallite (Kawamura and Stevens 2012, fig. 2:15). Its morphology closely resembles *Heritschioides separatus* Fedorowski and Stevens in Fedorowski *et al.*, 2014, a species based on one of the paratypes of *C. jagoensis* from the Brooks Range, Alaska.

Kawamura and Stevens (2012) described three species they included in the Permian genus *Pararachnastraea* Stevens and Rycerski, 1989. Indeed, some features of the Bashkirian specimens from the Klamath Mountains resemble this genus, first described from the Asselian or Sakmarian of the Stikine Terrane, Pacific Coastal Province. However, those characters are more comparable to the Bashkirian genus *Arctistrotion*. Only the lack of data concerning the microstructure of the Klamath Terrane specimens’ intercorallite walls, i.e., either cerioid or cerioid-aphroid growth form, precludes their firm identification as *Arctistrotion*, to which these species are provisionally transferred herein. At my request, Dr. Calvin H. Stevens (letter dated 28 April 2021) commented on my suggestions: “... I agree with you that *Dibunophylloides* is probable and *C. jagoensis* should be placed in *Paraheritschioides*.” However, he was “not quite sure about *Arctistrotion*.” So this re-identification must be left only as an alternative to *Pararachnastraea*.

Summing up the discussion, the following should be highlighted as of particular palaeogeographic value: 1) The appearance of several European genera in the upper Viséan and Serpukhovian strata in North America confirms an open connection between the two areas at that time, as suggested by Fedorowski and Bamber (2007), Rodríguez and Kopaska-Merkel (2016) and Bamber *et al.* (2017). 2) The close similarity and/or relationship of the Bashkirian rugose coral faunas of the Brooks Range, Alaska Province and the Klamath Terrane, Pacific Coast Province demonstrate the easy connectivity between these areas. 3) The occurrence of *Barytichisma* and *Yuanophylloides* in both the Donets Basin and the Midcontinent Province,

as well as the possibility of *Dibunophylloides* in the Klamath Terrane demonstrate a link between the Donets Basin and the North American provinces. However, this relationship was quite limited, as indicated by the many genera characteristic exclusively either of Euro-Asiatic, or of American provinces. 4) The current knowledge of the fauna of Serpukhovian/Bashkirian rugose corals in North America cannot serve as a step by step analysis of the entry and exit of individual genera. Also, the patchy occurrence and uneven representation across provinces makes a general summary difficult. This results in a lack of precision in determining the exact period of the Mississippian/Pennsylvanian faunal turnover in North America, as is the case in the Donets Basin. Only rare rugose corals were identified from the *Homoceras*–*Hudsonoceras* and lower *Reticuloceras* (R_1) biozones (e.g., Fedorowski and Bamber in Gunning *et al.* 2006). Thus that interval of time can be identified as characterized by the poorest representatives of the Rugosa.

China

The vast majority of Chinese rugose coral species are based on very limited collections, usually of single incomplete specimens. The widespread lack of complete studies on the major growth stages (early and late neanic, and early and advanced mature) has made the generic names applied by Chinese scientists to many incompletely studied coral genera and species unjustified. Thus, many (most?) Chinese rugose coral taxa should be carefully studied again, with detailed references to modern stratigraphic subdivisions, superimposed on the traditional Chinese lithostratigraphy, before they are ready for detailed analysis. Chinese papers published before 1980 are commonly not considered here. The reader of this opus is kindly referred to my earlier summary (Fedorowski 1981a) as regards these early Chinese achievements. Also, only selected papers from the vast Chinese literature published after 1981 on Carboniferous rugose corals are considered here.

The monumental opus “Carboniferous of the World” with resumes by Yang *et al.* (1983; Fengnianian), Gao *et al.* (1983; middle Carboniferous), and Li and Zhang (1983; upper Carboniferous) provide reference studies for the Carboniferous stratigraphy and some corals described by earlier Chinese stratigraphers and palaeontologists. Unfortunately, Yang *et al.* (1983) correlated Chinese lithostratigraphic units and major fossil assemblages from particular regions of China to the old Western Europe subdivision (Z, C, S, D, E, H). They correlated the *Yuanophyllum*

Biozone of Yu (1931) with Biozone D, i.e., Asbian and Brigantian in Europe, while they placed Biozones E and H, important in the context of this present paper, in the Datangian Stage together with the Viséan. This stage, referred to by Menning *et al.* (2006) as the Tatangian, lasts until the end of the Zapaltyubian Horizon in the Donets Basin, i.e., the end of the Serpukhovian. Index fossils from the Datangian Stage and associated rugose coral genera listed by Yang *et al.* (1983) from different regions of China vary: in their fig. 4a, *Eostaffella* Rauzer-Chernosuova, 1948 and *Homoceratoides* Bisat, 1924 are listed as accompanying *Aulina*, *Lithostrotion*, *Lonsdaleia*, *Melanophyllum* Gorsky, 1951, *Palaeosmilia* (+ *Palaeosmilia regia* = *Palastraea*) and *Yuanophyllum* Yu, 1931; in their fig. 4b, only *Eostaffella* is listed and the corals are restricted to *Lithostrotion* (possibly *Siphonodendron*), *Neoclesiophyllum* Wu, 1963 and *Yuanophyllum*; in their fig. 5, *Eumorphoceras* Girty, 1909 is listed as accompanying several taxa of rugose corals, most of which are the same as in the previously mentioned figures, with *Dibunophyllum* and *Kueichouphyllum* Yu, 1931 as additions to the former; in their fig. 9, *Eumorphoceras* is accompanied only by *Lithostrotion* (possibly *Siphonodendron*), *Palaeosmilia regia* (= *Palastraea*) and *Yuanophyllum*. Neither fusulinids nor ammonoids are mentioned in their fig. 7, and the long list of rugose corals includes all genera mentioned above + *Arachnolasma* and the heterocoral *Hexaphyllia* Stuckenbergh, 1904. The index fossils may indicate a Serpukhovian (*Eumorphoceras*) and/or early Bashkirian (*Homoceratoides*) age, while the listed genera of rugose corals are known to occur from the late Viséan (Asbian, Brigantian) to the Serpukhovian, and some up to and including the early Bashkirian. The lack of precise stratigraphic markings precludes the assignment of the listed rugose coral genera to different stages, and insufficient illustrations make checking their identification impossible.

In their discussion on the lower boundary of the middle Carboniferous, Gao *et al.* (1983, p. 86) listed the Zhaojiashan Formation as containing *Homoceras* spp. and *Eostaffella* spp., and thus by recent standards already belonging to the lower Bashkirian. This recognition is contrary to that of Fan (1988; see below). Gao *et al.* (1983, p. 86, fig. 17) placed the lower/middle Carboniferous boundary between the H and R_1 ammonoid Genozones in Europe and at the base of the *Pseudostaffella antiqua* Fusulinid Biozone. This position was accepted by most stratigraphers of that time, but analysis of rugose corals questioned this view. “The lower boundary of the Bashkirian, as concerns the coral fauna may well be lowered down into the

base of the Chokierian stage...” (Fedorowski 1981a, p. 132), i.e., to the stratigraphic level adopted by the 10th Carboniferous Congress in Madrid (1983) and still valid today. The summary by Gao *et al.* (1983) is mainly devoted to strata roughly correlated with the middle/upper Bashkirian and younger. Rugose corals are also rarely mentioned by them. From north-western China of the Kalawuyi Formation they mentioned *Caninia*, *Bothrophyllum*, *Neokoninckophyllum*, *Pseudozaphrentoides*, *Ivanovia* Dobrolyubova, 1935 and *Protoivanovia* Yu (X.-G.), 1977 together with *Ozawainella* Thompson, 1935, *Profusulinella* Rauzer-Chernousova and Belayev, 1936 and *Pseudostaffella* Thompson, 1942. These taxa can be regarded as upper Bashkirian, while *Caninia*, *Bothrophyllum*, *Heritschioides* from the Azigan Formation accompanied by *Pseudostaffella*, *Fusulinella* and *Fusulina* Fischer de Waldheim, 1829 are lower Moscovian. I have some reservations about the names of the genera mentioned, but the absence or paucity of illustrations precludes suggestions on their probable substitutes.

In her extensive English summary on the Carboniferous strata of Xizang (Tibet), Fan (1988, pp. 59–128) discussed the position of the lower/middle Carboniferous boundary in China. Her conclusions apparently agree with the statements of Gao *et al.* (1983), but at the same time are fraught with some disagreement. Fan (1988, p. 113) wrote: “... in the so called “Zhaojiashan” Formation of Dewu section ... abundant planktonic ammonoids and fusulinids such as *Homoceratoides*, *Proshumardites*, *Eostaffella ovooides* and *E. postmosquensis*... [occur]. However, there is no *Yuanophyllum*.” Thus, the index fossils point unambiguously to the lower Bashkirian. Further, she noted that “...the strata containing these fossils should be higher than the Zhaojiashan or Baisuo in level. The term Dewu Formation instead of the Zhaojiashan and the Baizuo are the only component part of the Shangssu Formation” (Fan 1988, p. 114). However, the latter formation was included in the *Yuanophyllum* Zone (Fan 1988, p. 101). Wang *et al.* (2021) recognised the validity of the Zhaojiashan Formation and included its upper part in the upper Viséan and lower Serpukhovian, while Aretz *et al.* (2020, fig. 23.5) listed the Shanghsian Regional Stage (as they called it) and correlated it with most of the Warrantian, but placed its upper boundary, marked by dashed lines, below the Viséan/Serpukhovian boundary. They clarified the position of the Dewuan Regional Stage (as they called it), somewhat ambiguously described by Fan (1988) as following the Shanghsian Regional Stage, and established its upper limit at the Serpukhovian/Bashkirian boundary. They also confirmed the lower

limit of the Lousuan Regional Stage, i.e., the lower limit of the Bashkirian, previously suggested by Fan (1988) as being in accordance with the appearance of *Declinognathodus noduliferus*.

The stratigraphic position of Bashkirian rugose corals from China remains ambiguous. Aretz *et al.* (2020, fig. 23.5) approximately equated the Lousuan Regional Stage with the Chokierian and Alportian substages and the Huashibanian Regional Stage with the Kinderscoutian and Yeadonian substages in Western Europe and extended the Dalaun Regional Stage from the Langsettian (lower middle Bashkirian) to the lower Cantabrian (lower Kasimovian). They did not list corals from any of these substages. Wang *et al.* (2021) wrote “The rugose coral zonation in the Pennsylvanian Subsystem is of very low resolution” and divided it into two formations: “the Weining Formation (Bashkirian to late Moscovian), and ... the Maping Formation (uppermost Moscovian to Gzhelian)”. This means that the stratigraphic position of the Chinese taxa important in the context of this summary remains uncertain.

I have several objections and suggestions regarding the identification of genera published in selected papers that followed the publications of Gao *et al.* (1983), Li and Zhang (1983) and Yang *et al.* (1983). These objections and suggestions are divided into three categories according to my subjective opinion: 1) The original generic names accepted here as correct with ‘perhaps?’ in brackets when some doubts remain. 2) Corrected names in brackets that follow the original names. 3) Unaccepted names, indicated by a question mark in brackets. In the latter case, the inadequacy of the original illustrations precludes the possibility of proposing substitutes. These three categories are introduced in the notes below. Taxa left in open nomenclature are omitted from consideration.

Xizang (Tibet) and Sichuan. This part of the discussion is based almost entirely on the works of Wu and Zhang (1979, 1985), Fan (1980, 1988), Wang and Yu (1982, 1986), Wu and Zheng (1982), Yang and Fan (1982), Gao *et al.* (1983), Li and Zhang (1983), and Fan *et al.* (2003). Unfortunately, the precision of age determinations in these papers is insufficient to closely compare the putative Bashkirian rugose coral fauna from these regions with other Bashkirian coral faunas worldwide. Neither Aretz *et al.* (2020) nor Wang *et al.* (2021) mentioned corals from Tibet. Wu and Zhang (1985) described their corals from the Zhapu Formation, the Dingpo Formation and the Aoqu Group (in ascending order). Gao *et al.* (1983, p. 72) cited *Fusulina*, *Fusulinella*, *Profusulinella*,

Pseudostaffella, *Eostaffella* and *Millerella* Thompson, 1942 from the Zhapu Formation. This formation therefore probably spans both the upper Bashkirian and Moscovian. These authors omitted the Dingpo Formation, but delimited two fusulinid zones in the Aoqu Group (Gao *et al.* 1983, p. 81): the upper *Fusulina*–*Fusulinella* Zone and the lower *Profusulinella* Zone with *Profusulinella parva* (Lee and Chen in Lee *et al.* 1930) and *Pseudostaffella laronovae* Rauser-Chernousova and Safonova in Rauser-Chernousova *et al.*, 1951. The fusulinid taxa allow the rugose corals of the lower zone to be considered as upper Bashkirian, but a more precise stratigraphic determination is not possible. Fan *et al.* (2003) considered the Aoku Group to represent the lower part of the upper Carboniferous, i.e., they followed Gao *et al.* (1983), a position that is also accepted in this paper. Fan *et al.* (2003) completed the list of corals described by Wu and Zhang (1985) from the Aoku Group and added a description of corals from the Sisuo Formation. Both of these formations were identified by them as representing the lower part of the upper Carboniferous, i.e., the Bashkirian and Moscovian.

The following taxa were described by Wu and Zhang (1985) from the Zhapu Formation in western Sichuan: *Amygdalophyllidium* Kato and Minato, 1975; *Axolithophyllum*; *Caninia* [C. cf. *vigilans* (Reed, 1959) = *Yuanophylloides* (perhaps?)]; *Caninostrotion* (?); *Carinthiaphyllum* Heritsch, 1936 (?); *Corwenia* (perhaps?); *Dibunophylloides* (?); *Durhamina* Wilson and Langenheim, 1962 (= *Opiphyllum* or *Protodurhamina*); *Gshelia* Stuckenber, 1888 [*G. xiangchengensis* = *Yuanophylloides* (perhaps?)]; *Kionophyllum*; *Lithostrotionella* Yabe and Hayasaka, 1915 (= *Petalaxis*); *Lytvophyllum* (?); *Melanophyllum* (?); *Sestrophyllum* Fomichev, 1953 (?) (colonial; resembles *Paraheritschioides* or *Protodurhamina*), and *Yuanophylloides* (perhaps?). Several taxa from the Zhapu Formation closely resemble those of the Aoqu Group from Xizang (Tibet) (see below). However, the nature of the fauna from western Sichuan indicates a closer contact with the mainstream Bashkirian–Moscovian fauna of the world than that from Xizang (Tibet).

The corals of the Aoqu Group described by Wu and Zhang (1985) are much less diverse than those of the Zhapu Formation. Only the following genera are described: *Amygdalophyllidium*; *Calophyllum* Dana, 1846; *Kepingophyllum* Wu and Zhou, 1982; *Lithostrotionella* (= *Petalaxis*); *Lytvophyllum* (?); and *Tschussovskenia* [= *Opiphyllum* (perhaps?)]. However, Fan *et al.* (2003) significantly supplemented this list. They identified the following additional taxa:

Acrocyathus d'Orbigny, 1849 [*A. jamdaensis* Fan, 2003 (perhaps?)]; *Arachnolasma* [*A. longbangnonense* Yu, 2003 = *Yuanophylloides* (perhaps?)]; *Axophyllum* [*A. tenellum* Fan, 2003 (perhaps?)]; *Durhamina* (*D. xizangensis* Yu, 2003 = either *Heintzella* or *Protodurhamina*); *Durhamina* (*D. intermedia* Yu, 2003 = *Paraheritschioides* or *Protodurhamina*); *Fomichevella*; *Guengdephyllum* Yu, 1991; *Hongzhengia* Fan and Yu, 2003; *Kapuphyllum* Yu and Wang, 1987b (= *Kumpanophyllum*; see Fedorowski 2019b); *Neokoninckophyllum* [*N. banagense* Yu, 2003 and, *N. jomdaense* Yu, 2003 = *Yuanophylloides* (perhaps?)]; *Nephelophyllum* Wu and Zhao, 1974; *Paraheritschioides* and *Opiphyllum* (both = either *Heintzella* or *Protodurhamina*); *Pavastephyllum* Minato and Kato, 1965a [*P. rivoqueense* Yu, 2003 (perhaps?)]; *Petalaxis*; *Pseudocarniaphyllum* Wu, 1962; *Pseudolytvophyllum* Yu and Wang, 1983 (in Yu C.C. *et al.* 1983; see Fedorowski 2021a); *Pseudosemenoffia* Yu, 1985 (= *Kumpanophyllum*; see Fedorowski 2019b); and *Youphyllum* Yu, 1984. The listed corals cannot be taken as indicative of either the upper Bashkirian or Moscovian. They are probably mixed in the list, as the Aoku Group spans both these stages (Gao *et al.* 1983; Fan *et al.* 2003; however not Wu and Zhang 1985).

Corals of the Aoku Group were included by Fan *et al.* (2003, p. 83) in The China Region of the Palaeotethys Realm, N.-W. Sichuan–Quinling Sub-region, Jamda area and subdivided into four groups: (i) Relicts (*Arachnolasma*, *Axophyllum*, *Amygdalophyllidium*), which disappeared from the fossil record close to the top of the Aoku Group. (ii) Pioneers that first appeared in this formation but continued until the Permian, including: *Guengdephyllum*, *Kepingophyllum*, *Nephelophyllum*, *Pavastephyllum*, and *Pseudocarniaphyllum*. Among these pioneers are a group of endemics, unknown from the Cordillera–Arctic–Uralian Realm. They may be Moscovian in age, having arisen when the connection between the latter realm and the Palaeotethys Realm through the Ural sea was already strongly restricted or closed (Fedorowski 1981a, 1986a; Fedorowski *et al.* 2007). Of the remaining taxa listed by Fan *et al.* (2003, p. 86) as belonging to the pioneer group, the taxonomic position of *Lonsdaleoides* is unknown, and *Paraheritschioides* was already excluded from this genus by Fedorowski *et al.* (2007, p. 96). (iii) This group has been characterised as “... the common elements of the early late Carboniferous” (Fan *et al.* 2003, p. 86). Indeed, *Durhamina* (= *Heintzella* or *Protodurhamina*), *Fomichevella*, *?Yuanophylloides*, *Lithostrotionella* (= *Petalaxis*), as well as *Neokoninckophyllum*, *Opiphyllum* and *Paraheritschioides* (all three = *Heintzella* and/

or *Protodurhamina*) are known to occur in several areas outside China. (iv) *Chielama* Minato and Kato, 1965 and *Youphyllum* Yu, 1984 of this group were endemic, while *Kapuphyllum* and *Pseudosemenoffia* (both = ?*Kumpanophyllum*) were widely distributed (Fedorowski 2019b). The latter two taxa were described by Fan *et al.* (2003, p. 86) as appearing “at the bottom of the Upper Carboniferous Series.”

Yang and Fan (1982) and Fan *et al.* (2003) described a few non-dissepimented genera from the Sisuo Formation in Xizang (Tibet), defined as representing the lower part of the upper Carboniferous. At least some of the cited taxa may be of Bashkirian age. However, the very poor state of preservation of most of them prevents an indisputable identification. None of the taxa listed here can be used as age indicators – *Amplexus* (?); *Gorskyella* Kachanov, 1973 (?); *Pleramplexus* Schindewolf, 1940 (?); *Plerophyllum* Hinde, 1890 (?); *Calophyllum* (*C. sisuonense* Fan, 2003); *Rhopalolasma* Hudson, 1936 (*R. sisuonense* Fan, 2003 = ?*Ufimia*); and *Cyathaxonia* (?).

South-eastern and central China. Application of older literature data such as Grabau (1922, 1928), Chi (1931, 1935), and Yu (C.C.) (1931, 1933) to modern stratigraphy is difficult. Also, not all the data from younger literature can be placed in a modern stratigraphic scheme (e.g., Wu 1962, 1964; Fan 1963, 1978; Wu and Zhao 1974, 1989; Wu *et al.* 1974; Yu X.-G. 1976, 1982, 1984, 1985; Jia *et al.* 1977, 1984; Wang H.-D. 1978; Lin Y.-D. *et al.* 1984; Wang Z.-J. 1987; Yu X.-G. and Wang Z.-J. 1987a, b; Lin Y.-D. and Wu S.-Z. 1988; Luo and Qi 1990; Wu S.Z. and Lin 1992; Lin B.-Y. *et al.* 1995; Wang X.-D. *et al.* 2001, 2004; Fan *et al.* 2003; Lin W. *et al.* 2012). The inconsistency in the composition and stratigraphic range of the *Yuanophyllum* Zone, the Zhaojiashan Formation, the Shangsian, Devuan and younger stages and the Weiningian Regional Series have been discussed above. The uncertainties mentioned above have resulted in the Chinese literature being limited to only a few selected samples and a rather cautious citation of their stratigraphic occurrences.

The characteristics at generic level of part of the rugose coral fauna from the *Yuanophyllum* Zone in SE China are comparable with those of the European and North African faunas. Such solitary, dissepimented genera as *Arachnolasma* (first described from China by Grabau 1922), *Auloclisia*, *Axophyllum*, *Clisiophyllum*, *Dibunophyllum*, *Kizilia*, *Koninckophyllum*, *Palaeosmia*, *Spirophyllum*, fasciculate colonial *Corwenia*, *Lonsdaleia*, *Siphonodendron* and massive colonial *Acrocyathus*, *Aulina*,

Lithostrotion and *Palastraea*, are almost cosmopolitan. Most of the rugose coral taxa mentioned occur in the Zhaojiashan Formation, characterised by Wu and Zhao (1989, p. 191) as yielding *Gigantoproductus lattissimus*, *Eostaffella paraprotvae* and *E. mosquensis*, which indicates their Serpukhovian age. Wang *et al.* (2021) considered the upper part of this formation to represent the upper Viséan and lower Serpukhovian. Cózar *et al.* (2011) accepted the stratigraphic position of *E. ‘paraprotvae’* as lower Serpukhovian. This position was confirmed by Sheng *et al.* (2018) and is accepted here. Thus, the list of rugose coral faunas from the Zhaojiashan Formation is not cited here as lying outside the main topic of this paper. However, two genera present in this fauna but omitted from my earlier discussion (Fedorowski 2021a) should be mentioned. *Lytvophyllum* (especially *L. minor*) and *Prolytvophyllum* are of particular value in the context of the Donets Basin fauna. *Lytvophyllum* shows all the main features of *Colligophyllum*, most likely including a solitary, gregarious growth form. *Prolytvophyllum* morphologically resembles *Colligophyllum*, except that it either lacks a dissepimentarium or has it very incomplete, i.e., exhibiting a primitive character of that lineage. Both these taxa appeared earlier in the stratigraphic column than *Colligophyllum dobroljubovae* from the Donets Basin, suggesting their ancestry and possible westward migration from southeastern China via the Urals into the Donets Basin.

Foraminifera cited by Wu and Zhao (1989) from the Weiningian Formation in the Zhanyi section (*Fusulinella bocki*, *Fusulina* cf. *chernovi* and *Pseudostaffella khotunensis*) and from the Weiningian Formation of the Weining section (*Fusulina quasicyclica megasphaerica*, *Fusulinella oviformis*, *Profusulinella prisca*, *P. fukujiensis* and *Pseudostaffella paradoxa*) indicate a Moscovian age for the corals they described. The coral taxa are therefore not listed here, although genera such as *Cystolonsdaleia*, *Opiphyllum* and *Yuanophylloides* suggest that some of this fauna may come from the Bashkirian.

I have had an opportunity to examine the collections of Yu (1985), Yu and Wang (1987a, b), This part of the commentary is therefore written in more detail. Yu (1985) introduced several new genera and subgenera and described several species of rugose corals from the “uppermost part of Lower Carboniferous” and the *Pseudostaffella* Zone of Shaanxi Province, east-central China. Poorly preserved foraminifera occurring in the “uppermost part of Lower Carboniferous” matrix with probable *Eoparastaffella* suggest the possibility of its lowermost Bashkirian

position. The following taxa have been described from these deposits: *Pseudosemenoffia* Yu, 1985 included in *Semenoffia* Poty, 1981 as a subgenus. Its distinctly tripartite tabularium and interrupted pseudocolumella allow its dubious synonymy with *Kumpanophyllum* (Fedorowski 2019b, p. 441); *Paranemistium* Yu, 1985, considered colonial by Yu (1985), is probably solitary and gregarious, as suggested by the three very young corallites attached to the mature corallite in the type species *P. typicum* Yu, 1985 (pl. 1, fig. 1a–d). Perhaps it will be synonymised with *Kumpanophyllum* if its gregarious growth form is indisputably documented; *Cystilophophylloides* Yu, 1985 includes three new species, each represented by a single, incomplete specimen. Perhaps they should be combined into a single species. The genus was considered by Yu (1985) to be most closely related to *Cystilophophyllum* Fomichev, 1953. However, the latter genus has an elongated counter, but not the cardinal septum, like the specimens from China. I provisionally consider *Cystilophophylloides* to be valid. *Carruthersella zhenanensis* Yu, 1985 is represented by one incomplete specimen with a slightly diagenetically damaged inner skeleton. The lack of a compact pseudocolumella excludes it from this lower Carboniferous European genus. Perhaps it should be placed together with specimens described as *Cystilophophylloides*.

The following taxa were described by Yu (1985) from the *Pseudostaffella* Zone: *Liuzhouia* Yu, 1985, introduced as a subgenus of *Carruthersella* Garwood, 1913, was based on *Carruthersella fongi* C.C. Yu, 1933. It resembles the Namurian *Darwasophyllum* in terms of morphology and the solitary, gregarious growth form recently established in the latter genus by Bamber *et al.* (2017); *Liua typica* Yu, 1985 is perhaps subcerioid as confirmed by offsets. Its main morphological features resemble those of the genus *Petalaxis*, already indicated by Yu (1985, p. 94), but the growth form proves the difference and the possibility of a distinct generic status. Yu (1985, p. 92) listed also *Acrocyathus*, *Carruthersella* (*Liuzhouia*) and *Koninckocarinia* from the *Pseudostaffella* Zone. His *Acrocyathys xikouensis*, however, is cerioid-aphroid in growth form and represents perhaps a new genus, while the other two taxa are represented by specimens too incomplete and too poorly preserved to comment.

The rugose coral fauna in the *Pseudostaffella* Zone characterised above may roughly correspond to the *Pseudostaffella* Zone in the Kapu Village section of Dushan County, Guizhou Province, South China, which lacks rugose corals (Yu and Wang 1987b, p. 74, table 1). The latter authors described several corals from the underlying strata, distinguished by them as

the *Ephippicaninia*–*Kapuphyllum* Zone. Wang *et al.* (2021) characterised this fauna as follows: “This assemblage might be latest Mississippian in age based on its position below the *Pseudostaffella* foraminifera biozone. It is the only coral assemblage in this time interval in South China.” I follow the age determination of Wang *et al.* (2021) but cannot agree with several identifications of Yu and Wang (1987b), repeated *in extenso* by Wang *et al.* (2021). Also, I am not able to decisively propose and document indisputable new substitutions, as the material studied by these authors and re-examined by me is very incomplete. However, I have the following comments:

The two specimens assigned to different species of *Corphalia* belong perhaps to the same species, but they cannot be included in the middle Viséan, European genus *Corphalia* Poty, 1975. Considering the axially concave tabularia recognisable in the Chinese ‘*Corphalia*’ and ‘*Caninophyllum*’ *dushanense* Yu and Wang, 1987b, I would rather classify both species as *Ephippicaninia* Yu and Wang, 1987b (pl. 1, figs 5b, 8c, 9b). The concavity of the tabularium in *E. typica* Yu and Wang, 1987b clearly differs from tabularia in the type species of *Caninia*, *Caninophyllum* and *Corphalia*, while the morphology in transverse sections of all Chinese species discussed herein resembles each other and differs from that of European genera. Thus, *Ephippicaninia* is accepted as a valid genus comprising all specimens discussed in this paragraph.

The morphology of both species (?) of *Semenoffia* of Yu and Wang (1987b) differs markedly from *Semenoffia viseensis* Poty, 1981, the type species of this genus, while *Kapuphyllum typicum* Yu and Wang, 1987b closely resembles the Chinese ‘*Semenoffia*’ (see Fedorowski 2019b, p. 437 for comments). Both these genera were questionably included by Fedorowski (2019b, p. 441) in *Kumpanophyllum*. Among the other species listed by Yu and Wang (1987b) from the *Ephippicaninia*–*Kapuphyllum* Zone, *Neokoninckophyllum guizhouense* (called *N. dushanense* in the caption to pl. 2, fig. 3 in Yu and Wang 1987b), resembles ‘*Neokoninckophyllum*’ *simplex* Moore and Jeffords, 1945 and ‘*Koninckophyllum*’ *oklahomense* Rowett and Sutherland, 1964. It was dubiously included by Fedorowski (2019a, p. 66) in synonymy with *Yuanophylloides*. *Protocarinophyllum dushanense* and *P. simplex* of Yu and Wang (1987b) belong to the same species, closely resembling *Cystilophophylloides typicum* Yu, 1985 in morphology and perhaps belonging to that genus. *Lithostrotionella crasseseptatum* should perhaps be included in *Petalaxis*, while the transverse section of *Para-*

thysanophyllum minor Yu and Wang, 1987b closely resembles the type species of this genus introduced by Fan (1978) from the *Yuanophyllum* Zone, southern China, provisionally accepted as valid.

Yu and Wang (1987b) described several species of rugose corals from the *Profusulinella* Zone. I question their generic identifications of several taxa. All their species identified as *Caninia* lack early ontogenetic growth stages, whereas any species identified as *Caninia* must follow *Caninia cornucopiae* in the early ontogeny, as established by Carruthers (1908) and confirmed by Fedorowski (2010b) on the basis of Belgian topotypes. *Pseudozaphrentoides breviseptatus guizhouensis* Yu and Wang, 1987b is most likely synonymous with '*Caninia*' *leptoseptata* Yu and Wang, 1987b, but the generic position of the two is uncertain. The assignment of *Opiphyllum intermedium* Yu and Wang, 1987b to *Opiphyllum* is probably correct, despite the rare lonsdaleoid dissepiments present in some corallites. A colonial growth form of '*Dorlodotia*' *elegantula weiningensis* Yu and Wang, 1987b is possible. However, that subspecies bears some features of the Subfamily Colligophyllinae Fedorowski, 2021a and may represent a new genus within that subfamily. Common features are: (i) median lamella rarely free, commonly connected to the cardinal septum, either monoseptal or supplemented by very few short septal lamellae; (ii) counter septum equal to remaining major septa; and (iii) tabularium normal with tabulae either slightly or moderately elevated adaxially. Two specimens, represented by a single fragment of a colony (?) each, were identified by Yu and Wang (1987, p. 83, pl. 4, figs 3a, b, 4a, b) as two species of *Darwasophyllum*. Bamber *et al.* (2017, p. 89) accepted this identification at the genus level, including them in the synonymy of this genus. However, the solitary, gregarious growth form of the Chinese species is not documented, and the morphology of their longitudinal sections differs (Yu and Wang 1987b, pl. 4, figs 3b, 4b). The longitudinal section of *D. parvulum* Yu and Wang, 1987b resembles the longitudinal section of *Huanglongophyllum megacystosum* Yu and Wang, 1987b. Apart from the uncertain growth form of both species of *Darwasophyllum* and *H. megacystosum*, the axial structure in all of them forms a loose lattice rather than the compact pseudocolumella typical of *Darwasophyllum*. Thus, the three species are very similar in several features and should be included in the same genus and, possibly, the same species. However, they differ from the type of *Darwasophyllum* and should perhaps be included in *Huanglongophyllum*, doubtfully accepted by Hill (1981, p. F403). *Lithostrotionella mohomo-*

kensis tenuepitheca Yu and Wang, 1987b belongs perhaps to *Cystolonsdaleia*, as suggested by the axial cones recognisable in its longitudinal thin section.

Wu and Lin (1992) described the rugose coral fauna of the Benxi Formation from the Taizihe River Valley in the eastern part of northern China. The lower member of this formation (*Taizheophyllum–Caninophyllum* assemblage), is correlated by them with the middle–upper Namurian in Western Europe, i.e., with the Kayalian Regional Stage in the Donets Basin. Corals from this member are much less abundant than those found in the upper member. The following taxa belong to that assemblage: the genus *Taizheophyllum* Wu and Lin, 1992 represented by two new species, i.e., *T. taizheense* (type species) and *T. kongjiabuziense*. I would refer the paratype *T. taizheense* to *Yuanophylloides*, and *T. kongjiabuziense* Wu and Lin, 1992 to *Bothrophyllum*. The illustrations are insufficient to make unequivocal comments, but judging by the existing ones, the specimens included in *Taizheophyllum* may represent two or three different genera. *Barrandeophyllum choniukouense kongjiabuziense* and *Barrandeophyllum* sp. of Wu and Lin, 1992 do not belong to *Barrandeophyllum* Počta, 1902 from the Lower or Middle Devonian of the Czech Republic, but insufficient illustrations preclude suggestion of a substitution. *Caninophyllum domheri* and *C. dobroljubovae*, illustrated mostly on the basis of mature growth stages, may represent any genus developing the so-called 'caninoid' mature growth stage. The elongated septum or pseudocolumella illustrated in the longitudinal section of the immature part of one specimen (Wu and Lin 1992, pl. 6, fig. 5b) may suggest its affinity with *Bothrophyllum*.

A much more diverse rugose coral fauna comes from the upper member of the Benxi Formation. However, it belongs perhaps to the Moscovian and/or younger strata and is not commented on. Only the occurrence of *Yuanophylloides* in this member (Fedorowski 2019b) is noteworthy.

Northwest China. Little is known to me about the Serpukhovian and Bashkirian corals from this region (Wang Z.-J. and Yu X.-G. 1986; Lin and Rodríguez 1993; Liao and Rodríguez 1999; Huang *et al.* 2021). Moreover, Lin and Rodríguez (1993) described their corals from the Huaitoutala Formation as correlated with the upper Viséan and lower Namurian (= perhaps Serpukhovian), but did not distinguish the fauna between these two substages. Also, the species list (Lin and Rodríguez 1993, pp. 43, 44) includes mostly taxa known from both the upper Viséan and lower Serpukhovian. Foraminifera are not listed.

Therefore, this paper has been omitted from further considerations. Liao and Rodríguez (1999) described corals from the Heshilafu Formation. The lower and middle part of this formation contains *Eostaffella mosquensis* and was considered by those authors to be Viséan. The upper part with *Pseudoendothyra directa* was characterised by them as “roughly Serpukhovian” (Liao and Rodríguez 1999, p. 541). Species fully identified by Liao and Rodríguez (1999) include: *Aulina (Pseudoaulina) sandoi* Wu and Zhao, 1989; *Axophyllum tazoultense* Semenoff-Tian-Chansky, 1974; *Caninostrotion xinjiangensis* Liao and Rodríguez, 1999; *Dibunophyllum bipartitum*; *Fomichevella shacheensis* Liao and Rodríguez, 1999; *Kueichouphyllum sinense* Yu, 1933; *Lithostrotion decipiens*; *Palaeosmilia murchisoni*; *Siphonodendron irregulare*; and *Yuanophyllum kansuense* Yu, 1931. The taxa listed are a mixture of cosmopolitan taxa, such as *D. bipartitum* or *P. murchisoni*, and Chinese and eastern Palaeotethyan taxa, such as *K. sinense* or *Y. kansuense*, but the assemblage does not point to either the upper Viséan or the Serpukhovian. Furthermore, the occurrence of North American *Caninostrotion* and North African *A. tazoultense* in north-western China is somewhat questionable, while *L. decipiens* appears to have a columnotheca, a feature absent in the genus *Lithostrotion*. Also, illustrations of *A. (P.) sandoi* and *O. huaitoutalaensis* are insufficient to distinguish the two taxa.

Two recent papers on Chinese Carboniferous corals (Wang *et al.* 2019; Huang *et al.* 2021) have clarified neither the taxonomy nor the stratigraphic occurrences of taxa described in earlier Chinese literature. Wang *et al.* (2019) provided an overview of the history of subdivisions of the Carboniferous Period worldwide and the history of subdivisions of this period in China, with a focus on conodonts, foraminifera and ammonoids as index fossils and brachiopods and rugose corals as auxiliary fossils (Wang *et al.* 2019, fig. 4). They proposed a very detailed zonation of conodonts and foraminifera, a much less detailed zonation of ammonoids and brachiopods, and eleven zones based on rugose corals. I omit the comments on index fossils and brachiopods except for one. According to the authors cited, the extent of the *Homoceras* Zone in China starts from the upper Serpukhovian contrasting with the zonation in Europe and North America, and even more with the zonation in North Africa (Cózar *et al.* 2015; see above). The coral zones, important for the present paper, are long-ranging. The *Aulina rotiformis* Zone covers the whole of the Serpukhovian, while the *Carinthiaphyllum–Acrocyathus* Zone extends from the

lowest Bashkirian to the lower half of the Moscovian inclusively. The latter is of particular value in the context of the present paper, as its wide stratigraphic range precludes establishing the exact position of rugose coral taxa during the most important period of post-crisis recovery. Furthermore, I question the correctness of the use of species and generic names, i.e., *Aulina rotiformis* and *Carinthiaphyllum–Acrocyathus* for zonal nomenclature. *Aulina rotiformis* was described by Smith (1917) from the Fell Top Limestone of the Millstone Grit, probably from the Brigantian. It is known from several areas such as the Voronezh Anteclise (Dobrolyubova 1958; Serpukhovian), Donets Basin (Vassilyuk 1960; upper Viséan–middle Serpukhovian), and China (e.g., Yu 1933; Smith and Yu 1943; Lin *et al.* 2012). All Chinese records are from the *Yuanophyllum* Zone. However, the upper limit of this zone varies (see discussion above). Such a record should not serve as an auxiliary index fossil for the entire Serpukhovian. I also do not understand the reason for establishing the *Carinthiaphyllum–Acrocyathus* Zone. *Acrocyathus* d’Orbigny, 1849 was first described and is most widely distributed in the Viséan of Europe. *Carinthiaphyllum* was described by Heritsch (1936) from the lower Permian of the Carnic Alps. The choice of Viséan and lower Permian genera as auxiliary for the Bashkirian–Moscovian strata is inappropriate. However, most significant in the cited paper is the lack of references to the earlier literature on rugose corals, clarifying the stratigraphic position of numerous Chinese taxa, uncertain as shown above.

The paper by Huang *et al.* (2021) brought limited clarification to the taxonomy of several taxa from NW China. The authors follow the Chinese ‘tradition’ in identifying and illustrating taxa, using single transverse and longitudinal sections or only the former, taken from indeterminate fragments of single corallites. I have the following comments on the definitely identified corals treated in this way by Huang *et al.* (2021): fig. 7:1 – I agree with the generic identification of this specimen as *Cyathaxonia*, but do not accept its species identification as *C. stereoseptata* Wu and Zeng, 1982. A single transverse section is insufficient for species identification in this highly variable genus; fig. 7:3. *Zaphrentites* cf. *pseudocrasusus* Wu, 1964 – the contrasting minor septa forming a triad with the counter septum eliminates this specimen from the genus *Zaphrentites*; fig. 4:5 – *Kinkaidia rhopaloides* Wu and Zeng, 1982 does not resemble *Kinkaidia trigonalis* Easton 1945, the type species for the genus in diagnostic characters. Its redefinition based on the illustration provided is impossible;

fig. 7:7 – *Meniscophyllum irregulare* does not resemble *Meniscophyllum minutum* (see Easton 1944 and Fedorowski 1990). It is most probably congeneric, perhaps conspecific with *Zaphrentites* cf. *pseudocrassus*; fig. 7:8 – *Fasciculophyllum longiseptatum*; Hill (1981, p. F310) stated that “In absence of suitable neotype, generic name is best not used.” The specimen of Huang *et al.* (2021) with dominant rhopaloid alar septa, and minor septa probably contralingent, may belong to a new genus; fig. 7:9 – *Amandophyllum intermedium* Yu, 1980 does not resemble the lower Permian *A. carnicum* (Heritsch, 1936) from the Carnic Alps, but shows some features in common with *Yuanophylloides*, revised by Fedorowski (2019b), and may belong to this genus; fig. 7:11 – *Arachnolasma sinense lophophylloides* Fan, 1963; I would tentatively agree with the author’s identification; fig. 7:12 – *Pseudozaphrentoides verticillatum* (Barbour, 1911); *Crataniophyllum* Lang and Thomas, 1957 is generally accepted as a valid alternate name for *Craterophyllum* Barbour, 1911. Besides, the pseudocolonial growth form must be documented to include the Chinese specimen in this species; fig. 7:13 – *Neokoninckophyllum tanaicum* Fomichev, 1953; the non-elongated counter septum and the Bothrophyllidae- or Dibunophyllinae-like axial structure eliminates the Chinese specimen from the genus *Neokoninckophyllum* (cf. also Fedorowski 2019b); fig. 7:14 – *Arachnolasma clisiohyllloides* Volkova, 1941; a peculiar axial structure in the longitudinal section, composed of sections of septal lamellae with a pseudocolumella indistinguishable (Huang *et al.* 2021, pl. 7, fig. 14b) is absent from both the Kazakh species and from *Arachnolasma*; fig. 8:1 – *Kueichouphyllum sinense gracile* Yu, 1933 is accepted here at species level; fig. 8:2 – *Aulokoninckophyllum carinatum* Huang, Zhang, Wang, Wang, Luan, Lin, Wang and Hu, 2021; the species name is occupied by *Campophyllum carinatum* Carruthers, 1909, selected by Sando (1976) as the type species for the genus *Aulokoninckophyllum*. Besides, the Chinese specimen shows a distinct cardinal fossula, a shortened cardinal septum and a peripheral tabularium composed of dissepiment-like tabellae, i.e., features that are absent in *Aulokoninckophyllum*; fig. 8:3 – *Gangamophyllum hamiense yamansuense* and fig. 8:4 – *Palaeosmia murchisoni stutchburyi* are tentatively accepted at genus level; fig. 9:1 – *Cystophora sparsa* Fomichev, 1953; *Cystophora* Yabe and Hayasaka, 1916 is occupied (Hill 1981, p. F403). Poor preservation and the lack of a longitudinal section make comments on Huang’s *et al.* (2021) specimen unjustified; fig. 9:4 – *Petalaxis vesiculosa* (Dobrolyubova, 1935) is accepted at genus level. The number of taxonomic

identifications questioned above is so large that the comparisons of coral assemblages from the Tianshan with assemblages from other Chinese areas (Huang *et al.* 2021, table 3) is misleading and cannot be followed.

To sum up: 1) The succession of rugose corals in China looks different from that in the other parts of the world discussed so far. It also differs from that in the Donets Basin (see below). Both of these differences, however, may be at least partly due to the inadequate level of study of many Chinese taxa, and their misidentifications. 2) The upper Serpukhovian/lower Bashkirian crisis was either much less pronounced in the Chinese area than in other parts of the world, or the stratigraphy used for these corals has masked its recognition. I was not able to prove either of these options on the basis of the available literature. 3) Modern stratigraphy of the Carboniferous, introduced in China on the basis of foraminifera and conodonts, is poorly, if at all, consistent with the stratigraphic positions of individual rugose coral species established by earlier authors. Therefore, my analysis of rugose corals from such an important area as China should be regarded as no more than the closest approximation I have been able to obtain. Also, this approximation, based on a few papers selected from the rich Chinese coral literature, should be taken only as an example.

Japan

The succession of the Carboniferous and its rugose coral fauna in Japan described by previous authors was summarised by Minato (1983), who analysed individual occurrences of rugose corals in the Carboniferous strata of the Japanese Islands and recorded their stratigraphic positions from foraminifer and conodont data. His summary showed many hiatuses corresponding to the time range important for the present paper (Minato 1983, fig. 5), but also showed a continuous succession in central Japan of the Akioshi Limestone Group, the Nagoe and Kodoni formations of the Atetsu Limestone, and the Ichinotani Formation. The stratigraphy and fauna of both the short-lived rugose coral formations such as the Onimaru Formation and the Nagaiwa Formation from the continental shelves (Kitakami Mountains, Hida Belt) and from the continuous successions in exotic blocks accumulated in central Japan (Akiyosi Terrane) have been studied by many Japanese palaeontologists, being both considered by Minato (1983) and published later (e.g., Igo and Adachi 1981, 2000; Yoshida *et al.* 1987; Kato 1990; Yoshida and Okimura

1992; Sugiyama and Haikawa 1993; Sugiyama and Nagai 1994; Yamagiwa *et al.* 2000; Niikawa 2001; Igo and Igo 2004; Ezaki *et al.* 2007). Most of the older contributions, summarised by Minato (1983) are not cited here, except for a select few that are important for this discussion. Minato (1983, p. 189) and Yoshida *et al.* (1987) listed numerous species of rugose corals from the Onimaru Formation and Omi Limestone, but these corals were omitted from consideration as belonging to the Viséan. Minato (1983, p. 195) listed several conodont species characteristic of the lower Bashkirian part of the Nagaiwa Formation, but did not list corals as occurring in this stratigraphic level. The occurrence of corals, described by Minato (1983, p. 195) as ‘especially dominant’, was listed by him from the higher part of the Nagaiwa Formation, i.e., from the stratigraphic level of *Profusulinella prisca*, considered by Minato (1983, p. 195) as “Upper Bashkirian to Moscovian”.

Following Minato and Kato (1974), Minato (1983, p. 195) listed the following rugose corals from the upper part of the Nagaiwa Formation: *Acroclyathus* sp., *Dibunophyllum bipartitum*, *Diphyphyllum delicatum*, *D. equiseptatum*, *Petalaxis kitakamienisis*, *Petalaxis* sp., *Sciophyllum japonicum* and *Thysanophyllum aseptatum*. The occurrence of most of these taxa, with the exception of *Petalaxis*, would be the youngest stratigraphically, if their identifications were confirmed. Kato (1990), in a brief review, confirmed the paucity of Bashkirian corals in Japan. He listed only *Lytvophyllum*, ‘*Kionophyllum*’ and *Caninia* as present in this stratigraphic level of the Ichinotani Formation. I question not only *Kionophyllum*, as Kato (1990) did, but also *Lytvophyllum* (see Fedorowski 2021a) and *Caninia*. The morphological conditions necessary to name a given specimen *Caninia*, are listed above. The Japanese specimen does not fulfil these conditions. The study of Igo and Adachi (2000) completed the list of Bashkirian species occurring in the Lower Member of the Ichinotani Formation (Igo and Adachi 2000, fig. 1). However, only six species from this list were described in the cited paper. Most were taken from various earlier papers cited by Igo and Adachi (2000). The taxa described belong to the following genera: *Arachnolasma*, *Carcinophyllum*, *Chienchangia* Lin and Fan, 1959, *Cyathaxonia*, *Heterocaninia* Yabe and Hayasaka, 1920, *Koninckophyllum*, *Kueichouphyllum*, *Lithostrotion*, *Lonsdaleia*, *Lytvophyllum*, *Neokoninckophyllum*, *Palaeosmia*, *Yuanophyllum* and *Siphonodendron*. Judging by the occurrence established by Igo and Adachi (2000), six species are of Serpukhovian and Bashkirian age. Only these species are commented on below. Stratigraphically younger

taxa, with the exception of ‘*Huangia*’ *mizuyagadensis* Kamei, 1957, included by Igo and Adachi (2000) in *Dibunophylloides*, are not commented on. The true *Dibunophylloides* includes only solitary, dissepimented corals having an axial column in the immature growth stage, but lacking it in maturity (Fedorowski 2017a). Thus, the colonial ‘*Huangia*’ *mizuyagadensis* does not belong to *Dibunophylloides*.

I cannot agree with some of the identifications made by Igo and Adachi (2000). The morphology of *Arachnolasma ichinotaniense* Igo and Adachi, 2000 and *Yuanophyllum pauciseptatum* Igo and Adachi, 2000, is so similar that I would suggest their co-specific position, unless their early ontogeny and septal microstructure differed. Furthermore, I have already expressed my doubts about the recent capacity of the genus *Arachnolasma* and the need to redefine it on the basis of Chinese types (Fedorowski 2015, 2017a). The corallite identified as *Actinophrentis?* sp. is misoriented. Its counter, but not the cardinal septum is shortened. This feature eliminates it not only from *Actinophrentis* Fomichev, 1953 discussed by Fedorowski (1987), but also from the Family Antiphyllidae Ilina, 1970. The unshortened cardinal septum and the very indistinct or absent cardinal fossula eliminate it from *Zaphrufimia* and suggest a new genus. I also suggest a new genus for *Koninckophyllum?* *nipponalpinum* (Igo and Adachi, 1981) (Fedorowski 2019a, p. 438).

The similar geological history and close recent position of the Akioshi and Omi Limestone Groups allows them to be considered together as belonging to the Akiyoshi Accreted Terrane. The continuous accumulation of carbonates, which started from the middle Viséan *Endothyra* Genozone and ended in the middle Permian (Guadalupian, Capitanian) *Yabeina–Lepidolina* Genozone was one of its peculiarities (e.g., Sano and Kanmera 1988; Yoshida and Okmura 1992; Ito *et al.* 2017, fig. 8). Another peculiarity is the mostly endemic rugose coral fauna (see below). Ota (1968) was the first to suggest the origin of the Akioshi Limestone as an atoll associated with a geosyncline, i.e., an accreted terrane in the recent meaning. The same is true for the Omi Limestone. Sugiyama and Nagai (1994) continued the palaeoecological study of the Akiyoshi Terrane, while Sugiyama and Haikawa (1993) completed the list of species described by earlier scientists of this terrane. Also, Ezaki *et al.* (2007) summarised studies of rugose corals derived from this Akiyoshi Terrane and suggested its isolated position in the Panthalassa Ocean. Matsusue (1986) established the foraminifera zonation of the lower part of the Akioshi Limestone Group succession,

while Ota (1997) summarised the foraminifera zonation of the middle Carboniferous and Permian part of that terrane. The succession of rugose corals in the Akiyoshi Terrane began with rare, non-dissepimented solitary corals, which were the pioneer fauna in the early Viséan (e.g., Minato 1955). In younger strata, this fauna was replaced by complex dissepimented solitary corals (e.g., Hayasaka 1924, 1939; Yabe *et al.* 1943; Minato 1951, 1955; Kato 1967; Kato and Minato 1974, 1975; Haikawa 1986; Yoshida *et al.* 1987; Yoshida and Okimura 1992; Sugiyama and Haikawa 1993). The Family Pseudopavonidae Yabe, Sugiyama and Ezuchi, 1943 forms the most distinctive group of this fauna, which is not only extremely morphologically complex and mostly endemic to the Akiyoshi Terrane, but also originated no later than the *Millerella* Zone. Kato and Minato (1975, fig. 4) summarised the appearance of this family in the latest Viséan by referring it to the *Endothyra* Genozone. They also documented its continuous occurrence up to and including the *Fusulina* Genozone. This marks the emergence of this family at the beginning of the Mississippian/Pennsylvanian boundary crisis in the Rugosa world and its flourishing during this critical period. The family includes genera such as: *Pseudopavona* Yabe, Sugiyama and Eguchi, 1943; *Taisyakuphyllum* Minato, 1955; *Omiphyllum* Kato, 1967; *Amygdalophyllidium*; *Hiroshimaphyllum* Kato and Minato, 1975; *Ibukiphyllum* Kato and Minato, 1975; and *Ozakiphyllum* Kato and Minato, 1975.

'*Amygdalophylloides*' of Yoshida and Okimura (1992) from the Serpukhovian–lowermost Bashkirian and two lithostrotionid species from the Viséan deposits of the Akiyoshi Terrane, i.e., *Lithostrotion* (*Siphonodendron*) *mitsuzaensis* Yamagiwa, 1977 and *Siphonodendron* *hinense* Yamagiwa, Suzuki and Okimura, 2000 require special comments. The position of '*Amygdalophylloides*' has recently been discussed as related or homeomorphic to *Krynkaephyllum* and is omitted from this discussion, except for the observation that the compact morphology of the Japanese species makes their homeomorphy to *Krynkaephyllum* more likely. Fedorowski (2008, p. 11) considered *S. hinense* to be "closely resembling the Australian species of '*Siphonodendron*'". Denayer and Webb (2015) considered *L. (S.) mitsuzaensis* as possibly belonging to their new genus *Pickettodendron*, but found only some morphological similarity of *L. (S.) hinense* to *Cionodendron* Benson and Smith, 1923, thus sharing the view of Ezaki *et al.* (2007) of its affinity with the European *Siphonodendron*. I do not share this view. The Japanese species, like the Chinese '*Siphonodendron*'

of Fedorowski (2008), considered by me to be directly related to Australian 'siphonodendrons', has a non-septothecal wall, as correctly pointed out by Denayer and Webb (2015). However, the morphology of their pseudocolumellae and tabularia clearly differs from European *Siphonodendron*, resembling much more these of Australian Lithostrotionidae than the European ones. Such an intermediate morphology may be an indication for the creation of a new genus or subgenus for specimens bearing these characters.

Fedorowski (1981a) and later Webb (1990) considered the Akiyoshi Terrane rugose coral fauna to be poorly related to the Australian fauna. Denayer and Webb (2015) challenged this view and considered the Australian fauna to be endemic. I had a similar concept (Fedorowski 1981a, p. 120) in establishing the Australian Province for the Australian Carboniferous Rugosa. Nevertheless, both the Akiyoshi Terrane and the South China microcontinental shelves bear some taxa of the rugose coral fauna resembling or related to the Australian fauna. Wu and Zhang (1979) included several species from the Xuchika Formation (Serpukhovian, western Szechuan) in the Japanese genera *Amygdalophyllidium*, *Hiroshimaphyllum* Kato and Minato, 1974, *Ozakiphyllum* and *Ramiophyllum* Wu and Zhang, 1979. Thus, these two areas are the only regions of the world resembling or related to Australian Carboniferous corals.

Despite the appearance of the Family Pseudopavonidae in the latest Viséan or early Serpukhovian, the coral fauna of Akiyoshi suffers from a Serpukhovian/early Bashkirian crisis in development. The much more abundant Viséan taxa, including many genera and several species in common with Asian and European fauna, and the relatively abundant fauna that emerged in the *Fusulinella*–*Fusulina* Zone and continued its development in younger strata, contrast with the limited number of corals in the strata between these two zones, marking the crisis.

Iran

Little is known about the Viséan to Bashkirian corals from Iran (Douglas 1950; Flügel 1963, 1974, 1975, 1991, 1994; Badpa *et al.* 2015, 2016), but the area should be mentioned in this review as being located in a place distant from Asian, European, North African and North American sites (Text-fig. 3) but bearing rugose coral faunas comparable to all those sites. The papers by Douglas (1950) and Flügel (1963) are the only contributions I am aware of on the Viséan rugose corals of Iran (Fedorowski 1981a, p. 119). However, the two *Kueichouphyllum* species

of Flügel (1963), his *Caninophyllum archiaci archiaci* (Milne Edwards and Haime, 1852), the holotype of *Bothrophyllum dobrolyubovae* Flügel, 1963 and *Bothrophyllum* n. sp. A show one important feature in common, i.e., most of the minor septa in these species are very thin and contratingent, some contratingent or free. They terminate in thickened tabular parts of the major septa, the dissepimental parts of which appear as thin bodies parallel to the minor septa. Such structures present in the mature growth stages of all species mentioned above closely resemble those in the mature growth stage of the holotype *Kueichouphyllum sinense*. Thus, I consider as congeneric all five species, classified by Flügel (1963) in three different families, but I exclude from this list the paratype of *B. dobrolyubovae*, native to Armenia. The taxonomic status of this specimen remains unknown.

Both illustrated subspecies of *Siphonophyllia cylindrica* McCoy, 1844 of Flügel (1963), i.e., the nominate subspecies and *S. c. latitabulata* (Gorsky, 1932) bear the main features of the mature part of the genus. The lack of early growth stages prevents more comprehensive comments. In the case of *Humboldtia ruttneri* Flügel, 1963, I would prefer to follow Hill (1981, p. F351), who synonymised *Humboldtia* Stuckenberg, 1895 with *Keyserlingophyllum* Stuckenberg, 1895, rather than accept the independent status of the former, but I would accept Flügel's (1963) species identification.

Flügel (1991) supplemented the Mississippian corals discussed above with several other species, but noted (Flügel 1991, p. 657; Abstract): "...the age of the fauna is according to the conodont-fauna at least partly Namurian." Unfortunately, he did not assign the taxa he described to a particular stage. Thus, the fauna is treated here collectively as upper Serpukhovian. Wang *et al.* (2021) repeated the generic names used by Flügel (1991), but considered the fauna to be "late Mississippian (Serpukhovian) and early Pennsylvanian (Bashkirian)." The following genera, exclusively solitary, were described by Flügel (1991): 1) Non-dissepimented taxa: *Amplexocarinia* Soshkina, 1928; *Amplexus*; *Claviphyllum* Hudson, 1942; *Cyathaxonia*; *Pentaphyllum* de Koninck, 1872; *Plerophyllum*; *Pseudowannerophyllum* Flügel, 1975; *Rotiphyllum*; *Sochkineophyllum* Grabau, 1928; *Ufimia*. 2) Dissepimented taxa: *Caninia* and *Siphonophyllia*. I have the following comments and concerns about these identifications. All of Soshkina's (1928) original Artinskian (Permian) specimens of *Amplexocarinia* were re-examined, redescribed and re-illustrated by me (Fedorowski 1986b, pp. 216–218,

fig. 18: 1–3) with the following suggestion: "A full definition of the genus *Amplexocarinia* Soshkina, 1928 and reconstruction of its affinities requires studies of well-preserved topotypes and is not proposed in this paper." Since there are no such studies, I still consider this genus doubtful and would recommend not applying this name to specimens older than the Permian. *Amplexus coralloides* of Flügel (1991) cannot be accepted as such until it is established at its earliest ontogeny is similar to that of British and Irish specimens of *A. coralloides* Sowerby, 1814 (see Fedorowski 1987, 2003; Berkowski 2006). The premature and mature morphology of *Amplexus* sp. A of Flügel (1991) resembles that of *Falsiamplexus*. Thus, the Iranian specimen perhaps belongs to this genus.

Flügel (1991, p. 664) synonymised *Antiphyllum* with *Claviphyllum*. I disagree with this suggestion. The type species of *Claviphyllum*, i.e., *Cyathopsis eruca* McCoy, 1851 shows contratingent minor septa, which are absent in *Antiphyllum* (Schindewolf 1952; Fedorowski 2012b). The illustrations of specimens identified by Flügel (1991, figs 23, 24) as *?Ufimia* sp. and *Plerophyllum* sp. were most likely transposed, as evidenced by the long counter septum in the illustration described as *?Ufimia* sp. The illustrations provided by Flügel (1991) are inadequate for a firm identification of his specimens. My recent discussion of the genera *Pentaphyllum* and *Cryptophyllum* Carruthers, 1919 (Fedorowski 2009a, 2021b) allows Flügel's (1991) species of *Pentaphyllum* to be transferred to *Cryptophyllum*, assuming their early ontogeny as cryptophylloid. Here, I confirm the independent generic status of *Pseudowannerophyllum*, accepted earlier (Fedorowski 1987, p. 137). The occurrence of *Sochkineophyllum* in the Viséan/Serpukhovian strata of Iran can either be accepted or regarded as a morphotype closely resembling the Artinskian (Permian) '*Plerophyllum*' *artiense* Soshkina, 1925, selected by Grabau (1928) as the type species of *Sochkineophyllum*. I would now rather lean towards the second option. My attitude towards the genus *Caninia* is expressed above. *Caninia densiseptata* Flügel, 1991 does not expose any diagnostic characters of *Caninia* and cannot be assigned to any existing genus. To sum up, it can be suggested that at this stratigraphic level in Iran there is a mixture of Far Eastern Asian and Western European rugose coral morphotypes, with a slight dominance of the latter.

Minatoa Flügel, 1974 is the oldest massive colony known so far from Iran. It was derived from the Bashkirian Sardar II member of the Sardar Formation (Flügel 1974, 1994). According to Badpa *et al.* (2016, p. 155), the strata "spans *Pseudostaffella*

compressa, *P. antique*, *Eostaffella ambilis* foraminiferal zone and *Idiognathoides sulcatus parva* conodont zone...” It therefore roughly corresponds to the Mandrykinian Regional Stage in the Donets Basin or to the Marsdenian and/or Yeadonian substages in Western Europe. Fedorowski and Stevens (2014) mentioned *Minatoa* in the discussion of their new genus *Arctistrotion*, but did not point out the most important difference between their genus and *Minatoa*, i.e., the microstructure of the intracoralite walls. Flügel (1974, p. 99) described it as follows: “It consists of a thin, dark middle line from which calcite fibres in a normal position radiate”. This description fully agrees with the definition of a dividing wall given by Fedorowski and Jull (1976). The wall in *Arctistrotion* is septothecal (Fedorowski and Stevens 2014, fig. 9A, C, D), which corresponds to the partition of Fedorowski and Jull (1976) and implies complete integration of polyps within the colony. I therefore maintain my position on the independent status of the two genera discussed. The affinities of *Minatoa* and *Arctistrotion* are perhaps close enough to place them together in the Subfamily Arctistrotioninae Fedorowski and Stevens, 2014 within the Family Lithostrotionidae.

It is difficult to make a definite statement about Flügel’s (1994) *Heritschioides* and *Paraheritschioides*. His reduction to subfamily level of the Family Heritschioididae Sando, 1985, included in the Family Aulophyllidae Dybowski, 1873 is accepted by Fedorowski *et al.* (2014a, b) and herein. However, several features characteristic of Flügel’s *Heritschioides* occur in his *Paraheritschioides* and *vice versa*. For example, a continuous axial column is present in *Paraheritschioides gracilis* Flügel, 1994 but absent in *Heritschioides vepres* Flügel, 1994, which also shows a narrow, simple dissepimentarium, whereas *H. pseudosolitarius* Flügel, 1994 has a continuous axial column and a peripheral dissepimentarium complex. The morphology of both *H. vepres* and *P. gracilis* resembles *Paraheritschioides compositus* Fedorowski and Stevens, 2014. Also, the extra septal lamellae, i.e., lamellae corresponding to minor septa, are absent in all Flügel’s (1994) species of *Heritschioides* and *Paraheritschioides*. This feature is considered by Fedorowski *et al.* (2014a) as important but auxiliary. The biform tabularium, another auxiliary feature of *Heritschioides*, is absent in Flügel’s (1994) specimens included by him in *Heritschioides*, but is well seen in *Paraheritschioides antoni antoni* Flügel, 1994. In summary, I would place both *Heritschioides* and *Paraheritschioides* of Flügel (1994), including those in the collection of Badpa *et al.* (2016), provisionally

in the Subfamily Heritschioidinae and probably in *Paraheritschioides*.

Of the further species described by Flügel (1994), *Fomichevella uralica* (Dobrolyubova, 1936) was correctly distinguished by Badpa *et al.* (2016) as the new species *Fomichevella najafi*. *Kleopatrina* (*Porfirievella*) *bashkirica* Flügel, 1994 displays similarity to *Minatoa* strongly suggesting assignment to the Lithostrotionidae probably as a new genus. *Opiphyllum?* sp. of Flügel (1994) more closely resembles *Protodurhamina* than *Opiphyllum*, whereas *Palaeosmia* sp. of Flügel (1994) lacks a key-hole cardinal fossula, making its generic position doubtful. *Heintzella fluegeli* Badpa, Poty, Ashouri and Khaksar, 2016, which I consider correctly identified, completes my recent knowledge of Bashkirian Rugosa from Iran. I agree with the conclusion of Badpa *et al.* (2016, p. 164) that “...the composition of the colonial corals of Central Iran indicates a close affinity of the Iranian fauna with that of the northern provinces of Ural, Novaya Zemlja, the Kuiu Island area and Brooks Range, Alaska.” SE Asia should be added to that list of sites as bearing *Kueichouphyllum* present in Iran as well.

SUCCESSION OF RUGOSE CORALS OF THE MISSISSIPPIAN/PENNSYLVANIAN INTERVAL IN THE DONETS BASIN

Geological setting

The fairly recent summary of the stratigraphic succession in the Donets Basin (Poletaev *et al.* 2011; Gozhyk (Ed.) *et al.* 2013; Nemyrovska 2017), and the sequence stratigraphy of the Serpukhovian to Moscovian strata of several areas, including the Donets Basin (Izart *et al.* 2002; Eros *et al.* 2012), allow me to reduce this section to some general remarks and to a few statements mainly related to the occurrence of rugose corals. The Donets Basin, formed in the Middle Devonian, is located between the Ukrainian Shield and the East European Platform and is considered a rift area (Izart *et al.* 2002, p. 145) or aulacogen (Eros *et al.* 2012, fig. 1C). Global sea-level change and subsidence of the area, continuous but with varying rates, resulted in cyclic marine and terrigenous sedimentation, characteristic of paralic coal basins. In general, however, the “downwarp was entirely compensated by sedimentation” (Nemyrovska 1999, p. 6) with thicker deposits in the central part of the basin and more numerous and better developed limestone intercalations than in its peripheral parts.

The Carboniferous deposits of the Donets Basin have been studied by many geologists and palaeontologists for utilitarian and scientific purposes (for main references see Fomichev 1953; Vassilyuk 1960; Aizenverg *et al.* 1983, 1985, 1987; Poletaev *et al.* 1988, 1990, 2011; Nemyrovska 1999, 2017, Izart *et al.* 2002; Eros *et al.* 2012; Gozhyk (Ed.) *et al.* 2013). To these papers the reader is referred to for details. Only the basic data are briefly discussed below as essential for understanding the succession of rugose corals. The paper by Poletaev *et al.* (2011), which describes the type sections, is the main source of reference for these comments.

In order to place the rugose coral occurrences of the Donets Basin in a well-documented context, the upper Viséan and Serpukhovian corals described by Vassilyuk (1960, 1964), and Vassilyuk and Zhizhina (1978, 1979), and the Bashkirian corals described by Fomichev (1939, 1953) are included and tabulated (Text-figs 1 and 2).

The Donetzian and Mezhivian Horizons (= C_1^{yf} and C_1^{vg} zones) in the Donets Basin do not correspond exactly to the upper Viséan Asbian and Brigantian substages of Western Europe. The Donetzian includes the upper Holkerian and does not extend to the Holkerian/Brigantian boundary, whereas the Mezhivian includes the entire Brigantian and the upper Asbian (Menning *et al.* 2006, fig. 1). However, the boundaries of the Viséan and Serpukhovian substages, including the Viséan/Serpukhovian boundary, remain disputed, depending to some extent on the index fossils used (see e.g., Poletaev *et al.* 1990; Sanz-Lopez *et al.* 2006; Kulagina *et al.* 2013; Cózar *et al.* 2015, 2019; Aretz *et al.* 2020; Nikolaeva 2020). Thus, both the Donetzian and the Mezhivian are treated here as corresponding to the upper Viséan.

The Viséan deposits in the Donets Basin were formed during a major transgression that extended into the lower part of the Serpukhovian (Izart *et al.* 2002, p. 147). Poletaev *et al.* (2011, fig. 4) equated the Donetzian Horizon with Zone C_1^{yf} and divided it into four sets of limestones, with a thickness of about 60 m in the stratotype section. Ogar (2012, p. 342) described the “first real bioconstructions ... in the central part of the Donetsk Suite (Zone C_1^{yf}) ... composed of large fasciculate colonies of *Siphonodendron junceum* (Fleming)” and added: “The biostromes are intercalated between coarse-grained bioclastic limestone beds and argillaceous limestone with inclusions of black chert of irregular shape.” Vassilyuk (1960, 1964), and Vassilyuk and Zhizhina (1979) described many corals from this horizon, but did not indicate the taxa for a given lime-

stone. This results in continuous bars of occurrences of taxa corresponding to this zone in Text-fig. 1.

The depositional environments changed drastically at the Donetzian/Mezhivian boundary. Vassilyuk (1960, p. 21) called this new series of deposits ‘geosynclinal’. Poletaev *et al.* (2011, fig. 5) described the stratotype section of the Mezhivian as a 480 m thick series of argillites, aleurites and rare sandstones with rather thin intercalations of limestones, indexed as Limestone B_{1-11} . The Mezhivian ends with a more than 20 m thick series of interbedding aleurites, argillites and sandstones, terminating the upper Viséan deposition. Corals occur in several limestone intercalations (Text-fig. 1). Izart *et al.* (2002, p. 147) characterised this deposit series as follows: “High transgression is known during SI (Serpukhovian in part), a lowstand near the base of Bashkirian, high transgression in the Donets Basin, no transgression in the Moscow Basin and low transgression in the Ural Basin during SII (Bashkirian). . . .”

The Serpukhovian Series, with a total thickness of more than 1300 m if the stratotype sections are taken into account (Poletaev *et al.* 2011, figs 6–9), starts from the deepest lowstand corresponding to the Sakmarian Horizon, comprising 400 m thick, mainly sandy deposits. In this part of the section, limestone intercalations are rare and corals are absent for environmental reasons (cf. Poletaev *et al.* 1990, fig. 5; Text-fig. 3). The 420 m thick Prokhorivkian Horizon (Poletaev *et al.* 2011, fig. 7) is dominated by sandy and aleuritic deposits, but the number of limestone intercalations increases and the first rugose corals reappear in the limestone named by Vassilyuk (1960, 1964) as C_1^a , here considered as corresponding to Limestone C_6 of Poletaev *et al.* (2011). Increasingly numerous intercalations of Limestone D, framed by thick series of argillites and aleurites with sparse sandstone intercalations (Poletaev *et al.* 2011, figs 8, 9), are characteristic of the two upper horizons of the Serpukhovian, i.e., Novolyubivkian and Zapaltyubian. Rugose corals occur in several of these limestones, most abundantly in Limestone D_1^5 (Novolyubivkian) and Limestone D_5 (Zapaltyubian). The Zapaltyubian Horizon and the Serpukhovian Stage are terminated by a thin layer of Limestone D_5^8 lower.

The Serpukhovian/Bashkirian boundary remains debatable due to the inconsistent first appearances of individual index fossils, i.e., ammonoids, conodonts and foraminifera, and a hiatus in the stratotype section (Arrow Canyon, Nevada, USA), commented on by Aretz *et al.* (2020). This inconvenience prevents a precise correlation of the faunal turnover in rugose corals among particular areas. Nevertheless, in the

case of corals the boundary certainly does not run at the original lower Bashkirian boundary, established by Semikhatova (1934) with the entrance of *Pseudostaffella antiqua* Dutkievich, 1934, but occurs much lower, i.e., more or less at the *Eumorphoceras/Homoceras–Hudsonoceras* boundary or near the entrance of *Pseudostaffella varvariensis*. Here I follow the suggestion of Poletaev *et al.* (2011) and Nemyrovska (2017), who placed this boundary in the Donets Basin between Limestones D₅^{8 lower} and D₅^{8 upper}.

Deposition of the Voznessenian Horizon, i.e., lower Bashkirian strata, resembles the Zapaltyubian in thickness of the stratotype section (140 m; Poletaev *et al.* 2011, fig. 10) and to some extent in deposit content, the main difference being a significant increase in the number of limestone intercalations. Most important, however, is the increasing number of new rugose coral taxa appearing in these lowermost Bashkirian limestone intercalations (Text-fig. 2 and comments below). Precise sea-level changes, best reflected in the limestone intercalations beginning with the upper Viséan Mezhivian Horizon, continuing through the Serpukhovian Stage and up to the Voznessenian Horizon, are difficult to correlate with global sea-level changes and should be assessed as local events. According to Eros *et al.* (2012, p. 13), “the driver of stratigraphic architecture [is attributed] to relative sea level variations at multiple scales given that long-term accommodation in the Donets Basin was undoubtedly influenced by multiple processes including eustasy.”

Bashkirian strata in the Donets Basin were characterised by Poletaev *et al.* (2011, p. 59) as a transgressive-regressive megacycle, divided into three regional stages: Olmezovian, Mandrykinian and Kayalskian, corresponding to the lower, middle and upper Bashkirian. The two lower regional stages are divided into two horizons, while the upper regional stage consists of three horizons. Most of the rugose corals described in the series of my papers summarised here (see citations above) are from the lower and middle Bashkirian. The Bashkirian transgression mentioned by Izart *et al.* (2002) developed fully in the Feninian Horizon, as suggested by the increasing thickness (340 m) and nature of the deposits. The stratotype section of the Feninian Horizon consists mainly of aleurites and argillites with admixtures of sandstones and widely spaced limestone intercalations E₂ to E₇ in most of its thickness. Almost all of these limestones are devoid of corals, which occurred mainly in the lowermost Limestone Group E₁, occupying 10 m of the oldest deposits of this horizon. This limestone group and its coral fauna essen-

tially end the Voznessenian sedimentary cycle. The middle Bashkirian, i.e., the Mandrykinian Regional Stage was characterised by Poletaev *et al.* (2011, p. 68) as the most marine part of the Bashkirian succession in the Donets Basin. Two horizons comprising this stage, i.e., the Manuilivkian (Limestones E₈ to E₉² inclusively) and Blagodatnean (Limestones F₁ to F₂³ inclusively) include cyclic intercalations of argillites and aleurites with subordinate intercalations of limestones and lagoonal sandstones. Limestone intercalations vary in number and thickness. Most of them are thin, at 0.1–0.65 m. However, Ogar (2012) characterised the thickness of Limestone F₁ as varying from 12 m in the type section along Krynka River near Donetsk and along Luhanchik River near Luhansk, but often reduced to only 2 m or less in other areas. The large thickness of Limestone F₁ in the northern part of the basin was due to the development of a large bioherm (Ogar 2012), yielding diverse kumpanophyllid rugose corals (Fedorowski and Ohar 2019).

Only a few of the specimens studied by me were from the upper Bashkirian Kayalian Regional Stage, all from its lower Zuyivkian Horizon with a thickness of 1000 m in stratotype sections (Poletaev *et al.* 2011, fig. 14) and from Limestone G. Most of the taxa of the Kayalian Regional Stage included in Text-fig. 1 are compiled after Fomichev (1953), to whom the reader is referred for geological and stratigraphic data of the taxa introduced by him. The Zuyivkian Horizon began a regressive phase of the Donets Basin succession, which can generally be characterised as a reduction of marine argillites and aleurites at the expense of lagoonal and coastal terrestrial sandstones. Limestone intercalations still occur, but their thickness is generally small (compare Poletaev *et al.* 2011, figs 14–16).

Most coral-bearing limestone intercalations are bioclastic coarse- and/or small-grained limestones, some argillaceous. The corals in these limestones occur mainly as worn bioclasts. Some have been removed from the growth position, but probably left *in situ*. Those from the bioherms and from bioherm covering layers may remain in growth position (e.g., Fedorowski and Ohar 2019).

Succession of rugose corals

The succession of the Carboniferous rugose coral fauna in the Donets Basin was described in numerous papers (Lissitzyn 1925; Fomichev 1939, 1953; Vassilyuk 1960, 1964, 1975, 1983, 1990; Vassilyuk and Zhizhina 1978, 1979; Fedorowski

1981a; Rodríguez *et al.* 1986; Kossovaya 1996; Fedorowski and Vassilyuk 2001). The present analysis uses older data, but mainly includes studies of Bashkirian species (Fomichev 1953; Vassilyuk 1960, 1983; Fedorowski 2009b, c; 2017a, b; 2019a, b; 2021a, b; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013; Fedorowski and Ohar 2019).

The most important papers on the taxonomy of upper Viséan and Serpukhovian corals were published by Vassilyuk (1960, 1964) and Vassilyuk and Zhizhina (1978, 1979). These papers are the main sources of the data compiled in Text-fig. 1. Most of the generic and species identifications by these authors were found to be correct. Therefore, only remarks on the following taxa are introduced: 1) *Allotropiophyllum kabakovitsche* Vassilyuk, 1960 (pl. 12, fig. 7, 7a). The major septa in this species are radially arranged, rather short and free axially, slightly resembling *Bradyphyllum*. This arrangement does not agree with that in the type species of the genus, i.e., *Allotropiophyllum sinensis* Grabau, 1928 from the Permian of China. The major septa in the type species are grouped in a kind of semi-aulos including all major septa from counter quadrants, dominated in number, and some septa from cardinal quadrants. Thus, I disagree with the identification of Vassilyuk (1960). However, the lack of early growth stages in her specimen prevents precise generic identification. 2) *Amplexus coralloides constaseptata* Vassilyuk, 1960 (pl. 12, fig. 1, 1a) is insufficiently illustrated for me to comment. General issues concerning the genus *Amplexus* are discussed above. 3) *Amygdalophyllum nexilis* Vassilyuk, 1960 was included by me (Fedorowski 1970) in the new genus *Spirophyllum*, which is followed here. 4) *Claviphyllum eruca* (McCoy, 1851) of Vassilyuk (1960, pl. 12, fig. 6, 6a; 1964, pl. 3, figs 3–5) lacks contrasting minor septa, present in *Cyathopsis eruca*, the type species of *Claviphyllum*. Short and free minor septa, commonly hidden in the thickness of the outer wall, radially arranged major septa, cardinal septum shortened, and counter septum elongated fulfil the main features of *Antiphyllum* (see Fedorowski 2012b). Thus this generic name is applied to the Donets Basin specimens, while a new species name should be created for them. 5) *Enniskillenia curvilinea* (Thomson, 1881) of Vassilyuk (1964) was doubtfully excluded by Bamber *et al.* (2017, p. 37) from *Enniskillenia* Kabakovich in Soshkina *et al.*, 1962. I provisionally agree with that suggestion, although the shortened counter septum in both Vassilyuk's (1964, pl. 3, fig. 2) specimen and *Enniskillenia multiseptata* Bamber and Rodríguez, 2017 (Bamber *et al.* 2017, pl. 3, figs 3, 4, 7, 8, 10,

11) may suggest an affinity between the two species groups. Unfortunately, the single transverse section illustrated by Vassilyuk (1964) does not allow me either to confirm her identification or to suggest an alternative taxonomic position for her specimen. 6) The identification of two species as *Clisaxophyllum* Grabau, 1922 (according to Vassilyuk 1960, p. 146) or Grabau in Chi, 1931 (according to Hill 1981, p. F360) requires some comments. *Clisaxophyllum brazhnikovae* Vassilyuk, 1960 from Zone C₁^ve differs in many details from *C. sapaltjubensis* Vassilyuk, 1960 from Limestones D₄ and D₅⁷. These differences are significant enough to place the two species in separate genera. *Clisaxophyllum brazhnikovae* is omitted from further discussion as it occurs in strata older than those selected for this analysis. *Clisaxophyllum sapaltjubensis* should be transferred to *Cyathoclisia* Dingwall, 1926 if the synonymy of *Clisaxophyllum* with *Cyathoclisia* suggested by Hill (1981, p. F360) is accepted. However, the features of *C. sapaltjubensis* do not correspond to those of *Cyathoclisia modavense* Dingwall, 1926, the type species of the genus. The presence of extra septal lamellae in the axial structure of *C. sapaltjubensis*, absent in *C. modavense* and several other differences exclude the congeneric position of the two species. A new genus should be introduced for *C. sapaltjubensis*. 7) The identification of Vassilyuk's (1960, 1964) specimens as *Koninckophyllum interruptum* has previously been questioned (Fedorowski 1971, p. 82) due to the presence in her specimens of an axial tube, called columnotheca by Fedorowski (2009d). Such a structure is absent from *Koninckophyllum magnificum*, the type species of the genus. Thus, I stand by my earlier position, but cannot identify a genus to which the specimens of Vassilyuk (1960, 1964) should be included. 8) The name *Lophophyllum* cannot be applied to corals with a dissepimentarium such as those of Vassilyuk (1960, pl. 5, fig. 9). Lecompte (1955), Hill (1981) and Fedorowski (1990) re-examined the type collection of *Lophophyllum konincki* Milne Edwards and Haime, 1850, the type species of the genus, consisting of five, non-dissepimented specimens. Hill (1981, p. F333, fig. 219a–c) selected one of those specimens as lectotype. Vassilyuk's (1960) specimen does not belong to *Lophophyllum*, but it may be considered a predecessor of the specimens named *Lophophyllum* by Fomichev (1953), requiring a new generic name. 9) '*Permia*' *stuckenbergi* Vassilyuk, 1964 is a non-dissepimented coral with a kind of an aulos. Vassilyuk (1964, p. 68) correctly compared her specimen with some species included in this genus by Hudson (1943, 1944, 1945). However, the loss of

Stuckenberg's (1895) types has already been documented (Fedorowski 1971, p. 24). I have also studied (1969, unpublished) the 'Permian' topotypes from the collection of Dr. N.V. Kabakovich (Palaeontological Institute, Moscow) and established their identity with the early growth stages of *Aulophyllum* Milne Edwards and Haine, 1850. Accordingly, synonymy between the two genera has been suggested (Fedorowski 1971, p. 24). This position is maintained here, and a new generic name is required for both British and Ukrainian 'Permian' if they prove to be congeneric. 10) The illustration in Vassilyuk (1960, pl. 12, fig. 4) of *Tachylasma tenue tanaica* Vassilyuk, 1960 is inadequate for exhaustive comment and identification of her subspecies. However, my recent analysis of the occurrence of *Tachylasma* Grabau, 1922 (Fedorowski 2021b) allows me to exclude Vassilyuk's (1960) specimen from this genus. 11) *Zaphrentites subcarruthersi* Vassilyuk, 1960 exposes all the main features of *Zaphrufimia*. Vassilyuk (1960, p. 50) drew attention to the 'tachylasmatoïd character' of the thickening of some major septa in her specimen. Hence, it was transferred herein to *Zaphrufimia*.

The taxa described by Vassilyuk and Zhizhina (1978, 1979) also require some comments: 1) *Pseudodordolodotia subkakimii* Vassilyuk, 1978 and its role in the phylogeny of *Colligophyllum* has been already discussed (Fedorowski 2021a, p. 88). 2) Both *Corwenia vaga* Smith and Ryder, 1926 from Zone C₁^vg and *Corwenia progressiva* Tschukina in Bykova, 1966 from Limestone D₅ resemble in transverse section the morphology of *Lonsdaleia rugosa* McCoy, 1849, the type species of *Corwenia*. However, they lack the axial column in longitudinal section, typical of *C. rugosa*. This feature, also present in the British specimen of *C. vaga*, is important enough to consider their bearers, both British and Ukrainian, as differing from *C. rugosa* at genus level. 3) *Palaeosmilia regia* of Vassilyuk and Zhizhina (1979) is a colonial specimen. It is therefore included in *Palaeostraea*. 4) Both *Lithostrotion* species, i.e., *L. kwanghsiense tanaica* Zhizhina, 1979 and *L. longiseptata* Vassilyuk, 1979 are fasciculate colonial and are included in *Siphonodendron*. 5) The identification by Zhizhina (in Vassilyuk and Zhizhina 1978) of her new species as *Diphyphyllum* is tentatively accepted but may be incorrect. The axial offsetting, fundamental for *Diphyphyllum* is not documented in *D. fasciculatum lateseptatum* Zhizhina, 1979, while *D. carinata* Bykova, 1966 may belong to *Tizraia* Said and Rodríguez, 2007. Unfortunately, poor preservation precludes more precise suggestions. 6) The illustrations of *Orionastraea phillipsi* (McCoy, 1849),

Aulina grandis Vassilyuk, 1979 and *Solenodendron ramosa* Vassilyuk, 1979 are not good enough to comment in detail, and have therefore been marked with question marks in Text-fig. 1.

Almost all the species described by Vassilyuk (1960, 1964) and Vassilyuk and Zhizhina (1978, 1979) from the upper Viséan Donetzian and Mezhivian horizons (Text-fig. 1) were included by them in existing genera. Some of these genera are commented above as doubtful and/or possibly new. *Pseudoclaviphyllum* Vassilyuk, 1964 from the Mezhivian Limestone B₁ is the only new, upper Viséan genus represented by one species. Eighteen of forty-two upper Viséan species included in Text-fig. 1 are restricted to the Donetzian. Only twelve of them are either new or are described from the Donets Basin by authors other than Vassilyuk (1960, 1964). Sixteen species are known from the upper Viséan strata elsewhere, most of them (10) from Western Europe. Ten other species occurring in the Donetzian appeared in various younger strata. Five of them ended in the Mezhivian Horizon, the other five entered the Serpukhovian Stage, reappearing in its various limestones.

Fourteen of the twenty-four species present in the Mezhivian appeared as new species in the different limestone intercalations of this horizon, forming a kind of mosaic in appearance. Twelve of these are restricted to the Mezhivian, while the remaining twelve occur together with older (10) or younger (2) horizons, making the Mezhivian rugose coral fauna less diverse compared to both younger and older strata. Treating the Mezhivian as equivalent to the Brigantian Substage, its rugose coral fauna is very impoverished compared to faunas not only from Europe, northern Africa or China, but also from the Moscow Basin, the Urals and Novaya Zemlya. However, four species appearing for the first time in the Zapaltyubian of the Donets Basin, i.e., *Actinocyathus heckeri* (Dobrolyubova, 1958), '*Caninia*' *amplexoides* Stuckenberg, 1904, *Bothrophyllum* (= *Nina* Fedorowski, 2017b) *berestovensis* Vassilyuk, 1960 and *Dibunophyllum dobroljubovae* crossed the Serpukhovian/Bashkirian boundary. *Dibunophyllum dobroljubovae* reappeared in Limestone D₆ and *N. berestovensis* in Limestones D_{6,7} (Text-fig. 2).

The growth forms of the genera present in the two upper Viséan horizons differ considerably. This difference is obviously environmentally determined (see Geological Setting). Only five of the fourteen genera present in the Donetzian are solitary, dissepimented taxa, the remaining nine are colonial taxa, among which *Siphonodendron* dominates. None of these gen-

era is new. Three genera, i.e., ‘*Caninia*’, *Orionastraea* Smith, 1917 and *Pseudodorlodotia* are questionable. Solitary, non-dissepimented corals have not been fully described from this horizon. In contrast, five of the twelve genera that first appeared in the Donets Basin during the accumulation of the Mezhivian, are solitary, non-dissepimented taxa. Vassilyuk (1960, 1964) identified them as *Allotropiophyllum*, *Claviphyllum*, *Cyathaxonia*, *Enniskillenia* and *Permia* Stuckenber, 1895. The identification of most of these is questionable (see above), but their occurrence is important as an indicator of environmental change. Six of the new arrivals are solitary dissepimented genera. One of these, *Pseudoclaviphyllum*, restricted to the lowermost Mezhivian Limestone B₁ is a new genus. Only one genus (‘*Corwenia*’) of the newcomers is fasciculate colonial. Four other solitary dissepimented genera (*Aulophyllum*, *Dibunophyllum*, *Gangamophyllum* and *Palaeosmilium*) and two colonial genera: *Orionastraea* and *Siphonodendron* are common in the Donetzian (Text-fig. 1).

The observations on the upper Viséan species and genera can be summed up as follows:

1) The absence of new genera and the large number of widespread species, such as *Aulophyllum fungites*, *Dibunophyllum bipartitum*, *Palaeosmilium muchisoni*, *Palaeostraea regia*, and *Siphonodendron irregulare* found in the Donetzian, document the position of the Donets Basin in the middle of the mainstream of the upper Viséan rugose coral world. Fomichev (1953, p. 526) summarised his comments on this horizon as follows: “Thus, we have here a typical *Dibunophyllum*-zone of the Viséan Stage” (translated from Russian).

2) The significant difference in species and genus composition between the Donetzian and Mezhivian, superimposed on the paralic sedimentation type of the Donets Basin, suggests a significant difference in the life and creation centres of the rugose fauna occurring at the boundary between the two horizons. The vast and long-lasting carbonate platforms present in the Donetzian provided a friendly habitat for the rugose coral fauna within the basin, allowing for their differentiation. The overall depositional history of the basin changed at the beginning of the Mezhivian. Instead of carbonate platforms, carbonate intercalations, often thin, were deposited among the thick clastic deposits. Some carbonate build-ups and thick limestone intercalations may suggest the possibility of limited faunal formation within the basin (e.g., Fedorowski and Ohar 2019), but most do not. The rugose coral fauna appears to have found its refugia in oceanic platforms outside the basin.

3) Oceanic carbonate platforms developed in the

vicinity of the Donets Basin, but the basin itself was not a fauna-creative area for rugose corals. The accumulation time of most of the limestone intercalations in which corals occur was too short to allow the creation of new species within the basin. New species that appeared on oceanic platforms invaded the Donets Basin as a result of marine incursions. Such a process began in the Mezhivian, as indicated by the mosaic pattern of coral occurrence (Text-fig. 1). This also explains the pattern of occurrence of younger taxa in the Donets Basin (Text-fig. 2). The reduction of colonial corals at the expense of solitary dissepimented taxa, the absence of solitary non-dissepimented corals in the Donetzian, and their appearance in the Mezhivian suggest environmental changes in the fauna source area. Although theoretical, only such a model allowed for the continuous presence of Viséan genera during the Serpukhovian and the emergence of many new species throughout this stage.

The Serpukhovian Stage is the shortest Mississippian stage. According to Menning *et al.* (2006, fig. 3) it lasted 6.5 my; Torsvik and Cocks (2017) increased this age to 8 my, whereas Aretz *et al.* (2020) suggested slightly less than 7 my. Also, its lower boundary, correlated for a long time with the entrance of the conodont *Lochriea zieglerei* Nemirovskaya, Perret and Meischner, 1994 is disputed by several authors as summarised by Aretz *et al.* (2020, p. 818). Nemyrowska (2017, fig. 1) correlated this boundary in the Donets Basin with the onset of the *Cavusgnathus naviculus*–*Lochriea zieglerei* Biozone and extended the zone to the two lowermost Serpukhovian horizons: Samarian and Prokhorivkian. Moreover, she included the entire Limestone D₁ Group in the Novolyubivkian Horizon, while Poletaev *et al.* (2011, figs 7, 8) noted an 11 m thick Limestone D₁⁵ⁿ at the beginning of the Novolyubivkian Horizon, and placed all intercalations of Limestone D₁ lower than D₁⁵ⁿ in the Prokhorivkian Horizon. In this paper I follow the concept of Poletaev *et al.* (2011).

The distribution of rugose corals in the different Serpukhovian horizons varies considerably (Text-fig. 1). Only eight pre-existing species crossed the Brigantian / Serpukhovian boundary, but none of them reappeared in the uppermost Mezhivian limestones and the Samarian limestones. All of them are devoid of corals. This crisis coincides in time with the crisis of rugose coral fauna in Western and Central Europe, although the Sudetic Orogeny, responsible for changes in these parts of Europe, was not obviously active in the Donets Basin. Moreover, this deterioration cannot be regarded as an extinction, since almost all genera flourishing in the Serpukhovian are

Viséan relicts. The absence of corals in the Samarian Horizon should be treated as a local, environmentally induced event (see above).

The appearance of new rugose coral species started from the Prokhorivkian Horizon, in Limestone Group D₁ in particular (Text-fig. 1). Eight species (four of them new) appeared in the Donets Basin for the first time in this horizon. Two reappeared from the Mezhivian and three from the Donetzian. The new subspecies '*Tachylasma*' *tenuetanaica* with uncertain affiliation, is the only solitary non-dissepimented taxon among the thirteen species present in this horizon. Six species are solitary dissepimented and six are colonial. Five of these (*Aulina* and *Lithostrotion*) are massive colonial, and *Siphonodendron* is fasciculate. The occurrence of so many colonial and solitary dissepimented corals in a series of mainly sandy deposits with rare and thin limestone intercalations (Poletaev *et al.* 2011, fig. 7) is quite surprising. Only five of these taxa either prolonged their occurrence or reappeared in the Novolyubian Horizon and one species (*Aulina grandis*) appeared in the latter horizon and is restricted to its lower part (Limestone D₁⁵). The upper part of the Novolyubian is devoid of corals due to unsuitable environmental conditions (Poletaev *et al.* 2011, fig. 8).

The Zapaltyubian Horizon (Limestones D₃–D₅⁸ lower) has a rich and diverse rugose coral fauna. Four of the twenty-eight species present in this horizon reappeared from the Donetzian (Zone C₁^{vf}), one species reappeared from the Mezhivian (Zone C₁^{vg}) (both upper Viséan), and six species continued or reappeared from older Serpukhovian strata. The remaining seventeen species appeared in the Donets Basin for the first time near the upper Serpukhovian boundary. Eleven of these are new species. However, most of the genera (18) occurring in the Zapaltyubian are Viséan relicts. Unfortunately, six of them have uncertain affiliations; some may be new. Three genera are new: *Adamanophyllum* Vassilyuk, 1959 (probably endemic), *Nervophyllum* Vassilyuk, 1959 and *Nina*. *Nervophyllum* is in fact a late Mississippian relict, as its older representatives have been described from the Brigantian and lower Serpukhovian strata of Poland (Fedorowski 1971, 2015). *Nina* is of particular value as representing a possible intermediate taxon leading towards the Subfamily Dibunophyllinae Wang, 1950 (see Fedorowski 2017b). Only one genus, represented by one species, i.e., *Zaphruffimia subcaruthersi* (Vassilyuk, 1960), is a solitary, non-dissepimented taxon. All others are solitary dissepimented taxa (thirteen genera, sixteen species) or colonial taxa (seven genera, twelve species). In addition,

twenty-four of the twenty-eight species present in the Zapaltyubian occur in Limestone intercalations D₅¹⁻⁵, which ended approximately 30 m below the end of the Serpukhovian in the stratotype section. This rich fauna followed a slight decrease in diversity (thirteen species) in Limestone D₄, and ended abruptly with the onset of Limestone D₅⁶, devoid of corals. Only five species cross the Serpukhovian/Bashkirian boundary; of them *Dibunophyllum bipartitum* extended from the Donetzian, *Dibunophyllum dobroljubovae* first appeared in Limestone D₂, '*Caninia*' *amplexoides* first appeared in Limestone D₄, *Actinocyathus heckeri* and *Nina berestovensis* first appeared in Limestone D₅. The first four occur in Limestone D₅⁸ upper, while *Nina berestovensis* reappeared only in Limestones D₆, ₇, and *Dibunophyllum bipartitum* and *D. dobroljubovae* reappeared in Limestone D₆.

Corals from the upper Viséan (Donetzian and Mezhivian) and Serpukhovian of the Donets Basin (Text-fig. 1) are included in this analysis in order to: (i) demonstrate their abundance in the upper Viséan and close similarity to Western and Central European, North African and Chinese faunas in generic content over that time; (ii) document the occurrence in the upper Viséan of several species shared with Western Europe and North Africa and several shared with China, accompanied by several new species; (iii) indicate the occurrence of many new species in the Serpukhovian; almost all of them, except for the new genus and species *Pseudoclaviphyllum tenuiseptata* Vassilyuk, 1964 and *Nina berestovensis* (1960) belong to Viséan genera; (iv) emphasise the environmentally controlled depletion of fauna in the Mezhivian, in contrast to the abundance of contemporaneous fauna in several other regions of the world; (v) show a strong reduction of coral taxa in the latest Serpukhovian to only five species crossing the Serpukhovian / Bashkirian boundary, and, finally, (vi) show the peculiar mosaic pattern in the appearance of species, in particular limestone intercalations, beginning with the Mezhivian and continuing through the Serpukhovian (see below for details; Text-fig. 1).

The sequence of Serpukhovian rugose corals in the Donets Basin shows several peculiarities, which are at least partly due to the cyclic sedimentation characteristic of paralic coal basins. The absence of corals in some parts of the section, such as the upper part of the Novoljubivkian, is obviously environmentally determined. In contrast, the appearance of relatively abundant colonial corals in the Prokhorivkian, which is dominated by sandy deposits, similar to the Novoljubivkian, with sparse and thin marine intercalations, is difficult to comment on. Differentiation at

genus level is very limited, while at species level it is intense. Moreover, the most abundant and diverse fauna appearing towards the end of the Serpukhovian confirms the continuing creative potential of Mississippian rugose coral genera. Thus, their absence in apparently better living conditions in the Voznessenkian is incomprehensible (see below). In this context, the direct affinities of the Mississippian *Rotiphyllum* and *Rozkowskia* Fedorowski, 1970 with Bashkirian taxa are uncertain, despite their close morphological similarity in all growth stages to the Mississippian ?ancestors (Fedorowski 2009b, 2017a). The succession of Serpukhovian rugose corals in the Donets Basin can be pointed to as a model for the Mississippian/Pennsylvanian faunal turnover in the sense that an extremely limited number of taxa from the Mississippian continued into the Pennsylvanian. However, the richness of the Mississippian fauna near the top of the Serpukhovian and its rapid disappearance, independent of environmental conditions, makes the reason for this turnover puzzling.

The turnover of rugose coral fauna from the Mississippian to the Pennsylvanian–Permian phase (Fedorowski 1981a) was already predicted earlier. Degtjarev (1973) was not only the first one to suggest a turnover of rugose coral fauna, but he was most precise in his suggestion, pointing to the equivalent *Homoceras–Hudsonoceras* Genozone as the period of this turnover (see above). Vassilyuk (1974, p. 10) wrote: “Thus, a high-level turnover in coral development occurred at the Protvinian and Krasnopolyanian boundary ... This boundary should correspond to a high-level stratigraphic boundary” (translated from Russian). Note that the Serpukhovian/Bashkirian boundary in the most common recent sense was not accepted at the time of Vassilyuk (1974). Hill (1981, p. F62) clarified and accepted Vassilyuk’s (1974) suggestion by writing that she “considered that a great faunal change occurred between Namurian A and Namurian B, i.e. approximately at the end of the Mississippian.” Fedorowski (1981, p. 132) indicated that the “lower Bashkirian boundary, so far as the coral fauna is concerned, may as well be lowered to the base of the Chokierian Stage, at which level a number of new taxa first appeared.”

To my knowledge (see discussion above), both the precision of the Mississippian / Pennsylvanian rugose coral turnover and its sharpness are best documented and most prominent in the Donets Basin. Nearly all Mississippian taxa, at both genus and species level, disappeared near this boundary. However, Mississippian relicts are the only representatives of rugose coral fauna in the Bashkirian boundary

Limestone D₅^{8 upper}, while only a single, very incomplete specimen, identified as ?*Kumpanophyllum* sp. by Fedorowski (2019b) was found in Limestone D₅⁹, about 10 m above the base of the Bashkirian. Doubts about its taxonomic position have already been expressed (Fedorowski 2019b, p. 459).

Several of the sixteen limestone layers found in the Voznessenkian stratotype section (Poletaev *et al.* 2011, fig. 10) bear remnants of rugose corals, several of which belong to new taxa (Text-fig. 2). The first Pennsylvanian genus *Dibunophylloides* accompanied by *Dibunophyllum medium* Fedorowski, 2017a appeared in Limestone D₅¹⁰, about 17 m above the lower Bashkirian boundary. The close morphological similarity of *D. medium* to *Dibunophylloides paulus* Fedorowski, 2017a and the co-occurrence of both species allow me to consider *Dibunophylloides* as a close descendant of *Dibunophyllum*. The genus *Nina*, considered by Fedorowski (2017b, p. 260) to be “a potential ancestor of *Bothrophyllum*”, is another new Pennsylvanian genus, despite the finding of one specimen near the top of the Serpukhovian. The similarity of the early growth stages of *Dibunophyllum* and *Nina* allowed Fedorowski (2017a, p. 509) to exclude Mississippian species from the genus *Bothrophyllum* and to consider *Nina* and the Family Bothrophyllidae as derived from the Subfamily Dibunophyllinae.

In addition to the Pennsylvanian genera listed above, four other Pennsylvanian genera appeared in the Voznessenkian. In ascending order of occurrence these are: *Kumpanophyllum*, *Voragoaxum* Fedorowski, 2017a, *Protokionophyllum*, and gen. nov. of Fedorowski (2021b) (Text-fig. 2). Thus, there are six new genera, eight relict Mississippian genera (the six listed above, of which two are probably new, as well as *Rotiphyllum* and *Pentaphyllum*), represented by six relict Mississippian species, and twenty-two new species in the Voznessenkian. Seven of the new species were left in open nomenclature. Four of these are listed in Text-fig. 2, whereas three others, i.e., *Arachnolasma?* sp. (Limestone D₅¹⁰), *Nina?* sp. 1 and ?*Siedleckia* sp. 2 (both from Limestone D₇) are described and illustrated, but have not been included in Text-fig. 2 as their taxonomic position is too uncertain (Fedorowski 2017a, b).

The lowermost part of the Feninian Horizon, i.e., its first 10 m in the stratotype section including three limestone layers (Poletaev *et al.* 2011, fig. 11), is an obvious continuation of the first phase of differentiation of Bashkirian rugose corals in the Donets Basin. The oldest representative of the genus *Yuanophylloides* and three new genera appeared at this stratigraphic level, i.e., *Colligophyllum*, represented by *C. dobrol-*

jubovae, *Cordibia* Fedorowski and Ogar, 2013, represented by *C. pumila* Fedorowski and Ogar, 2013 and *Krynkhaphyllum*, represented by *K. validum* and *K. multiplexum*, both of Fedorowski, 2021a. They are accompanied by several taxa (Text-fig. 2), including the re-appearing Mississippian *Rotiphyllum*, *Rozkowskia* and *Axisvacuus*. The latter genus with the type species *A. verus* Fedorowski, 2009c was first described from the Limestone F₁ (Blagodatkian Horizon = Yeadonian Substage, upper lower Bashkirian) of the Donets Basin. However its oldest representative is known from the lower Pendleian (lower Serpukhovian E₁ Genozone) of the Lublin Coal Basin (Fedorowski 2015). Only a single specimen of *Axisvacuus semicirculatus* Fedorowski, 2009c has been described by Fedorowski (2009c) from the middle part of the Manuilivkian (Limestone E₈⁵). However, most of the Feninian and almost the entire Manuilivkian are devoid of rugose corals, separating the first phase of their differentiation from the second. Scattered, thin and sparse limestone intercalations in most of the Feninian and in the lower half of the Manuilivkian may suggest an environmental cause for this absence. In contrast, limestone layers are quite abundant in the upper part of the Manuilivkian, and two of them are 1.5 m thick (Poletaev *et al.* 2011, fig. 12), but both are devoid of corals. The reason for the absence of corals remains unknown.

The genera *Protokionophyllum*, *Voragoaxum*, and gen. et sp. nov. of Fedorowski (2021b) appearing successively in the Voznessenkian, and *Nina* appearing in the latest Serpukhovian, should be considered as endemic for now, but representatives of *Dibunophylloides*, *Kumpanophyllum* and *Yuanophylloides* (Text-fig. 2) are widely distributed (Fedorowski 2017a, 2019a, b). Some Chinese taxa included in the Family Kumpanophyllidae Fomichev, 1953 may have been ancestral to representatives of this family from the Donets Basin, as suggested by the general directions of ocean currents. However, the lack of detailed stratigraphic data from China precludes an indisputable recognition of such affinities. *Dibunophylloides*, on the other hand, may suggest a distant association of the Donets Basin not only with China, but also with the Coastal Province of North America (see Palaeogeographic Overview above).

The relatively rapid diversification of rugose corals in the early Bashkirian, Voznessenkian and early Feninian allows me to make the following summary: 1) The rugose coral fauna of the Voznessenkian and lower Feninian is a mixture of relict and new coming species and genera, with newcomers predominating among the species. 2) Dibunophyllid corals

(*Dibunophyllum*) rooted in the Viséan, and their descendants *Dibunophylloides* and *Nina*, dominate, but the earliest appearance in the early Bashkirian of the families Kumpanophyllidae and Krynkhaphyllidae Fedorowski 2021a, both of uncertain provenance, should be noted. 3) Most species and some genera are short-lived, but long-lived and widely distributed lineages have emerged, such as the Bothrophyllidae, Kumpanophyllidae and Krynkhaphyllidae, and the Dibunophyllinae have continued their occurrence. 4) The content of the rugose coral fauna makes the Donets Basin (see above) a faunal creative centre rather than a typical refugium, although some species and genera are relicts from the Mississippian, which also documents this refugial role. 5) The lack of colonial taxa and the dominance of solitary dissepimented corals were probably environmentally induced, as suggested by Vassilyuk (1974).

The strong depletion or absence of rugose corals from Limestones E₃ to E₉ (upper Feninian and Manuilivkian) may have been partly environmentally induced, as indicated by both the limited number of limestone intercalations and the lithology of several of them. However, the composition of other fossil groups listed from these limestones (Poletaev *et al.* 2011, pp. 65–75) is not significantly depleted. Therefore it is possible that both environmental and other factors were at work here. One theoretically possible factor could have been the limited population content of individual rugose coral species, insufficient to follow marine incursions and recolonise floodplains. Fomichev (1953, p. 527) did not find corals “in upper [i.e., above Limestone E₁] deposited limestones of Suite C₁⁵ E [i.e., Limestones E₂₋₉]” (translated from Russian). Suite C₁⁵ terminated the lower Carboniferous at Fomichev’s time (1953). He summarised his earlier remarks as follows (Fomichev 1953, p. 527): “The short overview above of the coral fauna of Suites C₁¹–C₁⁵ has shown that all of them represent typical Lower Carboniferous groups of forms...”. However, he also added: “... the upper part of the Lower Carboniferous section (Suites C₁³–C₁⁵) already contains Namurian forms ... and should be correlated with the Upper (Middle) Carboniferous” (translated from Russian).

The stratigraphically oldest corals described by Fomichev (1953) include those from Limestone F₁. *Stereophrentis* (= *Axisvacuus*) *mandrykinensis* Fomichev, 1953 (Text-fig. 2), *Lophophyllidium* cf. *grabau* Fomichev, 1953 and *Axolithophyllum?* sp. found above a series of coral-depleted deposits allowed him to consider Limestone F₁ as the entrance of an upper middle Carboniferous fauna. A similar opinion was expressed by Fedorowski and Vassilyuk (2001), while

Vassilyuk (1974) lowered this entrance down to the Krasnopolyanian, i.e., the Feninian Horizon. Recent studies (Fedorowski 2009b, c, 2017a, b, 2019a, b, 2021a, b; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013; Fedorowski and Ohar 2019) established two stages of rugose coral diversification in the Donets Basin. The older stage established here, i.e., the true turnover of the Mississippian/Pennsylvanian fauna began from the deposition of the lower Voznessenian. This stage was unknown to Fomichev (1953) due to lack of data, with the succession of genera and species summarised in Text-fig. 2 confirming Fomichev's (1953) suggestion, but in the sense of the second stage introduced here.

The second stage of the faunal turnover includes forty-six species. Only four of these (*Axisvacuus verus*, *A. semicirculatus*, *Rotiphyllum abnorme* Fan, 2003 and *R. asymmetricum* Fedorowski, 2009b) continued from the first stage. Also, of the twenty-four genera present in the second stage, only six genera are continued from the first stage (non-dissepimented *Axisvacuus*, *Cyathaxonia* and *Rotiphyllum*, and solitary dissepimented *Kumpanophyllum*, *Yuanophylloides* and *Dibunophylloides*). Thus, not only the ecologically-caused interruption of coral occurrence, but also the significant difference in faunal content at specific and generic level, confirms the distinction between the two stages.

Most of the genera introduced by Fomichev (1939, 1953) are accepted here, but some of those occurring in the second stage require comment. 1) *Stereophrentis* Fomichev, 1953 with the type species *Zaphrentis delanouei* Milne Edwards and Haime, 1851 (Fomichev, 1953, p. 144) lost priority at the expense of *Zaphrentites*, since the same type species was chosen for both. However, the Tournaisian type species of *Z. delanouei* is unnecessarily congeneric with taxa from the middle Bashkirian and Moscovian included by Fomichev (1953) in *Stereophrentis*. *Stereophrentis mandrykinensis* has been already transferred to *Axisvacuus* (Fedorowski 2009c), while the other species introduced by Fomichev (1953) into *Stereophrentis* may represent a new genus/genera. 2) Kossovaya *et al.* (2012) negated the identifications of some species by Fomichev (1953) as *Cyathaxonia* and included them in the new genus *Sloveniaxon*. This new identification may be correct if/when the morphology of columellae in Fomichev's (1953) species confirms the similarity to *Variaxon*. Such similarity is lacking in the work by Kossovaya *et al.* (2012), while undoubted *Cyathaxonia* was described by Fedorowski and Vassilyuk (2011) from Limestone F₁. 3) *Carcinophyllum* was included by Hill (1981, p. F398)

in the synonymy of *Axophyllum*. However, the species from the upper Bashkirian included by Fomichev (1953) in his new species *Carcinophyllum ivanitzkyi*, may as well belong to a different genus. 4) The generic name *Cystophora* Yabe and Hayasaka, 1916 is occupied (Hill 1981, p. F403). Hill (1981) dubiously synonymised this genus with *Ivanovia* Dobrolyubova, 1935, but the taxonomic position of the latter is uncertain. It is the second colonial taxon occurring in the Donets Basin Pennsylvanian strata, after the Mississippian *Actinocyathus heckeri*, extending to the Voznessenian (lowermost Bashkirian) (Text-figs 1 and 2). 5) The identification of the Bashkirian specimen as the lower Carboniferous *?Spirophyllum*, is uncertain. 6) *?Sestrophyllum ancestor* and *?S. complexum* both of Fomichev, 1953, differ from the type species of the genus (*C. astraeforme* Fomichev, 1953) to an extent that makes their congeneric position questionable. 7) The identifications of '*Caninia*' and '*Campophyllum*', both early Mississippian taxa, require a careful study of their early growth stages and septal microstructure, lacking in Fomichev (1953). I would rather rule out the occurrence of these genera in upper Bashkirian strata. 8) *Stereolasma* is a genus from the Middle Devonian, occurring in the endemic New World Realm of Oliver (1976). The specimens included in this genus by Fomichev (1953) belong to a new genus. 9) The occurrence in the Donets Basin of *Falsiamplexus reductus* Fedorowski, 1987, first described from Texas, is important as an indicator of the faunal connection between Texas and the Donets Basin, already suggested by the occurrence of *Yuanophylloides inauditus* (Moore and Jeffords, 1945) in the two basins (see Fedorowski 2019a). 10) Six new genera that have arisen in the horizons from the Blagodatnean to the Krasnodonian: *Dirimia* Fedorowski and Ohar, 2019 (Limestone F₁), *Bothroclisia* Fomichev, 1953 (Limestone F₃), *Cystilophyllum* Fomichev, 1953 (Limestone G₁), *Monophyllum* (Limestone H₂), *Neokoninckophyllum* and *Orygmophyllum* (both Limestone I₂) are accepted here as important evidence for a distinct stage of differentiation of the Rugosa in the Donets Basin. The subdivision of *Dirimia* species can be questioned as most of them originate from a single biohermic cover site. The reason for their introduction and the introduction of a new Subfamily Dirimiinae is discussed by Fedorowski and Ohar (2019, p. 589).

Almost all species, except *Bothrophyllum kalmiussi* Fedorowski, 2017b, *B. gorbachevense* Fedorowski, 2017b, and *Rotiphyllum simulatum* Fedorowski, 2009b, occurring above Limestone F₁ in Text-fig. 2 were taken from Fomichev (1953, Enclosure; Priložhenyie). Only

a few of these species were checked by me for correct taxonomic affiliation and stratigraphic rank. Thus, very long-lived species, especially those revealing long gaps in occurrence, may in fact be morphotypes rather than true species. For species that I have verified in some aspects, see Fedorowski (1987, 2009b, c, 2017a, 2019a, b) and Fedorowski and Vassilyuk (2011).

The last part of the succession of Bashkirian Rugosa in the Donets Basin began within Limestone I₁ (uppermost Makiivkian), but intensified in the lower Krasnodonian (Limestones I_{2,3}), when six previously existing species reappeared and eight new species appeared after a brief hiatus in rugose coral occurrence. Four of the new species, the new genera *Orygmophyllum* and *Yakovleviella* both of Fomichev, 1953, continued to occur in the Moscovian (Text-fig. 2), allowing this stratigraphic level to be considered to be the probable beginning of the next rugose coral diversification stage in the Donets Basin.

DISCUSSION

My idea of the criteria necessary for the correct identification of a species of rugose coral is discussed in the chapter Material and Methods (see above). I consider this reminder necessary in the context of the comments that follow.

The paper *Carboniferous biostratigraphy of rugose corals* by Wang *et al.* (2021), mentioned in some aspects above, is briefly discussed in this chapter due to its general nature. While attempting to illuminate the stratigraphic value of the Rugosa, it documents the need for careful restudies of coral collections in many areas of the world, rather than offering a comprehensive solution. This is due, among other things, to the omission of many fundamental papers at the expense of summaries and the simple repetition of names used in included papers regardless of their correction. The brief comments on some of the correlation tables in their Serpukhovian to Bashkirian sections exemplify this.

The names *Carinthiaphyllum*–*Acrocyathus* chosen by Wang *et al.* (2021, fig. 2) to characterise the Bashkirian and most of the Moscovian stages for Southern China are already questioned in the subsection above. *Caninia pishanensis* listed as co-characterizing the upper Bashkirian in Northern China has no documentation of early ontogeny and is unlikely to be congeneric with the Tournaisian European type species of the genus. Both names used for the *Lithostrotionella*–*Lytvophyllum* Zone in the Jungganhing Region of China are probably incorrect.

Lithostrotionella is a younger synonym of *Petalaxis*, while specimens identified as *Lytvophyllum* need to be re-examined before they can be included in this Artinskian (Permian) genus. Almost all of the genera listed as characteristic of the Serpukhovian–lower Bashkirian of Iran have been questioned above (see subsection Iran).

Only two provinces instead of five are included in Wang's *et al.* (2021, fig. 4) in North America, which creates a false view of the representation of rugose corals in that continent. Also many papers are not included (see section North America above). The name *Orygmophyllum* used as characteristic of the Bashkirian in the Western Interior Province is incorrect. Fomichev (1953) introduced it for solitary corals, whereas the North American forms are colonial. Besides, *Caninia* and *Neokoninckophyllum* are not found in North America, and the name *Rhodophyllum* is a younger synonym of *Dibunophyllum* (see Hill 1981, p. F360), also not found in North America.

The content of Wang's *et al.* (2021) figure 5 is highly misleading. 1) The choice of the areas discussed is subjective. For example: why is such an important area as the Voronezh Anticline not included? 2) Corals are known from the Serpukhovian of Great Britain. Also there is a rugose coral-bearing episode in the upper Bashkirian of Great Britain and Belgium. Both are missing from the figure. 3) The fundamental studies by Vassilyuk (1960, 1964) on the Mississippian corals from the Donets Basin and my papers on the lower Bashkirian corals cited above and available from an open access journal are not considered. The latter renders the lower Bashkirian in the Donets Basin empty of corals, whereas several new species and some new genera appeared there at that very important time for rugose coral evolution. 4) The statement in the figure: "To date, the Carboniferous rugose corals of the Moscow Basin are not well studied" is incorrect. Many papers, beginning with Fischer v. Waldheim (1830), Trautschold (1879), and Stuckenberg (1904), supplemented by Dobrolyubova (1932, 1952a, b, 1958, 1970) and Kabakovich (1952a, b), are devoted to Mississippian Rugosa from this basin. The secondary paper cited by Wang *et al.* (2021), i.e., Hecker (2001) is in its Russian part almost entirely based on these earlier fundamental achievements. The statement "based on the identifications by Dobrolyubova and Kabakowitsch (1948) and later revisions by Fomichev (1953)" is incorrect and also misleading. Firstly, there are several papers by Dobrolyubova (1935, 1937, 1940, 1948) and Kabakovich (1937), on the Pennsylvanian corals from the Moscow Basin, whereas only Dobrolyubova and

Kabakovich (1948) is cited by Wang *et al.* (2021). Secondly, Fomichev (1953) corrected only two species names of T.A. Dobrolyubova, transferring them to new genera, i.e., *Cyathoclisia symmetrica*, renamed *Dibunophylloides*, and *Lonsdaleia portlocki*, renamed *Cystolonsdaleia*. However, he did not revise those papers. 5) The column for the Urals and adjacent areas is misleading as well. First, such important reports as Gorsky (1932, 1935, 1951, 1978), Dobrolyubova (1935, 1936), Degtjarev (1965, 1973a,b, 1975, 1977, 1979) and Sayutina (1973) are not cited and, most likely, not taken into account. Secondly, Kossovaya's (1996, 1997, 2009) attempts to place at least some taxa from this important area in the modern stratigraphic scheme and to correct some names are not used. The first of her cited papers is only mentioned. I may disagree with some of her identifications, but her attempts are important enough to be considered rather than leaving part of the Pennsylvanian column of the Urals devoid of corals. The erroneous or undocumented generic names given by the authors, such as *Amandophyllum*, *Amplexus*, *Campophyllum*, *Caninia*, *Hapsiphyllum*, *Lophophyllum*, *Lytvophyllum*, and *Profischerina*, are less important compared to the other issues discussed above.

I fully agree with Wang *et al.* (2021) that “more detailed works on coral taxonomy are required, which are helpful for providing precise coral biostratigraphy and correlations“. This issue was already addressed in my plenary lecture at the Sendai Symposium (Fedorowski 2001), but not much has happened with regard to this issue since then. The paper by Wang *et al.* (2021) does not improve the matter.

The global succession and the lower/middle Carboniferous turnover of rugose coral fauna proposed in this paper is broadly consistent with my statement (Fedorowski 1981a, p. 132) that the “lower boundary of the Bashkirian, as far as the coral fauna is concerned, may be lowered to the base of the Chokierian Stage, at which level a number of new taxa first appeared.” However, new data collected since then and new boundaries proposed for the Viséan/Serpukhovian and Serpukhovian/Bashkirian have necessitated several modifications. I continue to consider the development of the Carboniferous and Permian rugose coral fauna in “a single evolutionary cycle ... divided into three phases” (Fedorowski 1981a, p. 141), subdivided into subphases. The present discussion begins with the third subphase of the lower Carboniferous phase, comprising the Viséan and the Serpukhovian, because “there is no evidence to support the separation of Namurian Series [= lower Namurian A, i.e., Pendleian and Arnsbergian

Substages], or Serpukhovian Series as independent phases in coral evolution” (Fedorowski 1981a, p. 141). The new data fully support this early conclusion.

Although Viséan corals are treated together with the Serpukhovian corals as belonging to a common subphase in the evolution of rugose corals, most of the upper Viséan coral fauna in the world is omitted in these considerations. Only brief mention is made of new and important developments in the study of rugose corals, such as the collections from southern Spain, North Africa and Canada. The detailed discussion on the succession of upper Viséan rugose corals in the Donets Basin is an exception. It is treated here as a necessary introduction to the Serpukhovian/Bashkirian rugose corals turnover. The generic content of the upper Viséan Rugosa of the Donets Basin closely resembles that of the Moscow Basin, the Ural Mountains, Novaya Zemlya, Western and Central Europe, and North Africa. North American upper Mississippian corals (with the exception of the Maritime Coral Province) are difficult to correlate with European and Asian taxa if only stages or lithostratigraphic units are indicated as their occurrences. However, new data (see Palaeogeographic Overview) have documented several upper Viséan North American taxa in common with Eurasian taxa. Thus, the almost worldwide, except for Australia, relationship of upper Viséan rugose corals is well-documented. The Serpukhovian, on the other hand, was a period of rapid or gradual separation of particular rugose coral species sites worldwide, both due to glaciation as a global factor and local tectonic changes. Environmental changes during the Mezhevian in the Donets Basin can be cited as an early example.

The Serpukhovian succession of rugose coral fauna in the Donets Basin and in the North African basins have been studied at a comparable level of detail. Moreover, the content of genera in these two areas is similar. Both areas can be considered as refugia, although the upper Viséan species, which continued to develop in the Serpukhovian, significantly predominate in the North African assemblages. In the Donets Basin, species common for both the upper Viséan and Serpukhovian are limited to a few at the expense of new species (Text-fig. 1). This difference may document an early stage of patchy distribution of rugose coral sites. The Ural Mountains, Novaya Zemlya and the southern provinces of China also contain several upper Viséan species in Serpukhovian strata, but their successions are not detailed enough for a thorough comparison. The Akiyoshi Terrane in Japan should be mentioned as the site of a rugose coral fauna poorly responsive to the Serpukhovian/

Bashkirian crisis. Moreover, its peculiar and mostly endemic Family Pseudopavonidae flourished during this critical period. This may have been due to both the continued friendly environment and the geographical isolation of the area. The great diversity of rugose corals in the Donets Basin near the upper Serpukhovian boundary (Limestone D₅⁵) and their almost complete disappearance from the uppermost Serpukhovian deposits is a peculiarity of this basin, so far not recognised in any other area.

In contrast to the aforementioned areas representing refugia for the Viséan rugose corals, the Rugosa from several other areas of the world have been either impoverished or eliminated in different stratigraphic levels of the Serpukhovian. Impoverished Serpukhovian coral fauna is found in northern and southern Spain and in the south-eastern and western Interior Provinces of North America. A somewhat impoverished fauna of upper Viséan rugose corals continued to occur in southern Scotland, but the rest of Western and Central Europe lost its rich Brigantian (upper Viséan) corals. Those of the Pendleian of the Lublin Coal Basin (Poland) may be noted as an exception. However, this basin represents the western part of the Ukrainian Lviv Basin and should rather be correlated with the Eastern European basins. A short-lived Serpukhovian fauna of the Upper Silesian Coal Basin is mentioned below as an exception.

To summarise the succession of Serpukhovian rugose corals, the following points should be made: 1) The turnover of the upper Viséan/Serpukhovian fauna is accentuated differently in different parts of the world. It may be poorly recognised, as in the Canadian Cordillera and the Akyoshi Limestone in Japan, or relatively sudden and drastic, as in Western and Central Europe. In general, the persistence, reduced diversity and/or disappearance of the rugose coral fauna depend on local environmental changes. For example, the Sudetic Orogeny, which uplifted many coral-rich areas up to and including the late Viséan, was the main factor acting in Europe, whereas glaciation can be pointed to as a global cause; 2) The disappearance of the uppermost Viséan and Serpukhovian, time- and area-differentiated rugose coral fauna resulted in the formation of their patchy occurrences during the Serpukhovian (Text-fig. 3).

Bashkirian rugose corals are documented from many areas of the world (see Palaeogeographic Overview). Some areas, such as the former Yugoslavia, Czech Republic or Indochina have been omitted from this discussion as they have no new data. Also, the detailed sequence of the disappearance of Mississippian genera and the appearance of Pennsylvanian genera

cannot be established worldwide in comparable detail. Thus, the detailed successions documented in the Donets Basin and the North African basins will remain as examples until a revised coral taxonomy, superimposed on modern stratigraphy, is established for such important areas as the Urals, Novaya Zemlya and China. The Palaeogeographic Overview has shown how much doubt remains in both these aspects. It can only be pointed out that the *Eumorphoceras* Genozone was a period of worldwide deterioration of the Rugosa. The extinction reached its peak with the end of this genozone, while the *Homoceras* Genozone hosted both several Mississippian genera and the first appearances of representatives of Pennsylvanian genera. Unfortunately, the lack of rigid comparable data precludes the establishment of the exact level of appearance of several of the most common Bashkirian genera and the directions of their migrations. Thus, only the following are listed: *Bothrophyllum*, *Colligophyllum*, *Cystolonsdaleia*, *Dibunophylloides*, *Fomichevella*, *Heintzella*, *Heritschioides*, *Kumpanophyllum*, *Opiphyllum*, *Paraheitschioides*, *Petalaxis*, *Protodurhamina*, *Protokionophyllum*, *Yuanophylloides*, and the Chinese genera related to *Kumpanophyllum* and *Colligophyllum*. Not mentioned are the names of endemic genera and of the so-called ‘*Caninia*’ and ‘*Protozaphrentoides*’ fauna occurring in the different Bashkirian strata of all the sites discussed in the Palaeogeographic Overview. In my opinion these names cover several different Bashkirian and younger genera.

The irregular distribution of corals, typical of the Serpukhovian, continued during the Bashkirian. The locations of sites with rugose coral fauna and their taxonomic content were environmentally controlled. Also, connection between individual basins, if any, was limited as evidenced by the diverse rugose coral fauna of individual basins. The Donets, Moscow and Voronezh Basins, located in close proximity to one other, illustrate this suggestion well. The uplifted Moscow Basin lacks Bashkirian corals, the Donets Basin contains only solitary corals, both dissepimented and non-dissepimented (Text-fig. 2), while in the Voronezh Basin there are mostly colonial taxa, such as *Fomichevella*, *Lytvophyllum* (= *Colligophyllum*), ‘*Dorlodotia*’, *Opiphyllum*, *Protodurhamina*, ‘*Pseudodorlodotia*’, *Petalaxis* and *Aulina*. The ‘sudden’ appearance of such a diverse fauna suggests its immigration from somewhere, but the area of origin cannot be indicated. Probably the earlier occurrence of *Fomichevella* in northern Spain and North Africa may point to these areas, while the whole assemblage, the ‘*dorlodotias*’, and *Aulina*, may

suggest immigration from southern China, but the lack of rigid stratigraphic data in the occurrence of most Chinese taxa precludes well-supported conclusions on this matter.

The patchy differentiation in the occurrence and content of the rugose coral faunas can also be applied to some other basins. The Cantabrian Mountains have an impoverished Bashkirian fauna, southern Spain lacks Bashkirian corals, while a rich and diverse fauna has been described from basins in North Africa and the Midcontinent Province in North America. In contrast, other provinces of North America are either depleted of early and middle Bashkirian corals or the coral fauna in these provinces is impoverished (see Palaeogeographic Overview).

The rare taxa common to the Donets Basin, appearing among the rich and diverse fauna of rugose corals found in the *Reticuloceras* Genozone in the Midcontinent Province of North America, suggest a limited relationship between the two basins (see above). However, most of the genera, both non-disseminated and disseminated, differ. The latter, commonly identified by American scientists (e.g., Newell 1935; Moore and Jeffords 1945; Rowett and Sutherland 1964; Cocke 1970) as *Dibunophyllum* and *Neokoninckophyllum* are of particular value because they are very common in North America up to and including the lower Permian (Ross and Ross 1962, 1963). Some common features in the early ontogeny of *Yuanophylloides* and the primitive North American '*Dibunophyllum*' may suggest an affinity between these two lineages. This will eliminate the North American '*Dibunophyllum*' from the Subfamily Dibunophyllinae when/if proven. The Bashkirian Rugosa from North America, found mainly in the upper Bashkirian, cannot be arranged in a well-documented succession (see Palaeogeographic Overview). The same is true for the Cantabrian Mountains in northern Spain, where the Bashkirian corals form a kind of introduction to the rich and diverse Moscovian fauna. Rare corals occurring in the Hassi Kerna Formation in North Africa have been recognised by Cózar *et al.* (2015, p. 8) as late Bashkirian. These rare and poorly preserved specimens ended the occurrence of Rugosa in North Africa.

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