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Rimma R. Khodjanyazova
Boise State University

Vladimir I. Davydov
Boise State University

Isabel P. Montañez
University of California - Davis

Mark D. Schmitz
Boise State University

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Climate- and Eustasy-Driven Cyclicality in Pennsylvanian Fusulinid Assemblages, Donets Basin (Ukraine)

Rimma R. Khodjanyazova
Department of Geosciences
Boise State University
Boise, ID

Isabel P. Montañez
Department of Earth and Planetary Sciences
University of California
Davis, CA

Vladimir I. Davydov
Department of Geosciences
Boise State University
Boise, ID

Mark D. Schmitz
Department of Geosciences
Boise State University
Boise, ID

Corresponding author: Khodjanyazova1960@gmail.com

Abstract

A model of cyclic recurrence (~0.6 – 1.2 myr) of three fusulinid assemblages in the Middle Pennsylvanian siliciclastic-carbonate succession of the Donets Basin is proposed. Each cycle records progressive turnover of assemblages in shallow marine environments in response to sea-level and regional climate change. A *Hemifusulina*-assemblage (A), adapted to cooler and reduced salinity seawater records the onset of sea level rise accompanied by humid climatic conditions. Sea level high stand is captured by the *Beedeina*–*Neostaffella*–*Ozawainella*–*Taitzeoella* (or *Beedeina*-dominated) assemblage (B), characteristic of relatively deeper-water environments. The B assemblage is successively replaced by the most diverse population of the warm-water *Fusulinella*-dominated assemblage (C). This assemblage, which occurs in the upper limestones of each fusulinid cycle records the onset of sea level fall accompanied by a shift to drier conditions and likely increased seawater salinity.

The proposed model permits robust interbasinal correlation of the Pennsylvanian successions of the Tethyan realm. Fusulinids of the A and C₂ assemblages are the most provincial and therefore the most useful for paleogeographic reconstructions. Specifically, they delineate originally contiguous regions that subsequently were dispersed hundreds to thousands of kilometers, whereas fusulinids of the B assemblage hold the highest potential for global correlation. Extinction at the Moscovian – Kasimovian transition of fusulinid genera of the A and B assemblages, which inhabited predominately cooler and normal salinity (perhaps hyposaline) waters, can be explained by the onset of global warming in the earliest Late Pennsylvanian. Fusulinid assemblages define various types of distribution patterns that differ by tectonic setting of the studied basins suggesting that fusulinid assemblage patterns hold potential for reconstructing the paleogeography and tectonic evolution of Pennsylvanian basins of eastern Laurasia.

Keywords: Donets Basin; foraminifera; paleoecology; late Paleozoic sea level; Pennsylvanian paleoclimate; sequence stratigraphy

1. Introduction

Collision of Gondwana and Laurussia during the Pennsylvanian created the Trans-Pangean mountains belt that spanned much of the tropical region of Pangaea (Becq-Giraudon et al., 1996; Keller and Hatcher, 1999; Martinez Catalan et al., 2002; Martin, 2011). Widespread paleotropical rain forests (Greb and DiMichele, 2006) extended to the north of this orogenic belt leading to the formation of economically productive coal seams in the Donets Basin, western Europe, North America, and northern China (Aisenverg et al., 1975; Phillips et al., 1985). Permo-

Carboniferous stratigraphic cyclothems, the hallmark of deposition in the shallow epicontinental seas surrounding Laurussia (Heckel, 2008), have long been inferred to record global sea-level fluctuations (glacioeustasy) in response to the waxing and waning of vast continental ice sheets in southern Gondwana continent (e.g. Wanless and Shepard, 1936; Veevers and Powell, 1987; Heckel, 1994, 2008).

Evolution of our understanding of the Late Paleozoic Ice Age (LPIA) over the past few decades suggests a series of multiple discrete (1-7 myr duration) and possibly asynchronous glaciations separated by interglacial intervals of comparable duration and associated with substantially diminished ice volume (Isbell et al., 2003; Montañez et al., 2007; Fielding et al., 2008a; Bishop et al., 2010; Montañez and Poulsen, 2013). Study of Permo-Carboniferous terrestrial successions further document shifts in regional climates and paleotropical floral distributions that appear to have occurred in concert with glacial-interglacial fluctuations over a range of temporal scales from eccentricity to millions of years (summarized in DiMichele et al. 2009; Montañez and Poulsen, 2013). Near-shore coal-bearing basins, such as the Donets Basin, Ukraine, offer the unique opportunity to evaluate the response of terrestrial and marine ecosystems to glacioeustasy and climate change. The most persistent middle Pennsylvanian (the late Bashkirian, Moscovian, and early Kasimovian, or the most of Westphalian and Cantabrian) humid episode (Aisenverg et al., 1975), recorded in the Donets Basin, lasted about 10 myr. This time coincides with an appearance of several genera, such as *Beedeina*, *Hemifusulina*, *Neostaffella*, *Taitzeoella*, which became extinct at the Middle – Late Pennsylvanian boundary, when the climate became more arid. Aridization in the Donets Basin is recorded by a considerable reduction of moisture-like plants and deposition of evaporate in the late Pennsylvanian (Aisenverg et al., 1975; Fisunen, 2000; Eros et al., 2012). Simultaneous biotic crises, both on land and in shallow epicontinental seas, point on a sensitivity of marine benthos to climate changes. Although previous studies have been documented the impact of sea-level fluctuations on biodiversity and extinction events (Bretsky and Bretsky, 1975; Heckel and Baesemann, 1975; Hallam, 1981; Baird and Brett, 1983; McGhee, 1991; Magniez-Jannin, 1992; Brett et al., 1990, 2007), little is known about the effects of sea-level changes on the distribution of the late Paleozoic fusulinids.

This paper addresses the response of Pennsylvanian fusulinids to global sea-level fluctuations and regional climate change using integrated paleontological and sedimentological observations. The Pennsylvanian succession from the Donets Basin (Ukraine) provides a near continuous record of the response of epicontinental deposition to environmental change during the dynamic climate history of the LPIA given the documented high rates of Pennsylvanian subsidence (Izart et al., 2003; Eros et al., 2012). High-precision radiometric ages (Davydov et al., 2010) provide a calibrated chronostratigraphic framework for detailed lithostratigraphic, biostratigraphic, and cyclostratigraphic study. We document repetitive, low frequency (0.6 – 1.2 myr) fusulinid distribution patterns and propose a new paleoecological model, which is mechanistically linked to global sea-level fluctuations and regional climate. The proposed model is a useful tool for refine biostratigraphy, regional and global correlation. Symmetrical and asymmetrical patterns of fusulinid distribution documented in this study hold promise for the reconstruction of the paleogeography and tectonic evolution of Pennsylvanian basins that developed along the south-eastern and eastern margins of Laurussia.

2. Fusulinid paleoecology

A rapid evolutionary rate among fusulinids was noted in the last century by stratigraphers who successfully employed these fossils for detailed regional correlations. Groves and Lee (2008) documented that a taxonomic expansion of fusulinids coincides with the onset of the LPIA. Although most of the Late Paleozoic benthic foraminifera, including all larger foraminifera, such as fusulinids, became extinct by the end of the Permian Period, fusulinid paleobiology and their environmental constraints are relatively well understood, as they have been inferred from studies of recent benthic foraminifera (Leppig et al., 2005; Ross, 1982; Ross and Ross, 1995; Stevens, 1966, 1969, 1971; Vachard et al., 2004).

Fusulinids were confined to the tropical-subtropical belts 30–40° S and N of the equator, and occupied shallow-water depositional basins characterized by carbonate or mixed carbonate-siliciclastic sedimentation (Ross and Ross, 1995; Kobayashi and Ishii, 2003). The paleogeographic distribution of fusulinids, their sensitivity to paleoenvironments, and their high-resolution temporal framework during the Pennsylvanian provide a basis for this study. Temperature is generally considered to be the major physical factor that controls the distribution of species or assemblages (BouDagher-Fadel, 2008; Hohenegger, 2004). As the benthic foraminifers are poikilothermic organisms, (i.e. their body temperature is very close to the temperature of the ambient water), they likely responded quickly to small changes in water temperature (Beavington-Penney and Racey, 2004).

Many important observations on the spatial and temporal distribution of late Paleozoic fusulinids have been made over the past century. Early paleoecological studies revealed a differentiation of fusulinid assemblages with type of substrate, hydrodynamic activity, water depth, and their association with other benthic organisms (Rauser-Chernousova and Kulik, 1949; Ross, 1961, 1967, 1969, 1971, 1972, 1982; Ginkel, 1965, 1973; Bensch, 1982). Ross (1969) first recognized that fusulinids occur in two associations: (1) a monospecific assemblage associated with siliciclastic rocks, and (2) a diverse fusulinid assemblage, found in carbonates, associated with an overall diverse marine biota.

Monospecific fusulinid occurrences have been noted in many previous Carboniferous studies (Bogush, 1963; Ginkel, 1973; Bensch, 1982; Villa and Bahamonde, 2001; Baranova and Kabanov, 2003). Two Pennsylvanian genera, the Moscovian *Hemifusulina* and the mid-Kasimovian *Ferganites*, commonly occur as monospecific assemblages. In the orogenic belts of the Cantabrian Mountains and Central Asia, the *Hemifusulina*- and *Ferganites*-assemblages are associated with lenses of sandstones and siltstones within thick conglomerates (Bogush, 1963; Villa and Bahamonde, 2001). In intracratonic regions, such as the Moscow and Donets Basins, monospecific assemblages of the *Hemifusulina* are associated with clay-rich limestones (Baranova and Kabanov, 2003; Khodjanyazova et al., 2011). The mid-Kasimovian *Ferganites* is absent in intracratonic basins. It is noteworthy that both of these genera (*Hemifusulina* and *Ferganites*) have a similar morphology: small proloculi, subcylindrical shape, rounded axial ends, symmetrically and regularly developed septal folding, and a porous wall structure.

Ross (1969), based on the spatial distribution of the genus *Triticites* in upper Pennsylvanian strata of Texas, proposed a relationship between test morphology and bathymetry. He suggested that some elongate subcylindrical species of *Triticites*, associated with silt-rich limestone and fine sandstone, may indicate shallow interdistributary bays and lagoons. Small fusiform representatives of *Triticites* are most common in poorly sorted limestones that were probably deposited in restricted waters or depths below fair-weather wave base. Large fusiform specimens of *Triticites* are associated with shallow-water algal meadows.

Stevens (1969, 1971) studied diversity and distribution patterns of the middle Pennsylvanian fusulinids from McCoy, Colorado with respect to water depth and distance from the shore. He proposed a model in which the shallowest assemblage is represented by juvenile forms which “are found in small numbers in rocks deposited in water as shallow as 4 meters” (Stevens, 1971, p. 410). Farther from the shoreline, abundant large mature fusulinids are found in “rocks deposited more than 3 km offshore in water with a minimum depth of 13 meters” (Stevens, 1971, p. 410). He suggested that the maximum depth limit for fusulinid habitation was approximately 22 m deep. The non-fusulinid, smaller foraminifers *Bradyina* and *Palaeotextularia* occur abundantly in rocks “deposited in water 15 meters deep, 3.5 km offshore” (Stevens, 1971, p. 411).

Dzhenchuraeva (1975), using algae as a proxy of bathymetry, recognized three assemblages among the late Bashkirian – early Moscovian fusulinids of Central Asia. The shallowest-water *Schubertella*–*Pseudostaffella* assemblage co-exists with the green algae *Beresella*. The deeper-water predominately *Profusulinella*-assemblage is associated with a mixture of the green algae, *Beresella* and the red algae, *Ungdarella*. The deepest-water *Neostaffella*–*Ozawainella* assemblage occurs solely with the red algae *Ungdarella*. Subrhomboidal species of *Beedeina* and *Taitzehoella*, their first occurrence documented as early Kashirian, are also associated with the deeper-water assemblage (Dzhenchuraeva, 1975).

The first documentation of the stratigraphic recurrence of Pennsylvanian fusulinid assemblages was made in the Moscow basin (Rauser-Chernousova and Kulik, 1949; Rauser-Chernousova, 1953; Rauser-Chernousova and Reitlinger, 1962; Reitlinger and Balashova, 1954). Rauser-Chernousova and Reitlinger (1962) demonstrated that the cyclic occurrence of fusulinids delineate evolutionary trend, with turnover of assemblages recorded in each depositional cycle (cyclothems). They concluded that within each depositional cycle, the repeated occurrence of Pennsylvanian fusulinid assemblages records the adaptation of different genera to environmental change (Rauser-Chernousova and Reitlinger, 1962). They distinguished a monospecific *Hemifusulina*-assemblage from the other diverse assemblages of fusulinids and linked the occurrence of this genus with a specific type of substrate, in particularly, with clay-rich limestone.

This study, based on correlation of the Moscovian strata in the Donets and Moscow Basins and analysis of the distribution of fusulinid assemblages in the other Tethyan basins with various tectonic and depositional settings, recognizes that the *Hemifusulina*-dominated assemblages simultaneously and repeatedly appeared over a broad area of tropical belt in the eastern margin of Laurussia in the short periods of geological time and were replaced consistently by *Beedeina*-, *Fusulinella*-, and *Fusulina*-dominated assemblages. In this paper, we discuss possible causes of reoccurrences of fusulinid assemblages in stratigraphic successions. We suggest that cyclic pattern in fusulinid distribution was governed by two main driving forces: global sea-level and regional climate changes, both of which were responsible in the fluctuation of physical parameters of shallow-water marine paleo-environment, in particularly, water temperature and salinity.

3. Geologic setting and lithostratigraphy of the Donets Basin

The Donets Basin is the southeastern segment of the Pripyat–Dniepr–Donets intracratonic rift structure. The basin, approximately 200 km wide and 700 km long (Fig. 1), it is located on the southern rampart of the East European craton between the Voronezh crystalline massif to the northeast and the Ukrainian crystalline massif to the southwest, and extends from the Baltic Sea to the Caspian Sea across Belarus, Ukraine, and Russia (Aisenverg et al., 1975; Khain, 1985, 1994; Stovba et al., 1996; Stovba and Stephenson, 1999). The basin is filled with 7 to 16 km of Silurian–Devonian prerift and synrift volcano-siliciclastics and Carboniferous–Lower Permian postrift sedimentary strata with the thickness of the deposits increasing from the central and westernmost Dniepr–Donets Trough to the Donets Basin (Chekunov, 1994; Stovba et al., 1996; Ulmishek, 2001). The Donets Basin is generally considered to have been uplifted during the Early Permian in response to the buildup of stresses emanating from the Hercynian–Caucasus–Uralian orogenies (Milanovsky, 1992) or to the activity of an asthenospheric mantle diapir (Chekunov, 1994; Gavrish, 1989).

Carboniferous–Permian deltaic-marine strata in the Donets Basin include coals and shallow-marine limestones characterized by specific biotic communities. The limestone beds can be traced across much of the Donets Basin, reflecting the low slope ($< 1^\circ$) of the depositional ramp (Eros et al., 2012). The Donets depositional ramp extended for thousands of kilometers along the western and northern edges of the warm tropical Tethyan Ocean (Alekseev et al., 1996). Essentially isochronous biostratigraphically dated limestones provide laterally extensive marker beds that underpin a detailed chronostratigraphic framework for the Donets Basin (Aisenverg et al., 1963; Makarov, 1985). The Carboniferous – Permian cyclic sequences are divided into major cycles or suites designated by Latin letters (e.g., Aisenverg et al., 1975). Major marine limestones are designated by capital letters and numerals, which indicate the stratigraphic order (e.g., M₁ indicates the first limestone of the “M” formation). Lower case letters indicate coal seams; numbers indicate the stratigraphic order (e.g., m₃ is the third coal seam of the “M” formation). The Moscovian Stage in the Donets Basin comprises the upper part of the “K” formation, “L”, “M” formations, and the lower part of the “N” formation (Einor, 1996).

Recent lithostratigraphic studies (Izart et al., 1996; Eros et al., 2012) provide sequence stratigraphic models for the Donets Basin that define systematic high-frequency (100 kyr), which bundle into composite (~400 kyr) and longer-term ‘composite sequences’ (Eros et al., 2012). The internal architecture of composite sequences preserves a genetically related set of strata that collectively record a hierarchy of relative sea-level changes (Eros et al. 2012). Composite sequence boundaries commonly coincide with widespread unconformities that extend to the seaward margin of the study area.

4. Fusulinid biostratigraphy

During the first half of the twentieth century fusulinids became an important chronostratigraphic tool that was widely utilized in the Donets Basin. Putrja (1939, 1940, 1948, and 1956) and Kireeva (1951) developed the fusulinid biostratigraphy within the Moscovian – Kasimovian transition in the Donets Basin. They correlated the “L”, “M” formations as Kashirian and Podolskian respectively. The lower part of the “N” formation from limestone N₁ to the N₄ or N₅ limestone was correlated with Myachkovian strata in the Moscow Basin. Subsequent research (Solovieva, 1986; Vachard and Maslo in Izart et al., 1996; Ueno in Fohrer et al., 2007) accepted the biozonation proposed by Kireeva (1951). A recent detailed biostratigraphic study (Khodjanyazova et al., 2011; Khodjanyazova et al., 2012) revealed an inconsistency in the generally accepted Donets biostratigraphy and proposed a new biostratigraphic zonation (Fig. 2; see Section 7.1).

5. Methodology

Samples for this study were collected from 28 successive limestones within the “L”, “M”, and “N” formations (Kashirian, Podolskian, Myachkovian and Krevyakian Regional Substages). Existing fusulinid distribution data was integrated with the results of this study (Brazhnikova, 1939a, 1939b, 1951; Putrja, 1940, 1956; Manukalova, 1950a, 1950b; Pogrebnyak, 1975; Ueno in Fohrer et al., 2007; Davydov and Khodjanyazova, 2009).

More than 500 thin sections were examined for fusulinid diversity, taxonomy and morphology and to refine micro- and bio-facies using the approach of Flugel (2004). A detailed description of the facies from the “L” and “M” formation can be found in Supplementary Data (Supplementary Tables 1 and 2). Supplementary Table 1 presents a distribution of fossils within each cycle from limestone L₇¹ to M₁₀, whereas Table 2 provides fusulinid species and smaller foraminifer genera data.

Lithofacies packages containing climate-sensitive deposits (e.g., evaporates and coals) in which the fusulinid-bearing limestones are enclosed, were analyzed in order to interpret a response of different fusulinids to climate change. The relationship of each fusulinid-bearing limestone to the composite sequences proposed by Eros et al. (2012) was evaluated and used to reconstruct the sea-level history and assess changes in fusulinid assemblages during each sea-level cycle.

The geographic distribution of fusulinid assemblages was reconstructed by integrated paleobiogeographic and biostratigraphic analyses. A restricted paleogeographic distribution of a particular assemblage was inferred as a lowstand of sea level, whereas a broader geographic distribution of a particular assemblage is interpreted as high stand (Brett, 1998).

6. Cyclic patterns of fusulinid distribution and their relation to sea-level and climate changes: A model

Pennsylvanian fusulinid biostratigraphy of the Donets Basin documents a systematic repetition of fusulinid generic assemblages that show a consistent relationship with composite sequences, which were previously defined by Eros et al. (2012) (Fig. 3). These biocycles, referred to as fusulinid cycles, are recognized in the “K”, “L”, “M”, and “N” formations of the Moscovian–Lower Kasimovian succession. Each fusulinid cycle includes two composite sequences, which based on their estimated duration, suggests the biocycles record ~ 0.6–1.2 myr (Fig. 4). Available material permits a detailed study the interval of the “M” formation (Fig. 3). Each cycle consists of four to six successive fusulinid-bearing limestones and reveals a progressive increase in diversity accompanied by the gradual appearance or disappearance of certain genera of fusulinids (Fig. 4). The lower part of each cycle (LTST – lower transgressive system tract, or the limestones deposited during an initial sea level rise, Fig. 3) contains limestones with a monospecific population of *Hemifusulina* assemblage (A). The middle limestones (HST – highstand system tract, or the limestones deposited at high sea level stand) in each cycle are characterized by a moderately diverse *Beedeina* assemblage (B). The uppermost limestones (ULST – upper low sea level stand includes the limestones deposited during a lowering of sea level) in each cycle contain a highly diverse *Fusulinella* assemblage (C). The following assemblages are recognized within each fusulinid cycle:

- A₁ is a monospecific population of abundant *Hemifusulina* (Figs. 3, 5.13). Associated biota is represented by abundant heterozoans (Figs. 6A, 6B, 6C). This assemblage occurs in the limestone M₃^{up}, and M₇.
- A₂ is a mixture of abundant *Hemifusulina* (Figs. 3, 5.1, 5.2, 5.12, 5.17, 5.18) and scarce *Taitzeoella* (Figs. 3, 5.4, 5.16), *Beedeina* (Figs. 3, 5.10), *Ozawainella* (Figs. 3, 5.3, 5.6, 5.9, 5.14), and *Neostaffella* (Figs. 3, 5.5, 5.8, 5.11, 5.15). This assemblage is documented in the L₇¹, M₇^{up}, and N₁ limestones.
- B is a moderately diverse community of the mature subrhomboidal *Beedeina* (Figs. 3, 7.1–7.3, 7.9–7.11) and *Taitzeoella* (Fig. 3, 7.6, 7.17), large discoid *Ozawainella* (Figs. 3, 7.4, 7.5, 7.14–7.16) with highly compressed polar ends, and the large spherical *Neostaffella* (Figs. 3, 7.7, 7.8, 7.12, 7.13). *Hemifusulina* disappears or is scarce in this assemblage. The B assemblage occurs in the L₇, M₁, M₅, M₈, and N₁⁶, and N₄ limestones. Smaller foraminifers characterized by *Bradyina*, *Endothyra*, rare textulariid; attached foraminifers are also present (Figs. 8A, 8B; Suppl., Table 2). Red algae *Ungdarella* (Fig. 8A) and abundant, highly degraded detritus of heterozoan are associated with this assemblage. Scarce trilobite fragments are recognized.

- C_1 is a diverse population of the abundant *Fusulinella* (Figs. 3, 9.3, 9.17, 9.21, 10.11) and *Schubertella* (Figs. 3, 9.4, 9.5, 9.22, 9.24, 10.13, 10.14). Elongated fusiform species of *Taitzeoella* (Figs. 3, 9.2, 9.18) and *Beedeina* (Figs. 3, 9.1) replace subrhomboidal species of *Taitzeoella* and *Beedeina* documented in the B assemblage; *Ozawainella* (Figs. 3, 9.6, 10.19) is less compressed at polar ends; *Neostaffella* evolves into new species (Figs. 3, 9.7, 10.16) and is partly replaced by *Pseudostaffella* (Figs. 3, 9.19, 9.23, 10.17, 10.18). Associated biota occurs as abundant smaller foraminifers, especially, *Bradyina* and *Paleotexularia* and scarce heterozoan fauna (Figs. 8C, 11B). Genera of red and green algae are present (Figs. 8C, 11B; Suppl. Table 1). This assemblage occurs in the L_5 , M_2 , M_6 , M_9 , N_1^2 , and N_5 limestones.
- Each cycle is completed by the C_2 assemblage represented by diverse species of *Schubertella* (Figs. 3, 9.15, 9.16, 10.2, 10.7, 10.22, 10.23) and *Fusulinella* (Figs. 3, 9.10, 9.13, 10.3, 10.4, 10.21); the latter stratigraphically evolved into Krevyakian (early Kasimovian) *Protriticites* and *Obsoletes*. The elongated fusiform species of *Beedeina* (Figs. 3, 9.8, 9.9), which occur in the upper part of the lower Kashirian cycles, are replaced by elongated subcylindrical *Fusulina* (Figs. 3, 10.20) in upper Kashirian limestones (M_6^{up}). The latter evolved into Podolskian *Fusulina* (*Kamaina*) occurred in the limestone M_{10} (Figs. 3, 10.9), Myachkovian *Fusulina* ex gr. *cylindrica* documented in the limestone N_2 and Krevyakian *Quasifusulinides* occurred in the limestone N_5 . Large *Neostaffella* (Figs. 3, 9.12, 10.1, 10.25) occur together with abundant small species of *Pseudostaffella* (Figs. 3, 9.14, 10.5, 10.6, 10.26). Kashirian *Taitzeoella* (Figs. 3, 9.11, 10.24) is replaced by Podolskian elongated-fusiform *Fusiella* (Figs. 3, 10.8) in the limestone M_{10} , whereas *Ozawainella* is replaced by smaller subrhomboid species (Fig. 3). Only green algae present (Fig. 8D) and scarce corals occur with benthic fauna of the C_1 assemblage (Fig. 11D). This assemblage occurs in the limestones M_6^{up} , M_{10} , N_2 , N_3 , and N_5 .

For simplicity we consider three assemblages A, B, and C (Figs. 4, 12). A_1 and A_2 assemblages are combined into the *Hemifusulina*-dominated assemblage (A). B is the *Beedeina*-dominated assemblage; C_1 and C_2 are combined into the *Fusulinella*-*Fusulina*-dominated assemblage (C). From one biocycle to another all fusulinid genera exhibit evolutionary changes at the species level that enable a biozone definition and correlation with coeval strata from the Moscow Basin (Khodjanyazova et al., 2012; Khodjanyazova and Davydov, 2013) and other basins of the Paleotethys. A similar trend of the fusulinid distribution is recognized in the Moscow Basin (Khodjanyazova et al., 2012).

A paleogeographic analysis of the fusulinid distribution in the Tethyan realm documents the widespread occurrences of the B and C_1 assemblages (Fig. 13), documented in off-shore successions in the Pamir (Leven, 1998), central and eastern Iran (Leven et al., 2006), the Cantabrian Mountains (Ginkel, 1965), southern Urals (Ivanova, 2008), northern China (Lee et al., 1930; Sheng, 1958) and Japan (Ota, 1977). Widespread distribution of these assemblages in the Tethyan realm would have been favored during periods of maximum sea level rise (Brett, 1998). Therefore, we propose that the B and C_1 assemblages were adapted to deeper-water environments that expanded during sea level rises (EHSL – early high sea level stand, LHSL – late high sea level stand) (Figs. 4, 12, 13). The presence of abundant red algae, however, suggests water depths of their habitat were restricted to a few tens meters (Fig. 12), given that they utilize both the red (long wave) and blue (short wave) portions of visible light that penetrates into the surface water (Wray, 1977; Bjorlykke, 2010).

In contrast, two assemblages, the A and the C_2 have restricted occurrences in the Tethyan realm (near-shore Moscow and Donets Basins; Fig. 13). Basinward in the eastern part of the East European craton (Fig. 13), the A assemblage disappears, and biocycles are represented by fusulinids of the B and C_1 assemblages (Dalmatskaya, 1961; Ivanova, 2008). Very shallow near-shore marine environments, inhabited by both A and C_2 assemblages (ETSL – early transgressive sea level stand developed during initial sea level rise, ELST – early low sea level stand developed during a lowering of sea level) might be very sensitive to regional climate change within short time slices (Figs. 3, 12, 13).

Biofacies analysis of the *Hemifusulina*-bearing limestones (Figs. 6A, B, C, and D) reveals an abundance of the heterozoans fauna: suspension and sediment feeders, such as brachiopods, crinoids, bryozoans (See also Suppl. Table 1). Micro-facies analysis of these limestones indicates a presence of non-oxidized organic matter within cement (or, Figs. 6A, B, and C). Pre-compaction, microspar cements lining and partially occluding primary porosity in the *Hemifusulina*-bearing limestones (Figs. 6A, B, C, and partly D) are interpreted as having formed from the infiltration of meteoric water during early diagenesis, suggesting minimally subhumid to humid conditions (Neiman and Read, 1988; Moore, 1989; James and Choquette, 1990).

Analysis of climate sensitive lithofacies (coals, evaporates) in the Donets Basin reveals that the lower limestones (LTST) of fusulinid cycles, characterized by a *Hemifusulina* assemblage, are enclosed within a package of fine siliciclastics intercalated with abundant coal seams that further support their formation under relatively humid conditions (Cecil and Dulong, 2003a). Hypothesized high mean annual precipitation, elevated rates of river discharge to coastal regions, and increased geochemical and physical erosion of uplands and high mountains (Carey et al., 2006), would have increased input of nutrients and suspended and dissolved organic matter to near-shore regions of the shallow epicontinental seas (Cecil et al., 2003b, 2003c). High level of nutrients may have driven increased primary productivity and expansion of heterozoan fauna during deposition of the *Hemifusulina*-bearing lower limestones (LTST) of each fusulinid cycle.

Hemifusulina evolved from cycle to cycle permitting a robust correlation of strata successions deposited in various tectonic and lithological settings. Coeval *Hemifusulina*-bearing clay-rich limestones in the Moscow Basin are intercalated with dolomites (e.g. Smedva Formation), which have been interpreted to have formed in very shallow marine conditions (Makhlina et al., 2001).

The A assemblage also occurs in near-shore basins of the orogenic belts, the Cantabrian Mountains, Sama Fm. (Ginkel, 1973) and Central Asia (Bogush, 1963). In these localities, Moscovian strata are represented mainly by cyclic coarse-grained fining upward siliciclastic successions with thick conglomerates at the base of each depositional cycle. *Hemifusulina*-bearing sandy limestones documented within the lower (the most coarse-grained) part of each depositional cycle support the hypothesis that the occurrences of *Hemifusulina* are associated with the initial repetitive sea level rises. Moscovian *Hemifusulina* possesses the overall morphological resemblance with the mid-Kasimovian *Ferganites* (Villa and Bahamonde, 2001). Besides, both these genera occur as monospecific assemblages in similar environments.

Villa and Bahamonde (2001) studied mid-Kasimovian *Ferganites* in the Cantabrian Mountains. Monospecific assemblages of *Ferganites* occur in numerous stratigraphic levels of the mid-Kasimovian Puentelles Fm., which consists of cyclic alternations of calcareous breccias and conglomerates, pebbly sandstones, graded and laminated silty and sandy limestones, skeletal grainstones, and bioturbated marly limestones and marls (Villa and Bahamonde, 2001, fig. 2 therein). Three fining upward sequences are recognized in this cyclic succession, which is interpreted "as flood-dominated fan-delta and river-delta systems, which generated alluvial to shelfal lobes of hinterland derived sediment supplied by episodic river discharges" (Villa and Bahamonde, 2001, p. 176). Such deposits occur in tectonically-controlled basins characterized by small and medium sized fluvial systems with high-elevation drainage basins and high-gradient transfer zones located close to marine basins (Villa and Bahamonde, 2001 and references therein). The abundance of *Ferganites* and absence of other contemporaneous genera, such as *Rauserites*, *Triticites* and *Quasifusulina*, are attributed to *Ferganites* adaptation either to the high hydrodynamic conditions of the near-shore environment or to the relative low salinity created by the fresh water discharge into proximal areas of the basins proximal to river mouth regions. Similarly, the abundance of *Hemifusulina* in the Moscovian strata in the orogenic belts attests an adaptation of *Hemifusulina* to near-shore environment probably with low salinity water that was critical for contemporaneous *Beedeina*, *Fusulinella*, *Neostaffella*, *Ozawainella*.

The C₂ assemblage that defines the upper part of each cycle is associated with abundant photozoan skeletal grains and green algae (Figs. 5G, 5H, 12) suggesting warm, very shallow habitat depths (< 10 m), within the zone of penetration of the red spectrum of visible light. Photosynthesizing algae further require waters with limited suspended fine-grained mineral and organic matter transported from land by river and surface runoff. Furthermore, limestones of upper part of the Kashirian and Podolskian cycles are associated with disseminated quartz silt (Fig. 5M) and chert nodules. Similar silt-size detrital quartz and chert nodules in Pennsylvanian limestones of the North American Midcontinent have interpreted as eolian dust influx under relatively dry conditions (Cecil, 2004). A reduction in regional precipitation is also supported by absence of early diagenetic meteoric calcite cements. In the Moscow Basin, Makhlina et al., (2001) observed a similar shift to thick algal limestones with chert lenses and nodules, which contain scarce fusulinids of the C₂ assemblage (Khodjanyazova et al., 2012).

In the Donets Basin, the assemblage C is also associated with a considerable reduction in coal beds, which are absent in the upper parts of the Verean, Kashirian (~Westphalian B–C) cycles and mainly concentrated in the lower parts of these cycles that exhibits a high contrast of climate change from humid to semiarid within a time slice of ~1myr. In the Podolskian, Myachkovian and Krevyikian (~Westphalian D–Cantabrian – maximum humidity both in the eastern and western margin of the continent Laurussia), such contrast was minimized and coal beds recorded

both in the lower and upper parts of each cycle. However, the coals documented in the upper part of cycle (e.g. m₃ coal) contain *Calamites*, which were adapted to relatively dry subhumid conditions (Fisunen, 2000). We thus hypothesize that the proposed fusulinid cycles record low-frequency (~ 1myr) shifts from humid to dry subhumid, or arid climate in this region of paleotropical Pangaea in concert with changes in sea level fluctuations on the 0.6 to 1.2 myr time scale (Fig. 3, 4, 12). Climatic cycles of comparable duration (~0.6–1.2 myr) and nature have been inferred from Pennsylvanian mixed carbonate-siliciclastic strata from the North American Midcontinent (Feldman et al., 2005). Analogous wet-dry cycles, characterized by a successive increase in the duration and intensity of the dry portion of each cycle, have been documented in the Upper Pennsylvanian succession of several central and eastern Euramerican basins (Oplustil and Cleal, 2007). For the Donets Basin, each fusulinid cycle begins with the A assemblage (*Hemifusulina*-dominated) hosted within lower transgressive system tract (LTST) deposits interpreted to record initial sea level rise coincident with the wettest conditions of the cycle. The overlying B assemblage (*Beedeina*-dominated) records highstand conditions with minimal record of climate change. The C assemblage (*Fusulinella*-*Fusulina*-dominated) that caps each cycle and occurs in upper limestones records the onset of falling sea level coincident with a shift to drier climate.

A relationship of the fusulinid cycles and physical and sequence stratigraphy are shown on Figure 3. Each composite sequences proposed by Eros et al. (2012) comprise two biological fusulinid cycles. The boundaries of composite sequences are placed at the bases of thick sandstones and it seems they divide the strata deposited under humid conditions from the rocks accumulated during relatively drier episode.

7. Application of the cyclic fusulinid distribution model

The proposed model can be applied to a range of geologic issues including biostratigraphy and interbasinal correlation, paleogeography and paleoclimatology, and sequence stratigraphic and basin analysis. In addition, the fusulinid cycle model may provide a possible explanation for the fusulinid extinction event at the Moscovian – Kasimovian boundary.

7.1. Biostratigraphy and global correlation

Trends in evolution, biogeography and biodiversity that are recognized within the established biocycles possess a valuable application in biostratigraphy. All three assemblages have a very short temporal range (0.3 – 0.4 myr). The deeper-water *Beedeina*, which dominates in the assemblage B ('transgressive' fusulinids), is recognized in the L₇, M₁, M₅, M₈, N₁⁶, and N₄ limestones in the deeper part of the eastern Donets Basin (Putrja, 1939, 1956). However this genus is absent in some limestones, for example M₈ and N₄ in the shallower water in the western part of the Donets Basin (Gurkrovo and Kalinovo sections). In turn, the *Fusulinella*-assemblage ('regressive' fusulinids), which we infer as a proxy of shallower depth, might be expected primarily in regions proximal to the shoreline, in agreement with Walter's law; however neither *Beedeina*, nor *Fusulinella* occur in the limestones M₈ and N₄; these limestones are characterized by smaller foraminifers. These relationships suggest that these 'transgressive' and 'regressive' fusulinids were not only depth-related forms but are time-related assemblages. In other words, the fusulinid assemblages we have defined for different sea-level stands are not only associated with depth, but obviously with some other specific environmental conditions. Moreover, all three proposed assemblages are recognized in different lithofacies packages in the Moscow Basin, situated in an arid climatic belt (Kabanov et al., 2010), hundreds of kilometers from the Donets Basin. The simultaneous replacement of one assemblage by another every ~300–400 kyr and the widespread distribution of each assemblage indicates environmental changes happened synchronously over 100s of kms — a phenomenon that requires global drivers. Here, we suggest that variations in water temperature and salinity in response to sea-level and climate change was the primary driver of the turnover in fusulinid assemblages within each biotic cycle (see Section 7.2).

The proposed model of cyclic distribution of fusulinids has application to interbasinal correlation. A usage of this model permits almost bed-to-bed correlation of the Pennsylvanian strata in the Donets and Moscow Basins. The limestones M₇–M₁₀ in the Donets Basin which represent one fusulinid cycle are coeval with Podolskian strata of the Moscow Basin (Fig. 2). In this correlation, the Smedva Fm. characterized by the *Hemifusulina* species (A) is coeval with the M₇, M₇^{up} limestones; the Vaskino Fm. characterized by *Fusulinella* (C₁) assemblage is coeval with the M₉ limestone; and the Ulitino Fm. characterized by *Fusulina* (*Kamaina*) (C₂) assemblage is coeval with the M₁₀ limestone (Fig. 2).

Fusulinids from the early highstand (*Beedeina*-dominated assemblage) inhabited the seas during periods closest to maximum sea level rise and are thus have the most potential for global correlation. Comparison of the evolution of *Beedeina* species to the mid-to late Pennsylvanian sea level history inferred from North American Midcontinent cyclothems (Ross and Ross, 2009) documents a similar trend to that defined in the Donets Basin. Abundant and diverse *Beedeina* species occur more frequently in the lower Desmoinesian strata in the western margin of Laurussia and in the coeval Kashirian successions in the eastern margin of this continent. In the late Desmoinesian coeval to Podolskian – Myachkovian – early Krevyakian, the occurrence and diversity of *Beedeina* are steadily decreased. The simultaneous last occurrence of *Beedeina* is recorded in the latest Desmoinesian (the Lost Branch transgression) in the North America and in the early Krevyakian (limestone N₄) in the Donets Basin. More detailed work needs to be conducted in the correlation of the *Beedeina* evolutionary trends in distal regions. As this assemblage is considered to indicate the maximal highstand of sea level, their stratigraphic distribution throughout the Middle Pennsylvanian might be useful in reconstruction of the tempo and magnitude of the continuous deglaciation of Gondwanan ice caps.

By contrast, fusulinids of the *Hemifusulina*-dominated community which occur in the LTST are provincial and therefore have a low potential for interbasinal correlation. Only correlation of the geographically closest basins, such as the Donets and Moscow Basins, is reliable. Notably, the most diverse fusulinids occur in limestones deposited during sea level fall (ULST). Lowering of a sea level in epicontinental seas likely creates geographical barriers that in turn increased isolation of fusulinid populations promoting development of endemic and provincial species. Nevertheless, the *Fusulinella*-dominated 'regressive' populations also permit the correlation between proximal basins, such as the Donets and Moscow basins (Khodjanyazova et al., 2012).

7.2. Diversity and morphologic response of Moscovian fusulinids to environmental change

The Pennsylvanian fusulinids, by analogy with modern larger foraminifers (BouDagher-Fadel, 2008; Hohenegger, 2004), probably were thermally intolerant but could adapt to seawater temperatures varied within a short time period (~ 1myr). Seawater temperature and salinity in late Paleozoic epicontinental seas depended on insolation to each region, circulation, and regional climate (Poulsen et al., 2007; Montañez and Poulsen, 2013). Insolation within tropical regions would not have varied substantially in the paleotropics thus the observed shifts in fusulinid assemblages within an interval of ~ 1 myr (± 0.2 m.y.) is best explained by major changes in circulation, freshwater input, precipitation/evaporation, and air surface temperature in response to sea level fluctuations and climate change.

In the Donets Basin, the predominance of the *Hemifusulina*-dominated assemblage in the lower parts of each cycle (LTST) and its absence from comparable facies in the middle and upper parts of fusulinid cycles indicate a lack of facies dependence and provide support for a sensitivity of these fusulinids to seawater temperature and salinity (Fig 4). Introduction of cooler waters into epicontinental seas coupled with increased precipitation and surface freshwater discharge during initial sea level rise would have led to colder and less saline waters (e.g., Schmittner et al. 2013). The morphology of *Hemifusulina* species suggest that they were likely able to adapt to shallow cooler water environments. *Hemifusulina* species are variable in shape from elongated subcylindrical (most common) and ovoid with rounded polar ends to short fusiform with pointed polar ends (Figs. 4, 5). *Hemifusulina* differs from many other large fusulinids in having a very small proloculus, regular shape, regularly folded septa, and regular small rounded chomata symmetrically arranged around a regularly widening tunnel. Mature specimens of modern foraminifers (Dodd and Stanton, 1981) exhibit an increase in volution number in colder water characterized by upwelling of nutrient-rich water. Thus, tightly coiled volutions and an increase in volution number of *Hemifusulina* species may indicate the adaptation of this genus to the cooler water temperature. Furthermore, *Hemifusulina*-bearing beds are restricted to silty or sandy limestones intercalated with siliciclastics in a few regions Cantabrian Mountains (Ginkel, 1973), in Central Asia (Bogush, 1963), Donets and Moscow basins (Reitlinger and Balashova, 1954; Baranova and Kabanov, 2003). Although these basins were situated in different tectonic settings and climatic belts, they share a common proximity to the paleo-land, the source of siliciclastics and fresh water input. Such critical habitat was harmful for the other fusulinids but favorable for *Hemifusulina*, which, in an absence of competition, abundantly occupied the near-shore basins. A gradual decrease in the abundance of *Hemifusulina* populations in a seaward direction in the East European craton (Dalmatskaya, 1961) may suggest that salinity also played a role in constraining the geographic and temporal distribution of the *Hemifusulina*-dominated assemblage (Fig. 13).

The lack of immature fusulinids in the *Beedeina*-dominated assemblage and its occurrence in clean limestones of the upper transgressive and lower highstand systems tracts (Figs. 3, 12) reflect the development of offshore environments driven by sea level rise during this portion of each fusulinid cycle. Species of *Beedeina* and *Taitzehoella* (LTSL–EHSL) are smaller (Fig. 7) than their relatives (Figs. 9, 10) adapted to sea level fall (LHSL–ELSL). We hypothesize that the subrhomboidal to short fusiform test outline of species of *Beedeina* and *Taitzehoella*, the globular shape of the large *Neostaffella*, and discoid shape of the large *Ozawainella* indicate their adaptation to increased water depths above the bottom substrates where they lived. Moreover, an increase in the number of tightly coiled volutions (6 to 8) in *Beedeina*, *Taitzehoella* and *Neostaffella* species relative to their descendants (fewer than 6) found in limestones of the upper portion of fusulinid cycles probably indicate their ability to adapt to cooler water temperatures. *Beedeina* and *Taitzehoella* species are subrhomboidal in shape, and possess a greater number of volutions (six – eight) than their descendants, associated with low sea-level stand (ELSL), which have only five or rarely six volutions. *Beedeina* in this assemblage are distinct in having regularly folding septa and small proloculi. *Neostaffella* is represented by large species, and has seven–eight volutions. Large discoid species of *Ozawainella* are highly compressed at their polar ends and replaced by smaller subrhomboidal species in the successive *Fusulinella*-assemblage. A very important feature for the assemblage B is an absence of the *Hemifusulina* (common for the lower limestones) and *Fusulinella*, *Schubertella* genera (common of the upper limestones).

The warmest water was inhabited by the very diverse *Fusulinella*-*Fusulina* assemblages (C) (Figs. 9, 10). This diverse community of fusulinids includes the abundant species of *Schubertella* and *Fusulinella*. Putrja (1940), Kireeva (1951), and Solovieva (1986), based on the wall structure of fusulinids, proposed a polyphyletic fusulinid lineage, in which Bashkirian and Vereian *Profusulinella* evolved into Kashirian *Moellerites*; the latter in turn evolved into Podolskian and Myachkovian *Fusulinella*. *Fusulinella* gave rise two Krevyakian genera *Protriticites* and *Obsoletes*. *Beedeina* in this assemblage is usually represented by elongated fusiform species. Large species of *Beedeina* possess fewer volutions (maximum five) and are almost three to four times longer than species from a previous deeper-water assemblage, and often have very large proloculi. *Taitzehoella* also replaced by elongate fusiform species. In the Podolskian, species of *Fusiella*, evolved from *Taitzehoella*, became an important element of the C assemblage (Fig. 10.8). Large species of *Neostaffella* occur together with the small individuals of *Pseudostaffella*. In the very shallow limestone of the upper part of fusulinid cycle, *Pseudostaffella* is dominated. The *Fusulinella*-dominated assemblage is usually characterized by an absence of the *Hemifusulina*. Single specimens are recognized in the Podolskian, M₉ limestone. In the Myachkovian M₁₀¹–N₂¹ (~the upper part of Westphalian D – the lower part of Cantabrian) single specimens of *Hemifusulina* occur within the upper part of cycle. Large elongate-subcylindrical *Fusulina* appear at the end of cycle.

A smaller number of volutions in advanced fusulinids, such as *Fusulinella*, *Beedeina* and *Fusulina*, probably, indicate their adaptation to the warm water temperature. Marine water, oversaturated with respect to calcite under drier climatic conditions, might be able to precipitate an inorganic calcite resulting in lithification of sea bottom. A hard substrate might promote a hydrodynamic activity due to a decrease of friction in the water-bottom interface. An abundance of the immature individuals of *Fusulinella* and *Beedeina* with two-three volutions (Fig. 8 C, 8D, 9.20) attests a mass mortality of fusulinids in the highly agitated water.

7.3. Moscovian – Kasimovian boundary extinction event

In the first half of the last century, Carboniferous chronostratigraphy in the former Soviet Union was developed based upon fusulinid evolution, and divided into three subsystems: Lower (=Mississippian), Middle (=Lower and Middle Pennsylvanian) and Upper (=Upper Pennsylvanian) Carboniferous. The boundary between the Middle and Upper Carboniferous (Moscovian/Kasimovian) was established by extinction of many Middle Carboniferous fusulinid genera, such as *Hemifusulina*, *Beedeina*, *Taitzehoella*, *Neostaffella* (Fig. 14). These genera first appear in the eastern margin of Laurussia at the base of Moscovian, which coincides with the most humid episode inferred from the interval of the most productive coal seams in the Donets Basin (~Westphalian B–C–D and Cantabrian). In North American Midcontinent, diverse *Beedeina* species appeared ~2–3 million years later than along the eastern margin of Laurussia, at the base of Desmoinesian, which is considered as the most humid interval (~ part of Westphalian C–Westphalian D –Cantabrian) inferred from Midcontinent cyclothems. The subsequent extinction of

many fusulinid genera at the Moscovian – Kasimovian transition coincided with a substantial reduction of wetland flora throughout Laurussia at the Cantabrian/Stephanian A boundary (Meyen, 1987) in Europe and contemporaneous Desmoinesian/Missourian boundary in North America (DiMichele et al., 2009) that coincided with the onset of aridification.

The extinction event primarily affected the inferred cooler-water fusulinid genera, such as *Hemifusulina*, *Neostaffella*, *Ozawainella*, *Beedeina*, and *Taitzehoella*. In contrast, the inferred warm water fusulinids, *Fusulinella* and *Fusulina*, that may have tolerated elevated salinities, diversified and rapidly evolved following this event in the early late Pennsylvanian (the “O” formation). *Fusulinella* gave rise to two phylogenetic branches *Protriticites* and *Obsoletes*, which became the main dominants in the lowermost Upper Pennsylvanian strata in the Tethyan realm. *Fusulina* evolved into early Kasimovian *Quasifusulinoides* and late Kasimovian–Gzhelian *Quasifusulina*. We interpret the extinction of cooler water fusulinids, which were adapted to normal salinity and possibly hyposalinity, and the proliferation of warmer water, high salinity tolerant fusulinids to a major shift from perhumid conditions of the Moscovian to semi-arid climates in the Late Pennsylvanian that has long been noted in sedimentologic and paleobotanical records (Phillips et al., 1985; West et al., 1997; Hilton and Cleal, 2007; Kabanov et al., 2010). Notably, the fusulinid extinction occurs towards the beginning of a long-term (~7 m.y.) rise in sea level that is hypothesized to have been driven by major contraction of the Pennsylvanian ice sheets (Eros et al., 2012) in response to CO₂ forced global warming (summarized in Montañez and Poulsen, 2013). This hypothesized global warming and aridification would have led to warmer and more saline seawater in the shallow epicontinental seas leading to the observed disruption of the fusulinid cycle pattern represented by the only warm-water assemblages (C₁ and C₂), at least in the eastern margin of Laurussia.

7.4. Paleogeography

A comparative analysis of different groups of fusulinids from the Donets Basin and other regions of the Tethyan province reveals that fusulinids from highstand limestones exhibit a greater degree of similarity between them than fusulinid groups associated with lowstand limestones (ULST). *Fusulinella* is one of the most diverse genera among the Pennsylvanian fusulinids and therefore, is the most provincial. Among Donets *Fusulinella* we found many species in common with those in the Moscow Basin, but farther from the Donets Basin, fewer species appear to be similar. *Fusulinella* species from coeval limestones of the intracratonic Donets and Moscow basins exhibit similar elongated subcylindrical morphologies. Farther from the Donets Basin, however, the degree of similarity between species decreases. In the orogenic belt, situated closer to an open ocean, species of this genus possess ovoid and subspherical forms. We propose that the provinciality of the *Fusulinella* species has utility for recognition of originally contiguous regions which later may have been dispersed hundreds or thousands of kilometers by plate tectonics.

7.5. Sequence stratigraphy and basin analysis

The proposed model is a useful tool for definition of third-order sea-level fluctuations in shallow marine basins. Sequence boundaries can be drawn at a base of the beds containing *Hemifusulina* (LTST). Maximum flooding is marked by a *Beedeina*-dominated assemblage (HST), whereas the late highstand of sea level and the onset of sea level fall are recorded by the occurrence of an abundant *Fusulinella*-*Schubertella*-community (ULST).

The fusulinid cyclic model developed for the Donets Basin represents a stratigraphic ‘symmetrical pattern’ in the terminology proposed by Brett (1998, p. 249). He noted that: “Within a single stratigraphic section, habitat tracking may produce a predictable vertical stacking pattern of biofacies that appear in a nearly symmetrical cycle. Such ‘symmetrical tracking’ patterns represent simple lateral shifting of bathymetrically-zoned biofacies, perpendicular to facies strike (shoreline), in response to relative rise or fall of sea level ” (Brett, 1998, p. 249, see figs. 3–5 herein). Brett also proposed ‘asymmetrical patterns’, which are “observed in some sedimentary cycles and may be attributed to incomplete preservation of intermediate facies” (Brett, 1998, p. 249).

We observe three types of fusulinid assemblage successions that vary with subsidence and sedimentation rates, distance from land, and tectonic setting (Figs. 15 and 16). Fusulinid distributions in the Donets and Moscow basin exhibit a symmetrical pattern, where all three assemblages are represented and successively record all stages of the sea-level cycle. In the Moscow Basin, the *Beedeina* species is absent in the B assemblage, however other associated fusulinids, such as *Neostaffella*, *Ozawainella* and *Taitzehoella* exist that permit identification of the B assemblage.

The important feature for cyclicity is a late occurrence of *Fusulinella* within cycle that is also recorded in the Moscow succession. Other regions of the Tethyan realm exhibit yet other combinations of assemblages that define asymmetrical patterns. These cyclic temporal distribution patterns exhibit the omission of one or another assemblage, or the disappearance of some fusulinid genera within assemblages. Farther to the east, in the deeper marine Uralian Foredeep, the *Hemifusulina* assemblage (LTSL) disappears, whereas limestones that host the B and C fusulinid assemblages are well differentiated (Fig. 13). Asymmetric patterns characterize orogenic belts (Fig. 16). Cyclic, predominantly coarse-grained, fining upward siliciclastic successions contain lenses of sandy limestones, characterized mainly by the *Hemifusulina*-dominated assemblage. Fusulinid of the B and C assemblages are absent or rare (Bogush, 1963).

The observed patterns of succession of fusulinid assemblages can be explained in the context of changes in relative sea-level (RSL). RSL rise in intracratonic (Fig. 15) and foreland basins (Fig. 16) is a sum of subsidence rate (red arrow) and global sea level change or eustasy (blue arrow). Conversely RSL fall is the residual between accommodation provided by subsidence (red arrow) and global sea-level fall (blue arrow). The existence of fusulinid-rich successions in the foreland basins (Fig. 16) and deeper intracratonic basins (Fig. 15) suggest that subsidence rates were not much higher than those estimated for the Donets Basin. With greater subsidence rates these basins would have been drowned to depth unfavorable for a fusulinid survival. In orogenic belts (Fig. 16) such as the Cantabrian Mountains and Central Asia, RSL is a subtraction between eustasy and the rate of tectonic uplift. Due to the uplift of strandlines in tectonically active areas, relative sea-level changes can be expected to be distorted relative to those recorded by strata in intracratonic basins, i.e., the magnitude of rises will be dampened, whereas falls may be amplified. Consequently, the requisite accommodation space needed for sediment accumulation may exist solely during RSL rises as long as the rate of tectonic uplift is well less than the rate of eustatic rise. This scenario is likely recorded by asymmetric successions in orogenic belt successions which are characterized by a *Hemifusulina*-dominated assemblage and lack regressive fusulinid assemblages.

8. Conclusions

- i. A new paleoecological model, mechanistically linked to global sea-level fluctuations and regional climate, is proposed for the origin of the cyclic patterns of fusulinid assemblages exhibited by Pennsylvanian strata of the Donets Basin. High-precision ID-TIMS U-Pb ages on zircons from volcanic ashes distributed throughout the Moscovian succession in the Donets Basin permit an estimate of duration of fusulinid cycles of ~ 0.6 to 1.2 m.y.
- ii. Three types of fusulinid assemblages accompanied by specific microfacies and biofacies, and interpreted different sea-level stages are recognized. The *Hemifusulina*-dominated assemblage (**A**) captures the initial sea level rise (ETSL) characterized by perhumid regional climate and cooler seawater temperatures in the epicontinental seas. The *Beedeina*-dominated assemblage (**B**) records the highstand (LTSL–EHSL) with no clear shift in climatic conditions. This assemblage is successively replaced by the most diverse *Fusulinella*-dominated assemblage (**C**) that proliferated in a progressively shallowing sea (LHSL–ELSL). This time coincides with drier regional climate and warmer shallow seas.
- iii. The *Beedeina*-dominated assemblage of Middle Pennsylvanian M₁, M₅, M₈, N₁⁶, N₄ limestones in the Donets Basin are interpreted to record maximum sea level inundation of the region. This interval coincides with a previously hypothesized period of global warming and major contraction of the Gondwanan ice sheets. Such fusulinid events have the potential to be recognized globally and be very useful correlation tools.
- iv. Extinction at the Moscovian – Kasimovian boundary mainly affected fusulinid genera associated with cooler waters during sea level rises (*Hemifusulina*, *Neostaffella*, *Ozawainella*, *Beedeina*, *Taitzehoella*). This extinction can be explained by a global warming event and rising water temperature and salinity that were fatal for those genera, which were adapted to cooler and lower salinity waters.
- v. Symmetrical and asymmetrical patterns of fusulinid distribution documented in this study hold promise for the reconstruction of the paleogeography and tectonic evolution of Pennsylvanian basins that developed along the south-eastern and eastern margins of Laurussia.

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FIGURE CAPTIONS

Fig. 1. Geologic setting of the Donets Basin. Study area (white rectangular outline) in the Dnieper-Donets aulacogen (horizontal lined pattern).

Fig. 2. Chronostratigraphic scale and correlation of regional and biostratigraphic subdivisions in the Moscow Basin, Donets Basin, west Europe, and North America (modified from Davydov et al., 2010). Thick lines are new lower and upper boundaries of the Podolskian Substage, proposed based on evolution and cyclic model of fusulinid distribution.

Fig. 3. Three fusulinid cycles recognized in the Gurkovo section and their relation to the ‘composite cycles’ (Eros et al., 2012) within the upper “L” and “M” formations, Donets Basin. Repetitive occurrences of three fusulinid assemblages within each fusulinid cycle: (A – *Hemifusulina*-dominated, B – *Beedeina*-dominated, C – *Fusulinella*-dominated).

Fig. 4. Gradual replacement of fusulinids within a cycle (~0.6–1.2 myr). Morphological and taxonomical changes of main genera with respect to depth, temperature, and salinity. Assemblages: A1 – a monospecific population of *Hemifusulina*; A2 – a low-diverse community with the main component of *Hemifusulina*; B – a moderate-diverse *Beedeina*-dominated assemblage; C1 – high-diverse *Fusulinella*-dominated assemblage; C2 – a high-diverse *Fusulinella*–*Fusulina*-dominated assemblage. The curves on the right show the dynamics of taxonomic diversity of fusulinids, heterozoan and photozoan fauna through the cycle. ETSL – early transgressive sea level; LTSL – late transgressive sea level; EHSL – early high sea level; LHSL – late high sea level; ELSL – early low sea level.

Fig. 5. Fusulinids of the *Hemifusulina*-dominated assemblage: 1 – 9 (limestone M₇^{up}), 10 – 12 (M₇), 13 (M₃^{up}), 14 – 18 (L₇¹). 1 – *Hemifusulina communis acuta* Rauser, x 20; 2 – *H. sp. cf. H. splendida* Safonova, x 20; 3 – *Ozawainella krasnodonica* Manukalova, x 40; 4, 16 – *Taitzeoella sp. cf. T. globulus* (Manukalova), x 35; 5, 8 – *Neostaffella larionovae* Rauser and Safonova, x 35; 6 – *O. sp. 2*, x 45; 7 – *Pseudostaffella variabilis* Reitlinger, x 45; 9 – *O. angulata* (Colani), x 40; 10 – *Beedeina sp. cf. B. vaskensis* (Rauser), x 20; 11 – *N. sp.*, x 35; 12 – *H. pulchella* Rauser, x 20; 13 – *H. kashirica* Rauser, x 20; 14 – *O. paratingi* Manukalova, x 40; 15 – *N. ozawai* (Lee et Chen), x 35; 17 – *H. moelleri* Rauser, x 20; 18 – *H. pseudobocki* Putrja, x 20.

Fig. 6. Microphotographs of the *Hemifusulina*-bearing limestones in the “M” formation. A – limestone L₇¹; B – limestone M₃^{up}; C – limestone M₇; D – limestone M₇^{up}.

E – echinoids, Es – echinoid spines, B – brachiopods, Bs – brachiopod spines, Os – ostracods, G – gastropods, Bz – bryozoans, Os – ostracods, Sp – sponges; Ss – sponge spicules, Tr – trilobites. AIA – phylloid red alga *Archaeolithophyllum sp.*, Cb – Cyanobacteria, fusulinids: Hm – *Hemifusulina sp.*, N – *Neostaffella sp.*, Oz – *Ozawainella sp.*, smaller foraminifers: FE – Endothyridae; or – organic matter, ms – microstylolites.

Fig. 7. Fusulinids of the *Beedeina*-dominated assemblage: 1 – 8 (limestone M₅), 9 – 18 (M₁). 1 – *Beedeina bona* (Rauser-Chernousova), x 20; 2 – *B. dunbari* (Sosnina), x 20; 3 – *B. pseudokonnoi* (Sheng), x 20; 4, 5 – *Ozawainella adducta* Manukalova, x 40; 6 – *Taitzeoella librovitchi* (Dutkevitch), x 35; 7 – *Neostaffella unibilicata* (Putrja et Leontovitch), x 35; 8, 12 – *N. compacta* (Manukalova), x 35; 9 – *B. schellwieni* (Staff), x 20; 10 – *B. pseudoelegans* (Chernova), x 20; 11 – *B. elshanica* (Putrja and Leontovich), x 20; 13 – *N. ozawai* (Lee et Chen), x 35; 14 – *O. sp. cf. O. digitalis* Manukalova, x 40; 15 – *O. stellae* Manukalova, x 40; 16 – *O. crassiformis* Putrja, x 40; 17 – *T. kashirica* (Rauser-Chernousova), x 35; 18 – *Eofusulina sp.* x 15.

Fig. 8. Microphotographs of limestones of the “M” formation. *Beedeina*-dominated assemblage: A – limestone M₁, B – limestone M₅. *Fusulinella*-dominated assemblage: C – limestone M₂, D – limestone M₁₀. AIU – *Ungdarella* (red alga), AIB – *Beresella* (green alga). Fusulinids: Bd – *Beedeina*; Fl – *Fusulinella*; Fn – *Fusulina*; Sh – *Schubertella*, im – immature specimens of fusulinids. Smaller foraminifers: FTb – *Tuberitina*, FB – *Bradyina*, FP – Paleotextulariidae, FT – *Tetrataxis*, FAm – *Ammodiscus*, Fs – sessile forms (*Paleonubecularia*?), Fc – calcisphaeric forms (*Calcisphaera*?), Sc – syngenetic ?, or early diagenetic calcite.

Fig. 9. Fusulinids of the *Fusulinella*-dominated assemblage: 1 – 7 (limestone M₆), 8– 16 (limestone M₃), 17 – 24 (limestone M₂). 1 – *Beedeina keltmensis* (Rauser-Chernousova), x 20; 2 *Taitzeoella* sp. cf. *T. globulus* (Manukalova), x 35; 3 – *Fusulinella colanii* (Lee et Chen), x 20; 4, 5, 16, 22, 24 – Schubertellidae x 40; 6 – *Ozawainella adducta* Manukalova, x 40; 7 – *Neostaffella* sp. cf. *N. sphaeroidea* (Ehrenberg), x 30; 8 – *Beedeina pronensis* (Rauser-Chernousova), x 20; 9 – *B. bona* (Chernova and Rauser-Chernousova), x 20; 10, 21 – *Fusulinella* (*Moellerites*) *cylindricus* Solovieva, x 20; 11 – *T. kashirica* (Rauser), x 35; 12 – *N.* sp., x 30; 13 – *Fusulinella* (*Moellerites*) *paracolaniae* Safonova, x 20; 14, 23 – *Pseudostaffella confusa* (Lee and Chen), x 40; 16, 17 – *Fusulinella* (*Moellerites*) *schubertellinoides* Putrja, x 20; 18 – *Taitzeoella pseudolibrovitchi* Rauser-Chernousova, x 35; 19 – *Pseudostaffella khotunensis* Rauser-Chernousova, x 40; 20 – *Beedeina* sp., immature specimen, x 20.

Fig. 10. Fusulinids of the *Fusulinella*-dominated assemblage: 1 – 10 (limestone M₁₀), 11– 19 (limestone M₉), 20 – 28 (limestone M₆^{up}). 1, 16 – *Neostaffella sphaeroidea* (Ehrenberg), x 30; 2 – *Sshubertella lata* Lee and Chen, x 40; 3 – *Fusulinella tokmovensis longa* Reitlinger, x 20; 4 – *F. (M.) plana* Reitlinger, x 20; 5, 17, 26 – *Pseudostaffella khotunensis* Rauser, x 40; 6 – *Pseudostaffella variabilis* Reitlinger x 40; 7 – *Schubertella subkingi* Putrja, x 40; 8 – *Fusiella praetypica* Safonova, 9 – *Kamaina rossoshanica* (Putrja), x 15; 10, 19 – *Ozawainella* sp. cf. *O. vozghalica* Safonova, x 35; 11 – *Fusulinella* sp. cf. *vozghalensis devexa* Rauser, x 20; 12 – *Putrella donetziana* (Lee), x 20; 13, 14 – *Schubertella* sp. cf. *galinae* Safonova, x 40; 15 – *Kamaina chernovi* (Rauser-Chernousova), x 20; 18 – *Pseudostaffella compressa donbassica* Putrja, x 40; 20 – *Kamaina* (?) sp. cf. *K. rossoshanica* (Putrja), x 15; 21 – *Fusulinella colanii* (Lee and Chen), x 20; 22, 23 – Schubertellidae, x 40; 24 – *Taitzeoella librovitchi* (Dutkevitch), x 35; 25– *Neostaffella larionovae* Rauser and Safonova, x 35; 27 – *Ozawainella adducta* Manukalova, x 35; 28 – *Ozawainella* sp. x 40.

Fig. 11. Microphotographs of limestones of the “M” formation. *Fusulinella*-dominated assemblage C: A – limestone M₃, B – limestone M₉. C – silt-sized quartz grains, limestone M₉. D – the fragment of a solitary coral, limestone M₆^{up}. Sp – sponge, AlK – red alga, *Pseudokomia*.

Fig. 12. A time – depth model of fusulinid distributional patterns and associated algae within a fusulinid cycle (~ 0.6–1 myr.). A – *Hemifusulina*-dominated assemblage, B – *Beedeina*-dominated assemblage, C – *Fusulinella*–*Fusulina*-dominated assemblage.

Fig. 13. Spatial/temporal distribution of fusulinids in shallow tropical basins of the Tethyan realm in response to low-frequency sea level fluctuations and climate change.

Fig. 14. Extinction of fusulinid genera across the Moscovian – Kasimovian transition.

Fig. 15. Symmetrical cycles in intracratonic settings: A – *Hemifusulina*-dominated assemblage, B – *Beedeina*-dominated assemblage, C – *Fusulinella*–*Fusulina*-dominated assemblage. Red arrow is tectonic effect to RSL (relative sea level); blue arrow is eustatic effect to RSL.

Fig. 16. Basins in the south-eastern margin of Laurussia and the north-eastern margin of Gondwana. Asymmetric cycles in tectonically active basins: A – *Hemifusulina*-dominated assemblage, B – *Beedeina*-dominated assemblage, C – *Fusulinella*-assemblage. Red arrow is tectonic contribution to RSL (relative sea level); blue arrow is a glacial contribution to RSL.

Gurkovo section

1; 2; 4; 10; 12; 13; 16—18

3; 5—9; 11; 14; 15

1 mm 1—3; 8; 9; 10—13; 17; 18; 20; 21

1 mm 4—7; 14—16; 19; 22—24

1 mm 3; 4; 8; 9; 11; 12; 15; 20; 21; 24

1 mm 1; 2; 5—7; 10; 13; 14; 16—19; 22; 23; 25—28

Near-shore (the Donets and Moscow Basins)

Off-shore basins (the Pamir, the Cantabrian Mountains, northern China, southern Urals, Japan)

Donets Basin

Siliciclastic successions
proximal to the paleo-land
(source of siliciclastics)

Moscow Basin

Carbonate successions
proximal to the paleo-land

s. Urals, n. China

Carbonate-siliciclastic successions
distal from the paleo-land

The Cantabrian Mountains, central and eastern Iran, northern Pamir, Alai Ridge

Off-shore basins

Mixed carbonate-siliciclastic successions

Near-shore basins

Siliciclastic successions

— Donets Basin reference sea-level curve