

# Warm water benthic foraminifera document the Pennsylvanian–Permian warming and cooling events – The record from the Western Pangea tropical shelves



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## ABSTRACT

Shallow warm water benthic foraminifera (SWWBF), including all larger fusulinids (symbiont-bearing benthic foraminifera), are among the best indicators of paleoclimate and paleogeography in the Carboniferous and Permian. The distribution of benthic foraminifera in space and time constrain important tectonic, paleogeographic and climatic events at a global scale. The North American shelves during Pennsylvanian and Permian time – though geographically within the tropical belt – are characterized by temperate environments with significantly lower foraminifera diversification and rare occurrences of warm water Tethyan forms, that are in general appear in the region as a migration entities. Such environments allow documentation of warming episodes associated with sudden immigration of warm water and exotic forms of SWWBF that evolved elsewhere into the area. First occurrence datum (FOD) of the forms exotic to North America during warming episodes are always delayed in respect of their First Appearance Datum (FAD) elsewhere. The time of delay and taxonomic diversity of fusulinids in North America shelves depended on the scale and intensity of the warming episodes. Cooling events, on the other hand, are associated with decreased taxonomic diversity and appearances of endemic forms characteristic only of temperate water provinces. The occurrence of these forms in Boreal and North American provinces appears to be isochronous, as their environments are uniform and induce their uniform and isochronous distribution. Several warming and cooling episodes during Pennsylvanian–Permian time are recognized. The differences between taxonomic variations in each event could potentially be used for provisional estimation of the degree of climatic change. A strong link between biotic and climatic events in North American province and the similarity of biotic changes in the North American and other provinces suggests that paleoclimatic events in North American province were controlled by global factors.

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## 1. Introduction

The Late Paleozoic is commonly regarded as a time of alterations global greenhouse–icehouse climate. The most recent data suggest multiple phases of glaciation, although the number of phases and their age constraints are still debated (Isbell et al., 2003; Montanez et al., 2007; Fielding et al., 2008b; Isbell et al., 2012; Montanez and Poulsen, 2013). The constraints and nature of the interglacial phases are still poorly understood.

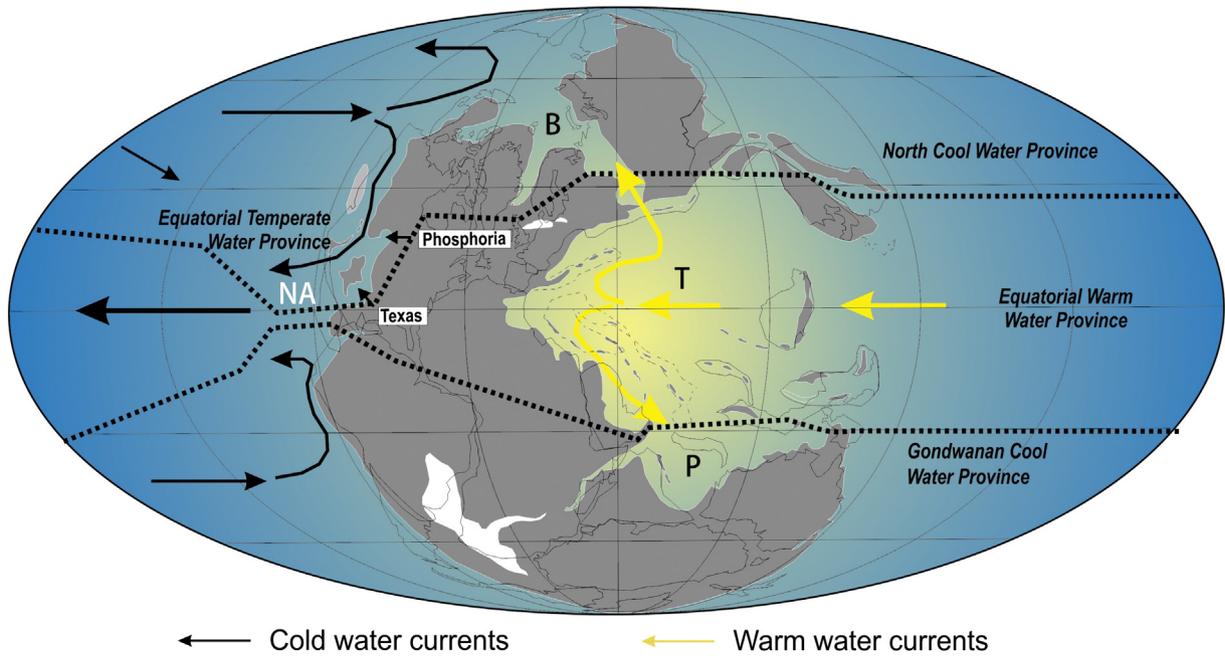
Marine biotas are sensitive to local, regional and global environmental changes and exceptionally well-studied shallow water benthic foraminifera are among the best indicators for paleoenvironments (Murray, 2006 and references herewith). The Cenozoic record of larger benthic foraminifera diversity (Hallock et al., 1991) shows a strong

correlation with well-studied climatic changes for that time (Zachos et al., 2001). Furthermore, several other recent studies suggest strong correlations of diversity of marine microorganisms, including those with symbionts, and sea surface temperature (Semenuk, 2001; Fuhrman et al., 2008; Mayhew et al., 2012).

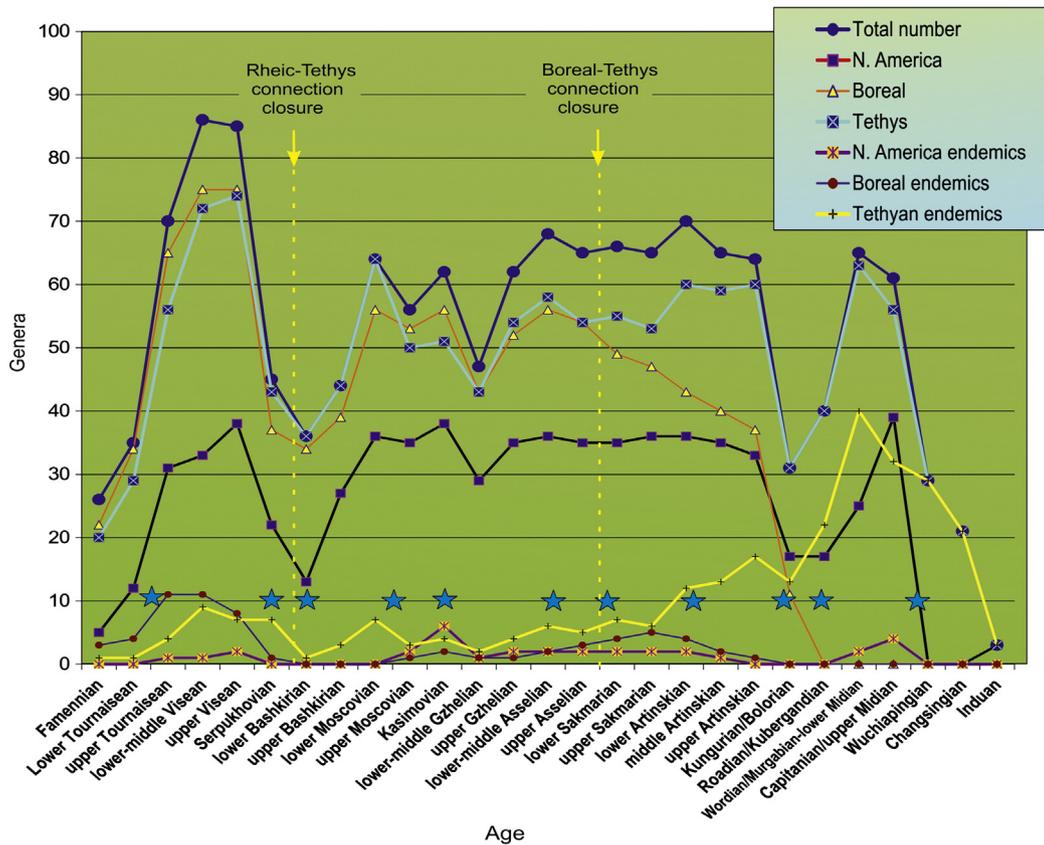
Several paradoxes exist in regards to the distributions of late Paleozoic faunas on North American shelves. During this time, Western Pangea shelves around Texas, and New Mexico and South Nevada were at tropical paleolatitude (Blakey, 2008) (Fig. 1). The taxonomic diversity of modern shallow-water organisms is assumed to be the highest at the tropic–subtropic environments (Huston, 1994; Buzas et al., 2002; Jablonski et al., 2006). However, the diversity of shallow benthic foraminifera in North American shelves is two to three times lower than that of the eastern shelves of Pangea (Urals, Donets Basins, Central Asia etc.) (Groves and Wang, 2009; Davydov et al., 2012). Even at higher Pennsylvanian paleolatitude in the present-day Arctic region (Timan–Pechora, Spitsbergen and North Greenland) the diversity of foraminifera was at least twice as high as on North American

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**Fig. 1.** Distribution of warm- and temperate water environments during Pennsylvanian–Cisuralian. The reconstruction is simplified after Ziegler et al. (1997). NA – North American province, B – Boreal, P – Peri-Gondwana and T – Tethyan provinces. Black lines – cold current, yellow lines – warm currents. Black dotted line – approximate border between warm and temperate paleoclimatic zones. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Fusulinid generic global and provincial diversity pattern (the raw data from Rauser-Chernousova et al., 1996). The foraminiferal diversity at the tropical paleolatitude in the North America shelves two–three times lower compare with those in Tethys province and even in mid-latitude Boreal province. The maximum diversity peaks are generally corresponds with global warming episodes, whereas the minimal diversity peaks perhaps indicate the cooling events. Some of the proposed cooling events coincided with known global glacial episodes (blue stars) documented in the literature (Fielding et al., 2008b; Grossman et al., 2008; Gulbranson et al., 2010; Isbell et al., 2012). Note a very low diversity of endemic genera in North American province through the time. For more details see the text. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tropical shelves (Fig. 2). Some workers might suggest that the apparent higher diversity of the eastern Pangea shelves is because Russian workers have been more prone to “splitting”, thus creating more taxa. However, taxa at generic level are generally accepted by excathedral international workers, including specialists from North America (Nassichuk and Wilde, 1977; Rui Lin et al., 1994; Ross, 1995). Some genera are recognized in North America when the concepts of the Russian taxonomy become available for the students in greater details (Wahlman et al., 1997).

The second paradox refers to the fact that the FOD of the majority of North American foraminifera genera in the western Pangea shelves possess the lag of 2–3 Ma and sometimes up to 5 Ma in comparison to the FAD of these genera elsewhere. At the same time, none of the genera occur in North American shelves earlier than elsewhere (Ross, 1995).

Finally, the third phenomena and paradox is the common occurrence of fauna characteristic of temperate climate including foraminifera, brachiopods, pelecypods and other fossils like *Palaeoaplysina* (Mamet, 1977; Ross, 1995; Wahlman and Konovalova, 2002; Weldon and Shi, 2003; Perez-Huerta, 2007; Clapham, 2010; Hanken and Nielsen, 2013) in North American at tropical paleolatitude.

A recently proposed model of the interaction between climate and tropical benthic foraminifera (Davydov and Arefeffard, 2013; Davydov et al., 2013a) and assessments of the Late Paleozoic climatic fluctuations are applied here in order to understand and evaluate paradoxes and problems mentioned above. The data on the global shallow water benthic foraminifera diversity variations are combined here with the pattern of their immigration from tropics into the North American shelves and the link between biotic and climate events is proposed and documented. Although Mississippian shallow water benthic foraminifera do not possessed symbionts, their evolution and distribution pattern are consistent with the larger symbiont-bearing shallow water benthic foraminifera such as fusulinids.

## 2. Paleobiology and paleoecology of fusulinaceans

Although extinct, Late Paleozoic shallow warm water benthic foraminifera (including Ammodiscida, Endothyroidea and Fusulinoida, by Vdovenko et al., 1993 and Rauser-Chernousova et al., 1996) played a leading role in benthic assemblages during the Late Paleozoic and: (a) dominated numerically in micro-benthic communities; (b) were globally wide spread within the tropics and subtropics; (c) evolved rapidly and reached highest taxonomic diversity among micro-benthic communities. These foraminifera, including the most important group such as fusulinids were mostly distributed within carbonate to mixed carbonate–siliciclastic shallow-water settings (Ross, 1995) in the tropical-subtropical belt (up to 35–40° S/N paleolatitude). Based on similarities in size and test morphology of fusulinids, as well as with the biofacies associations of modern larger benthic foraminifera (Beavington-Penney and Racey, 2004; Hohenegger, 2004; Murray, 2006), the majority of fusulinids are assumed to have hosted photosynthetic symbionts (Ross, 1982; Vachard et al., 2004). Benthic foraminifera are poikilothermic, i.e. their body temperature is very close to that of the surrounding water, and therefore, they responds very quickly to even small changes in the ambient water temperature (Beavington-Penney and Racey, 2004). Temperature is generally considered to be the most important physical factor influencing the distribution of benthic foraminifera and particularly on symbiont-bearing protists (Murray, 2006; Fuhrman et al., 2008; Afzal et al., 2011). Fuhrman et al. (2008) analyzed several parameters that control the taxonomic diversity of symbiont-bearing protists, such as salinity, food supplies, chlorophyll, average primary productivity and surface water temperature. It was clearly recognized that taxonomic richness strongly and positively correlates with water temperature at the time of sampling, and even more strongly with average annual sea-surface temperature. These data and analyses (Fuhrman et al., 2008) support the hypothesis that diversity of symbiont-bearing protists as well as

the other shallow water benthic foraminifera in a given habitat is largely generated and maintained by effects of temperature on the kinetics of metabolism. The metabolic rate, which increases exponentially with increasing temperature, sets the pace of life and hence the rates of nearly all biological activities.

Shallow-water assemblages of present-day shallow water benthic foraminifera in optimal water temperatures (20–30 °C) are generally much more diverse than those in temperatures greater than 30 °C or less than 20 °C (Fig. 3) (Beavington-Penney and Racey, 2004; Hohenegger, 2004; Murray, 2006; Afzal et al., 2011). Similar changes in diversity are apparent in the latitudinal distribution of the late Paleozoic benthic shallow water foraminifera and these are assumed to correspond to tropical-subtropical temperature changes (Ross, 1995). During global warm episodes, benthic shallow water foraminifera migrated to higher latitudes. By contrast, cooling led to migration of most of these foraminiferal faunas from higher to lower latitudes, stepwise extinction of some of the larger taxa, increasing provincialism, and the preferential survival of eurytopic faunas adapted for a broader range of facies and environments (Stanley, 1984; Ozawa, 1987; Kalvoda, 2002; Mayhew et al., 2012).

Climatic fluctuations and velocity of climate change are most significant at mid-latitudes, as has been shown in the modern-world (Burrows et al., 2011) and Permian models (Winguth et al., 2002). SWWBF faunas provide a particularly sensitive indicator for climate change in these areas. Permian climate simulation models (Winguth et al., 2002) suggest a significant 5–7 °C latitudinal shift in average sea-surface temperature and associated climatic belts under glacial versus non-glacial (warm) climatic states. This model for the mid-latitudinal regions has been successfully applied to help understand climate dynamics during late Gzhelian (latest Pennsylvanian of Timor and Australia) (Davydov et al., 2013a) and Guadalupian (Oman–Zagros areas) time (Davydov and Arefeffard, 2013).

## 3. Migrational pattern and dispersal of shallow warm water benthic foraminifera between Tethys and North America

In terms of the establishment of the direction pattern and interaction of shallow warm water foraminifera between different paleobiogeographic provinces, Thompson (1967) was the first

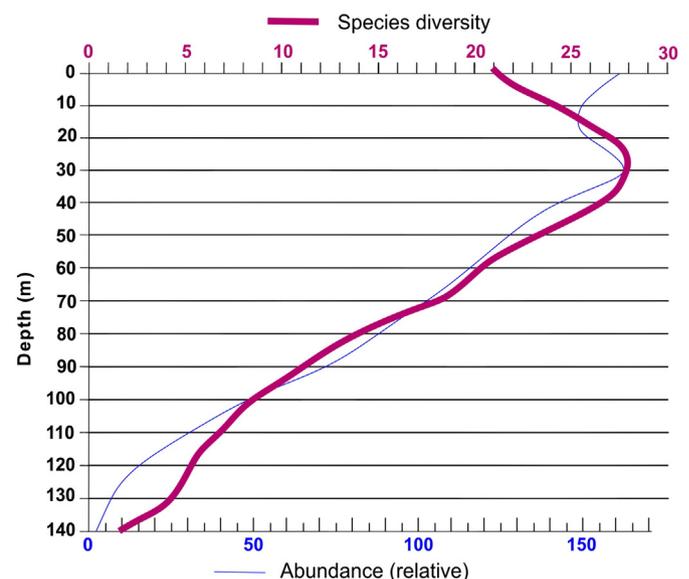


Fig. 3. Fundamental depth distributions of present day northwest Pacific symbiont-bearing benthic warm water foraminifera in clear ocean water (developed from Hohenegger, 2004). The low limit of the thermocline for these foraminifera is at 140 m. Foraminifera become abundant (>50 specimens and >7 species) at depth 110–100 m and reached their diversity/abundance at depth 40–30 m.

who noted the emigrational character of the occurrences of some important SWWBF forms in North America. For the pre-middle Permian forms he assumed east to west migration from Tethyan basins through the Arctic (North Greenland and Canadian Archipelago). Particular Uralian–Franklinian province that extends from the Urals in the east to the Nevada in the west has been proposed by Ross (1967, 1995). Because of uniform fauna within the province from Urals to Nevada it suggested frequent connections between these regions.

The Urals to North America migrational pattern specifically for *Triticites* was assumed by Davydov (1997b) and Villa and Wahlman (2007) and for *Profusulinella* by Groves et al. (2007). The latter genus appears in Tethys during early middle Bashkirian time and migrated to North America in the early Moscovian, as suggested by Groves et al. (2007), through the northern passage along northern margin of Pangea which was named Franklinian corridor. *Triticites* appears in western Tethys in the early middle Kasimovian (Davydov, 1990) and migrated to North America in late Kasimovian (Dennis cylothem) time (Davydov, 1997b; Villa and Wahlman, 2007).

It should be noted, however, that east–west migration through the Franklinian corridor was not the only way of dispersal for the SWWBF. The east–west migration potentially was possible only during Pennsylvanian–Cisuralian time until the northern margin of Pangea reached the temperate to cold climatic belt due to movement of the continent toward the north (Beauchamp, 1994). Thus, since Kungurian time the connection through the Franklinian corridor was not possible even potentially. At the same time, the migrations of the SWWBF in North American shelves occur in Kungurian and post-Kungurian times until the late Capitanian (Thompson, 1967). This clearly suggests the west to east migration of the SWWBF from eastern Tethys to North American realm. Therefore the interprovincial connections could potentially being permanent and migration of the new SWWBF faunas to North America could occur at any time during Pennsylvanian and Permian from both east–west and west–east directions, i.e. through the Franklinian corridor or from eastern Tethys directly to North American shelves. There are three cases where east to west connection between Arctic/Urals and North SWWBF is undoubtful. Moscovian *Wedekindellina*, early Kasimovian *Eowaeringella* and early Sakmarian *Eoparafusulina* were the genera that are endemic to Arctic/Urals and North America provinces. The two former genera are not known elsewhere. *Eoparafusulina* is widely distributed in Panthalassa and Peri-Gondwanan regions (Ueno, 2006; Davydov and Arefifard, 2007), but the earliest appearance documented in Russian Arctic (Grozdilova and Lebedeva, 1961).

#### 4. Temperate environments in North American shelves during Late Paleozoic

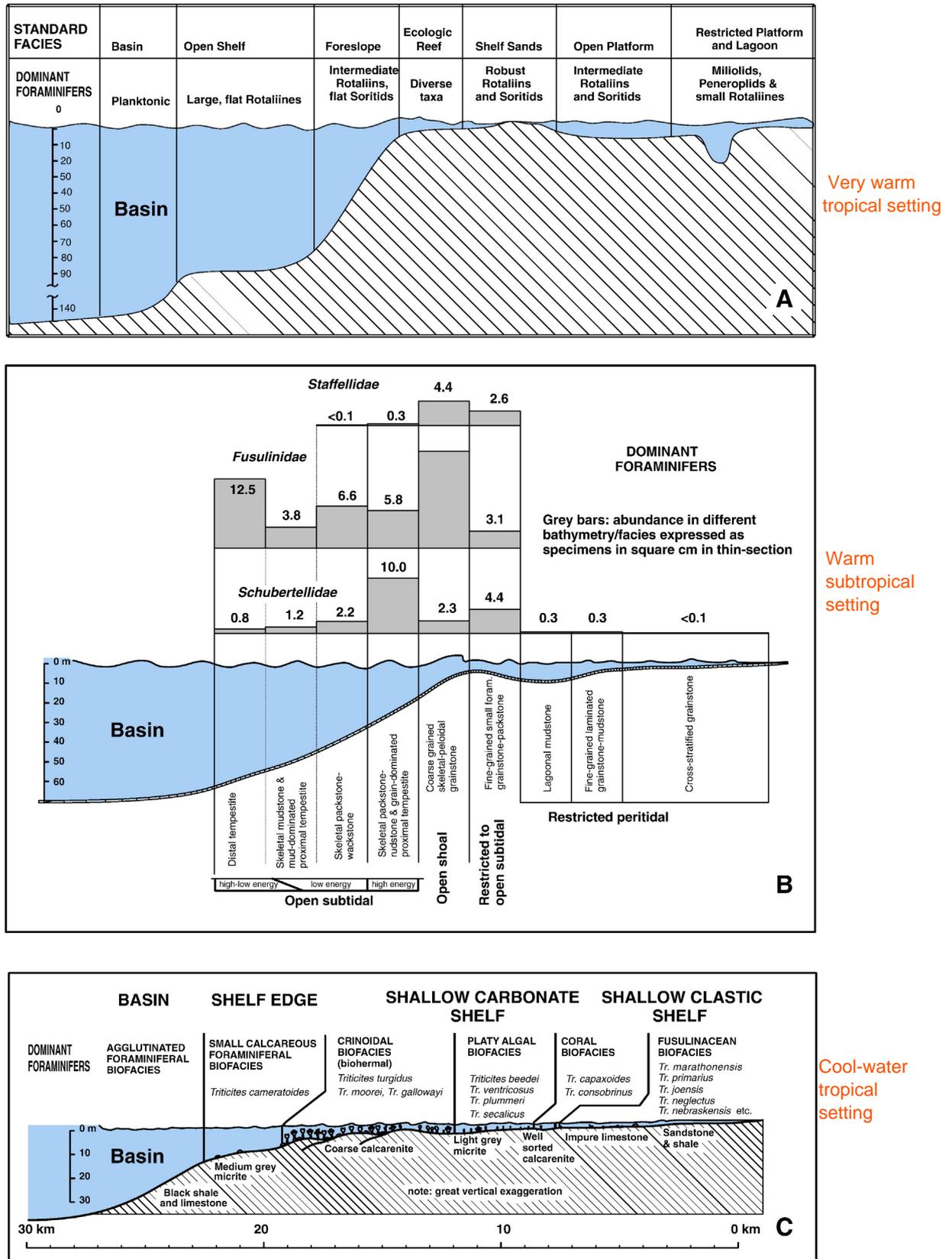
Several studies have noted a significantly lower diversity of Late Paleozoic foraminifera in North America when compared with corresponding assemblages in Tethys and even in Boreal faunas (Fig. 1) (Mamet, 1977; Davydov, 2008; Groves and Wang, 2009) but no reasons for this situation have been offered. A possible reason proposed here is that North American shelves in tropical paleolatitude had predominantly temperate paleoclimates (Davydov, 2008, 2013). The Permian regional climate cooling of western Laurentia has been documented from several benthic fossils (Clapham, 2010). Similarly, several temperate-index fossils, such as cold-water Conulariids and other pelecypods were documented within the North America shelves in Idaho, Nevada, and West Texas, (Kauffman and Runnegar, 1975; Meldon and Shi, 2003). Potential glendonites in the Bashkirian and middle Moscovian of Nevada were reported from the western margin of North American craton (Bishop et al., 2007; and personal data of the author). In addition possible evidence of alpine glaciation at this tropical paleolatitude zone has been presented for the Devonian (Brezinski et al., 2010) and also proposed for the Pennsylvanian in the Ancestral Rocky Mountains (Soreghan et al., 2008). Because of the shift of cool-water thermocline

southwards along the Laurentia, the environment in the shelves there was similar to as in the mid-latitudes elsewhere in Boreal and Peri-Gondwanan provinces (Davydov and Arefifard, 2013; Davydov et al., 2013a). Further evidence of late Paleozoic temperate paleoclimatic conditions in western Pangean tropical paleolatitude is the larger foraminifera thermocline, which is two to three times shallower than in eastern Pangean tropical to subtropical paleolatitude.

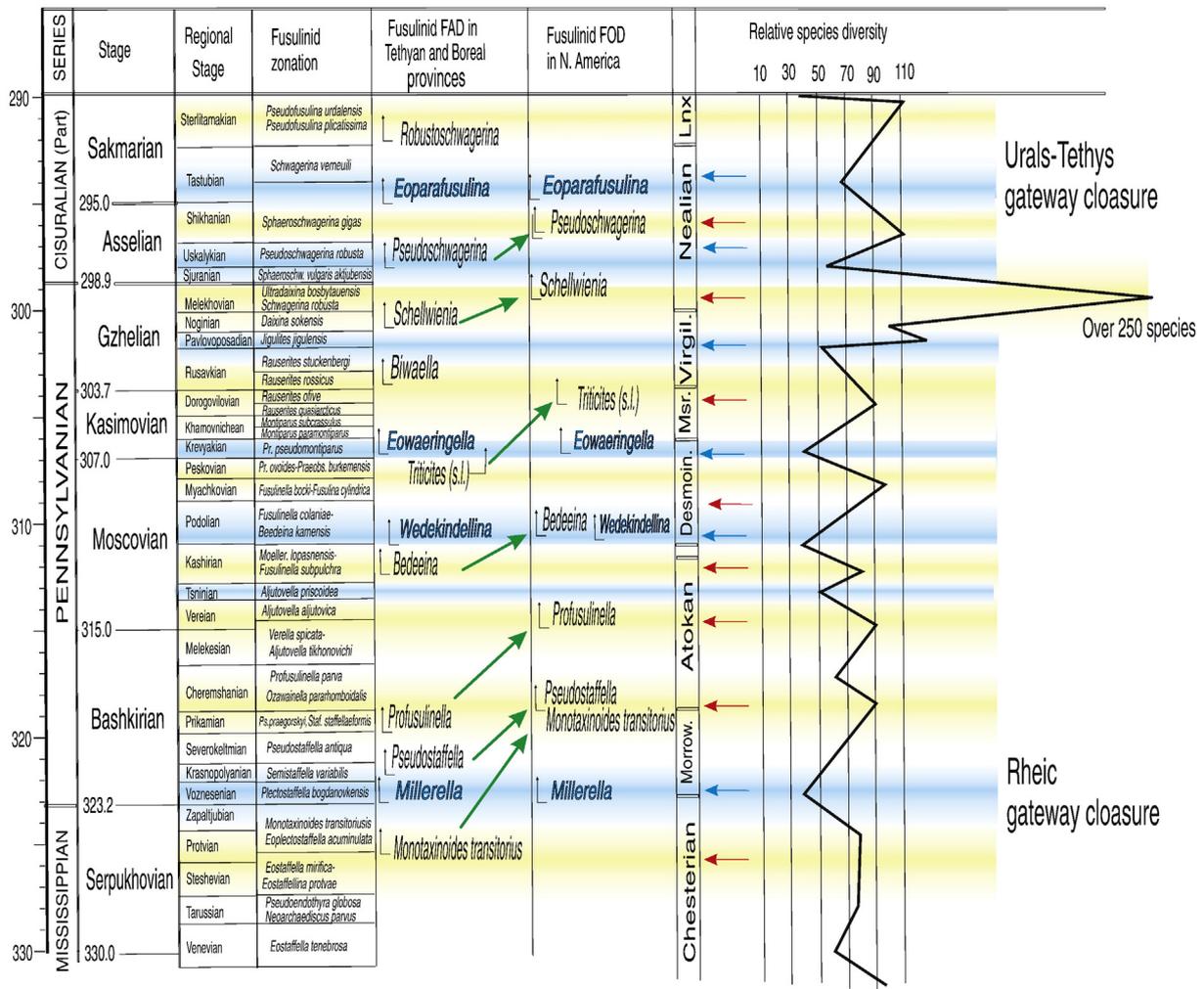
The data from modern tropical shelves suggest that the average thermocline range for the temperature sensitive foraminifera is 50–70 m with the maximum depth at 140 m (Figs. 2–3) (Beavington-Penney and Racey, 2004; Hohenegger, 2004). The studies in the Carboniferous subtropics in Moscow Basin at about 25–30° N paleolatitude in the eastern Pangea shelves suggest the fusulinid's thermocline range is at about 20–30 m with maximum depth at 40 m (Baranova and Kabanov, 2003). There are two studies on fusulinid paleobathymetric distributions in western North America. The paleobathymetry of most Desmoinesian fusulinids in Colorado was estimated at a range of 13–22 m with probable maximum depth of 30–40 m (Stevens, 1966, 1971). Ross (1968) also analyzed fusulinid paleobathymetric distributions in Desmoinesian, Virgilian and Wolfcampian strata, and suggested that the average paleobathymetric range was 3–10 m, with a maximum depth of near 12–15 m. Thus, the fusulinid thermocline in North American tropical paleolatitude shelves is at least twice as shallow as in the tropical shelves in eastern Pangea (Fig. 4). These interpretations of paleobathymetric distributions suggest significantly cooler water paleoenvironments on paleotropical shelves of western Pangea, perhaps to the degree of the environments in the mid-latitudes (subtropics to temperate zones). Of course, this suggestion requires serious consideration, and it is could be potentially tested with several independent techniques.

The diversity in the Western Laurentian tropical fusulinacean assemblages are two to three times lower than that of the eastern shelves of Pangea (Urals, Donets Basins, Central Asia etc.) (Fig. 2). Even at higher latitudes, i.e. around mid-latitudes in Arctic (Timan–Pechora, Spitsbergen and North Greenland) where the diversity usually low than in tropics, the diversity of SWWBF during Pennsylvanian was at least twice as high as in North American tropical shelves (Fig. 2). Besides this, North American realms that was within tropical paleolatitude, never been a center of origination of the taxa that dispersed outside of the realm as it was occurring in Tethys. Rather the majority of the taxa in North American realm are highly endemic, i.e. dispersed only within the shelves of the western Laurentia. The SWWBF of North American realm commonly include genera that commonly occur only at higher temperate mid-latitudes in Boreal and Peri-Tethyan provinces (i.e. *Pseudofusulinella*, *Wedekindellina*, *Eoparafusulina* etc.). However, typical warm water taxa occasionally and abruptly occur throughout the Late Paleozoic in North America and potentially provide valuable information on the dynamics of Late Paleozoic climate (Ross, 1995; Davydov, 2008; Davydov et al., 2012; Wahlman, 2013). In particular, the record of warming episodes within the successions is highlighted by the occurrence of warmer water tropical taxa that are exotic to this region fauna. These warmer water and exotic for the region elements appear in the local communities suddenly due to migration during warming episodes and do not have any evolutionary roots with local faunas. It appears that most North American fusulinid faunas evolved elsewhere and episodically migrated into the region (Figs. 5–6).

It also make sense to assume that North American province was predominantly cool-water with permanent factor (s) controlling and keeping water cool (upwelling and/or cold water currents). Global warming events will not affect North American shelves as much as the areas, where upwelling/or cold water currents are not significant, like in the Urals and Arctic, i.e. in mid-latitudinal subtropics of Northern Pangea. In the latter regions though the global warming events increase the diversity so much that it is nearly reached the diversity in tropics (Davydov et al., 2014). At the same time the global cooling events will stronger affect Urals



**Fig. 4.** Distribution of shallow warm water benthic foraminifera at different latitudinal and paleoclimatic settings. A – idealized distribution of major recent foraminiferal groups in reef-associated environments in tropics (from Beavington-Penney and Racey, 2004), shallow warm water benthic foraminifera thermocline is going to 90–100 m depth; B – distribution of fusulinid groups in Myachkovian (Late Moscovian) facies/environments in shallow-water carbonate subtropical (25–30° N) environments in Russian Platform. Gray bars indicate abundance of fusulinids in different bathymetry/facies expressed as a number of specimens in square cm in thin-section. Fusulinids in this mid-latitude, transitional from tropics to subtropics region, distributed down to the depth 60–70 m (modified from Baranova and Kabanov, 2003); C – reconstruction of depositional environments of the Pennsylvanian and Cisuralian at tropical paleolatitude carbonate shelves (western Pangea tropics) in Texas and distribution of species of fusulinids (modified from Ross, 1968). Fusulinids generally distributed at the depth 0–7 m and become rare around 10–15 m depth. The fusulinids thermocline in this tropical paleolatitude is abnormally shallow, i.e. 140 m in normal paleotropics vs 10–15 m in North American paleotropics.



**Fig. 5.** The warming and cooling events along the North American shelves during Pennsylvanian and early Cisuralian. The majority of fusulinid genera at the tropical paleolatitude in North America occur as result of the immigration to the region always with lag around 1.5–4 Ma in comparison with their origination in Tethys tropics. The immigration to North America occurred rapidly and abruptly and is likely to have been associated with warming events. At several levels (early Bashkirian, lower upper Moscovian, early Kasimovian and early Sakmarian) the appearance and dispersal of certain fusulinids in North American and Boreal provinces occur isochronous. These levels interpreted to have been associated with cooling events that make environments in both provinces uniform and favorable for the distribution these cool-water faunas. Abbreviations for the North American stages: Morrowan. – Morrowan, Desmoinesian. – Desmoinesian, Msr – Missourian, Virgil. – Virgilian, Lnx – lower part of Lenoxian.

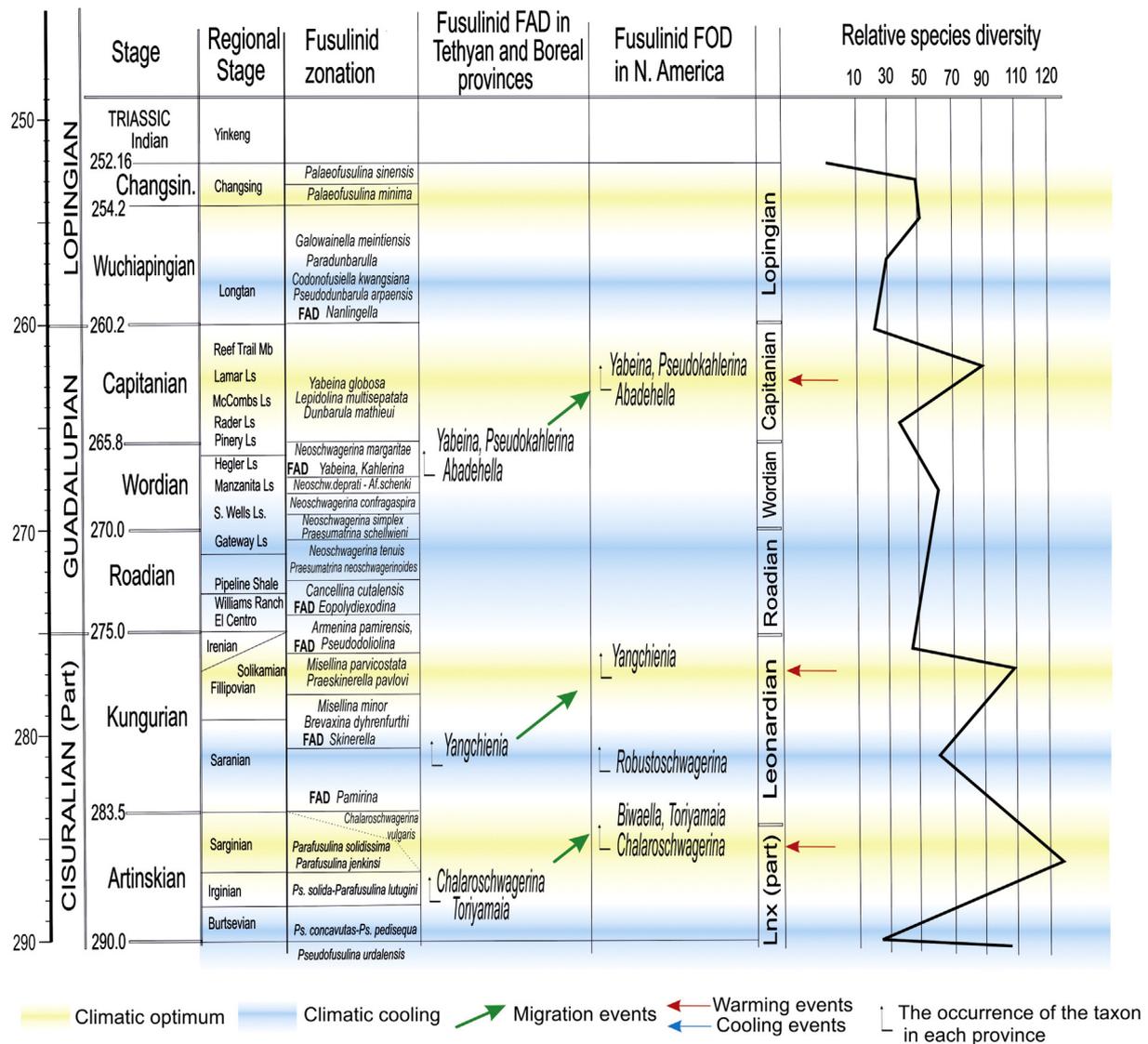
and Arctic regions and less significant North American province what will make climate more uniform between North American at tropical paleolatitude and northern Pangea subtropics (Arctic, Urals). This is consistent with the data from the recent foraminifera. As has been shown along the Western Australian coast the most pronounced changes of foraminifera diversity along the climate (temperature) gradient occur in summer, whereas during winter the foraminiferal assemblages along the gradient are more closely related (Semeniuk, 2001). Thus, during the warming events the greater diversity and taxonomic difference between permanently cooler North American shelves and Arctic-Ural shelves where climatic fluctuations were more dynamic might be expected. During the cooling events the difference between these regions perhaps was minimal.

**5. Late Paleozoic climate variation within the Western Pangea shelves**

At the very end of the Serpukhovian, North American shelves and Eastern Pangea share similar foraminiferal faunas even at species level. Several genera and important species such as *Monotaxinoides*

*subconicus* (Brazhnikova and Yartseva), “*Millerella*” *designata* Zeller, “*Millerella*” *tortula* Zeller, *Brenckleina rugosa* (Brazhnikova), *Eosigmoilina robertsoni* (Brady), *E. explicata* Ganelina, *Eostaffella proikensis* Rauser-Chernousova, *Eolasiiodiscus* sp., *Asteroarchaediscus rugosus* (Rauser) are common in the latest Serpukhovian of Donets Basin and Urals and latest Chesterian (Kinkaid Limestone and Grove Church Shale) of North America (Brenckle, 1977; Brenckle et al., 2005). Recently, the earliest representative of the typical Tethyan genus *Plectostaffella* has been found in the uppermost Chesterian in the type sections in southern Illinois (Kulagina et al., 2008).

At the beginning of Bashkirian time, after the probable closure of Rheic pathway, the connection of western and eastern shelves of Pangea was completely cutoff (Saltzman, 2003), which had a direct effect on the taxonomic composition of foraminifera faunas in the two regions. Provincialism of foraminifera rapidly increased subsequently and almost no common species occur in the western and eastern shelves of Pangea. Moreover, in the western Pangea (North American) shelves the taxonomic diversity of fusulinids decreased markedly compared to the eastern Pangea shelves (Fig. 2). The fusulinid diversity in North American shelves during the Morrowan, i.e. the major part of the Bashkirian, is the lowest within the entire Carboniferous and Permian.



**Fig. 6.** Warming and cooling events along the North American shelves during late Cisuralian through the end of the Permian. The warming events associated with diversity peaks and occur in late Artinskian, late Kungurian, Capitanian and Changsingian. The cooling events correspond to the low taxonomic diversity interval and proposed to occur in early Artinskian, early Kungurian, Roadian–early Wordian and early Wuchiapingian. Abbreviations for the chronostratigraphic units: Lnx – lower part of Lenoxian. Word. – Wordian; Changsin – Changsingian.

Two to three long-ranging species of *Millerella* and several rare species of *Eostaffella* occur in North American shelves during that time (Brenckle, 1977; Nodine-Zeller, 1977; Groves, 1986). The time correlative Bashkirian assemblages in Tethys include over 10 genera and 40–50 species (Brazhnikova et al., 1967; Vdovenko et al., 1984; Kulagina et al., 1992; Kulagina et al., 1997; Groves et al., 1999). Only one genus, *Millerella*, is common in both the western and eastern shelves of Pangean regions. The genus appeared at the beginning of the Bashkirian or slightly earlier and became rapidly distributed globally. The occurrence of that genus in all known regions is isochronous (Vachard and Maslo, 1996; Groves et al., 1999). The low foraminiferal diversity during the Morrowan can be linked with the Bashkirian glacial event recently constrained in Gondwana (C2 glaciation) (Fielding et al., 2008a; Gulbranson et al., 2010). Because of slow evolution and extremely low diversity during the early and middle Bashkirian (Morrowan) time, no zonation has been established in the Morrowan of North America (Groves, 1986; Wahlman, 2013). The Morrowan was probably the coldest in the North American shelves environment lasting for about 4.5–5.0 Ma (Fig. 5) (Davydov et al.,

2012). Long-ranging r-strategist *Millerella* was apparently one of the most environmentally tolerant fusulinid during early to middle Bashkirian time and the global cooling event allowed its isochronous dispersal in both western and eastern temperate Pangea shelves.

The first warming episode in North American shelves at the beginning of the Atokan time was associated with the immigration of *Pseudostaffella* and slightly later *Schubertella* and *Schubertina* (Groves, 1986; Davydov, 2011). The *Pseudostaffella* FAD (First Appearance Datum) in eastern Pangea and elsewhere in Tethys is in lower Bashkirian, approximately at 321.5 Ma (Reitlinger, 1971; Kulagina and Sinitsyna, 2003; Davydov et al., 2012) and the FOD (First Occurrence Datum) of the genus in North America is about 318.5–318 Ma, i.e. with the delay of 2.0–3.0 Ma (Groves et al., 1999; Davydov et al., 2012). The *Schubertella* and *Schubertina* FAD in Tethys are at about middle Bashkirian (Kulagina et al., 2001; Nikolaev, 2005) and its migration to North America was not delayed as much as *Pseudostaffella*.

The second important immigration event, and possible warming episode, is associated with the occurrence of *Profusulinella* in the upper Atokan time (Groves et al., 1999) at the beginning of the global

early Moscovian transgression (Makhlina et al., 2001; Schmitz and Davydov, 2012). The *Profusulinella* FAD in Tethys and Boreal provinces is at 320 Ma, compared with its FOD in North America at approximately 315 Ma (Davydov et al., 2012). The genus is widely distributed within the western shelves of Pangea and is well documented from Bolivia to the Great Basin and western Canada (McGugan and Rapson, 1979; Groves and Sanderson, 1990; Sakagami and Mizuno, 1994). The delay of the occurrence of *Profusulinella* in North America in respect to the FAD in Tethys was approximately 4.5–5.0 Ma (Fig. 5) (Davydov et al., 2012).

Two cooling events can be recognized within the Moscovian and the Moscovian–Kasimovian transition. The first one is marked by the sudden and isochronous occurrence of *Wedekindellina* in both North American and Arctic/Urals shelves. *Wedekindellina* is restricted only to these two areas and has not been reported from Tethys and/or Peri-Gondwana. In Boreal province, *Wedekindellina* is a very common form and is documented in Central and Northern Urals, Timan–Pechora and Spitsbergen–North Greenland and Canadian Arctic regions (Chuvashov and Dyupina, 1979; Rui Lin et al., 1991; Groves et al., 1994; Remizova, 1995; Davydov, 1997a; Davydov and Nilsson, 1999; Davydov et al., 2001). The southernmost occurrence of *Wedekindellina* in Boreal shelves is in the Southern Urals, where this genus is rare (Davydov, 1986). *Wedekindellina* is common in North American shelves where it occurs at the base Desmoinesian (Thompson, 1934; Waddell, 1966; Wahlman, 2013). The evolutionary roots of the genus are not clear. Most probably it is evolved from *Fusulinella* (Miklukho-Maclay et al., 1959). The first occurrence datum in both North American and Boreal shelves are well constrained and seem synchronous. This evolutionary event is also associated with the reduction of the fusulinid diversity in Podolskian in the eastern Pangaea and at the Atokan–Desmoinesian transition in the western Pangaea (Groves and Wang, 2009; Davydov et al., 2012) and increasing provincialism (Schmitz and Davydov, 2012). The isochronicity of the occurrence of *Wedekindellina* in temperate climatic zones (Arctic–Urals and North American shelves) is interpreted here as evidence of a cooling event where cool-water assemblages in both North America shelves and northern Pangea shelves become more uniform than the warm water assemblages in these regions (Fig. 5). The last occurrence datum of *Wedekindellina* in Timan–Pechora Basin is the middle Kasimovian (Remizova, 1995; Davydov, 1997a). In North America *Wedekindellina* considered lower Desmoinesian genus (Thompson, 1954; Wahlman, 2013). However, rare *Wedekindellina* ranged up to the top of Desmoinesian (personal data of the author from Nevada). The second potential cooling event corresponds with the major extinction event in the fusulinid evolution at the Moscovian–Kasimovian boundary (Kireeva, 1964; Reitlinger, 1969; Davydov, 1990; Davydov and Nilsson, 1999; Khodjanyazova et al., 2014). This extinction is well expressed in Tethys (Leven and Davydov, 2001) and at the global scale (Groves and Wang, 2009; Davydov et al., 2012) and is associated with the unconformity in many regions in Pangaea (Davydov and Nilsson, 1999) and with the turnover of the early–middle Pennsylvanian fusulinid fauna into the late Pennsylvanian–Permian schwagerinid fauna. In Boreal and North America provinces this event is marked by the occurrence *Eowaeringella*. At the boundary in the North America there is also a marked unconformity and an interval that lacks any significant fusulinids. *Eowaeringella* genus in North America characterizes the lowermost Missourian (Thompson et al., 1956; Stewart, 1968; Wahlman, 2013). In the Boreal region it is known to occur in the early to middle Kasimovian of Timan–Pechora (Remizova, 2004). These two occurrences are essentially isochronous (Schmitz and Davydov, 2012) (Fig. 5). The genus range is very short.

Early–middle Kasimovian is also approximates with the first occurrence datum of a poorly known genus *Oketaella* in both North America and Timan–Pechora Basin. In the first region, it co-occurs with *Eowaeringella* and in Timan–Pechora it is reported from early to middle Kasimovian (Thompson et al., 1956; Remizova, 1995; Davydov, 1997a;

Wahlman, 2013). The next warming event in the North American shelves is marked by the immigration of *Triticites* from Eurasia (Thompson, 1967; Davydov, 1997b; Villa and Wahlman, 2007). The genus evolved in Tethys during early to middle Kasimovian (late Desmoinesian–early Missourian) and appeared in North America only in the early middle Missourian (upper Kasimovian) (Thompson et al., 1956; Davydov, 1997b; Wahlman, 2013). The time lag in the appearance of the genus in North America is 1.5–2.0 Ma (Fig. 5).

Another warming event during the late Gzhelian in the Tethyan and Boreal provinces is associated with the maximum peak in foraminiferal diversity and the global distribution of many fusulinid species (Groves and Wang, 2009; Davydov et al., 2012; Davydov, 2013; Davydov et al., 2013a). In North American shelves it is marked by the occurrence of *Occidentoschwagerina* (= *Advenella* of Wilde, 2006), *Likharevites* (= “*Alpinoschwagerina*” of Wilde, 2006) and *Schellwienia*, which is thought here to include many North American species traditionally placed in *Schwagerina* or *Pseudofusulina*. (Davydov et al., 2014).

*Occidentoschwagerina*, *Likharevites* and *Schellwienia* are exotic to the region, possess no evolutionary relationship with any local fusulinid faunas and are most likely migrated to the region from the Tethys. *Schellwienia* in Tethys appears in the late Gzhelian *Daixina sokensis* zone (Davydov, 1986), whereas in North America the genus appears in the latest Gzhelian (Schmitz and Davydov, 2012; Wahlman, 2013). The difference between the occurrences in the Tethys and North American shelves is around 1 Ma or less (Fig. 5) suggesting a very rapid onset of global warming event at this time (Davydov et al., 2013a). This event is coincident with the highest global foraminiferal diversity during the Pennsylvanian–Permian time (Groves and Wang, 2009; Davydov et al., 2012). *Occidentoschwagerina* and *Likharevites* are typical Tethyan genera and in the Boreal province occur only in Spitsbergen and Central Urals (Nilsson and Davydov, 1997; Vilesov, 2000). In North America these genera are found only in New Mexico (Wilde, 2006).

The proposed here global warming event contradicts with several recent papers that cite the maximum late Paleozoic glacial event around the Carboniferous–Permian boundary, i.e., Late Gzhelian (Montanez et al., 2007; Fielding et al., 2008b; Isbell et al., 2012). This contradiction definitely requires special attention and multidisciplinary studies. It can be noted, however, that the proposed here late Gzhelian global warming event are precisely constrained biostratigraphically whereas the direct record of glaciation over Carboniferous–Permian transition interval remains equivocal given the paucity of chronostratigraphic constraints (Montanez and Poulsen, 2013).

Middle Asselian appearance of *Pseudoschwagerina*, is well-documented in the Tethys (Scherbovich, 1949; Rauser-Chernousova, 1961; Bensch, 1972; Leven and Scherbovich, 1978). In the Boreal province and in North America it appeared during late Asselian time (Thompson, 1954; Konovalova, 1991; Nilsson and Davydov, 1997; Schmitz and Davydov, 2012), which suggests a warming event at that time. There are several other lines of evidence of the warming event during late Asselian in the North American and Boreal shelves. For example, *Biwaella*, which appears in the Tethys in the early Gzhelian (Davydov, 2011), migrated into the Boreal province in the late Asselian (Nilsson and Davydov, 1997). The typical warm water fusulinid *Sphaeroschwagerina* first appears at the beginning of the Asselian in the Tethyan province (Scherbovich, 1949; Kireeva et al., 1971; Leven and Scherbovich, 1978; Davydov, 1984) occurs only in the late Asselian in Spitsbergen and Canadian Arctic (Rui Lin et al., 1994; Nilsson and Davydov, 1997). Also during the late Asselian time, the species *Pseudofusulina attenuata* Skinner and Wilde from Klamath microcontinent migrated to the North American shelves, being reported in Nevada (Stevens et al., 1979; Davydov et al., 1997b) and western Canada (Zubin–Stathopoulos et al., 2012). The difference in the occurrences of *Pseudoschwagerina* in Tethys and North America is minimal and does not exceed 1–1.5 Ma. Therefore, the late Asselian warming event was shorter and not as extensive as the late Gzhelian event as

indicated by the overall lower foraminiferal diversity in the late Asselian (Groves and Wang, 2009; Davydov et al., 2012).

The widespread and isochronous occurrence of *Eoparafusulina* in Boreal and North American shelves at the beginning of Sakmarian perhaps indicates another cooling event. In Timan–Pechora and Spitsbergen this genus is very abundant in the earliest Sakmarian and becomes rare during middle Sakmarian (Grozilova and Lebedeva, 1961; Nilsson and Davydov, 1997; Remizova, 1997). In North America, the earliest occurrence of *Eoparafusulina* is reported from the single horizon in the upper part of the Neal Ranch Formation in Glass Mountains, Texas (Ross, 1967), which correlates with early Sakmarian (Wardlaw and Davydov, 2000). The range of *Eoparafusulina* in Boreal province is very short, within the lower Sakmarian only (Davydov, 1997a; Remizova, 2004). In North America, *Eoparafusulina* occurs as two acme-zones. The first one is in the early Sakmarian (Neal Ranch Formation in Glass Mountains) and it is restricted to Texas only. The second is in the latest Artinskian through early Kungurian in age and is widely known from Texas to Nevada (Dunbar and Skinner, 1937; Stevens et al., 1979; Davydov et al., 1997b). This second acme zone potentially might also represent the cooling event, but such a suggestion requires further evaluation. *Eoparafusulina* is also known from Peri-Gondwanan sections (Leven, 1993; Ueno, 2006; Davydov and Arefifard, 2013), where they occur in the assemblages with uncertain late Sakmarian to early Artinskian age.

The position and expression of the Late Sakmarian warming event in North American shelves is not clear. In the Urals and Arctic this event is associated with thick reef buildups (Rauser-Chernousova, 1950; Chuvashov, 1983; Rafaelsen et al., 2008) and significant transgression (Davydov et al., 1997a), but it cannot be readily recognized in the North American succession. It should be post-Nealian, early Lenoxian in age. However, early Lenoxian is already Artinskian in age as the upper Lenoxian possesses the late Artinskian fusulinid *Chalaroschwagerina hawkinsi* and conodont *Neostreptognathodus transitus* (Wardlaw and Davydov, 2000). Besides, the lower Lenoxian *Perigondwanania tersa* (Ross) has been found recently in lower Artinskian of Carnic Alps (Davydov et al., 2013b). In summary, the recognition of this event in North American succession requires further studies.

A late Artinskian warming event in the North America temperate zone is associated with the occurrence of several genera. The most prominent genus is *Chalaroschwagerina*, which appears in Tethys in the middle Artinskian (Davydov et al., 2013b) and is widespread in Tethys and the Klamath microcontinents through the late Artinskian–Kungurian. It occurs in North American shelves in the late Artinskian (*Ch. hawkinsi*, *Ch. nelsoni*, *Ch. solita*) (Dunbar and Skinner, 1937; Davydov et al., 1997b; Stevens and Stone, 2009). The delayed occurrence of the genus in North America is about 2–2.5 Ma. Another typical Tethyan Sakmarian–Kungurian genus *Robustoschwagerina* has been documented from lower Kungurian (middle Leonardian) in Texas (Dunbar, 1953; Ross and Ross, 2009). Also, *Bivaella* and *Rugosochusenella* occur in the Gzhelian of Tethys (Davydov, 1986, 2011), but do not appear in the south of North America (New Mexico) until the upper Artinskian (Skinner and Wilde, 1965). Because of strong provincialism of North American fusulinid assemblages in Kungurian–Wordian and perhaps overall temperate global climate at that time, no Tethyan elements have been reported, except for the occurrence of rare *Yangchienia iniqua* in the upper Kungurian part of the Road Canyon Formation (Yang and Yancey, 2000). The genus *Yangchienia* appeared in the Tethys in the early Kungurian (Leven et al., 1992). The late Kungurian in Tethys is characterized by a high fusulinid diversity peak within the Guadalupian (Figs. 1B and 4) and possibly with a warming episode. The time lag of the *Yangchienia* occurrences in Tethys and North America is about 4–4.5 Ma (Fig. 6).

The last prominent warming event and major fusulinid migration to North America occurred during the late Capitanian and included the Tethyan fusulinids such as *Yabeina*, *Pseudokahlerina*, *Paradoxiella*, *Reichelina*, *Codonofusiella*, *Rauserella* and *Lanchichites*. Also, the very

characteristic Tethyan smaller foraminifera *Abadehella* has been found above the *Yabeina* in Texas (Dunbar and Skinner, 1937; Skinner and Wilde, 1955; Nestell et al., 2006). The neoschwagerinid *Yabeina* is the most important taxon. Neoschwagerinids are a very climatically sensitive foraminifera that survive only in very warm paleoenvironments where surface water is thought to have exceeded an annual temperature of about 20–22 °C (Ueno, 2006; Davydov and Arefifard, 2013). It seems the shallow-water paleoclimatic condition in Texas at the time was marginal for neoschwagerinids because *Yabeina* in the area is rare and is represented by only a small and primitive form. The rest of the fusulinids, most of which were schubertellids and ozawainellids, are more resistant to the temperate environments (Davydov, 2011) and are thus more diverse and abundant in the upper Capitanian in North America. *Yabeina* appear in Tethys sometime in late Wordian time (early Midian in Tethys) together with other diverse verbeekids/neoschwagerinids and the schubertellids and ozawainellids mentioned above. In North America, *Yabeina* occurs with the time lag of about 4–4.5 Ma (Fig. 6).

## 6. Western Pangea climate: regional vs global signal?

The observations made here regarding western Pangean paleoclimatic fluctuations are based on interpretations of fusulinid diversity patterns and migrations events. The parallel tracking of the provincial and global fusulinid generic diversity curves (Fig. 1B) suggests that paleoclimatic and taxonomic trends were linked and global in nature. (Groves and Wang, 2009; Davydov et al., 2012). A very similar pattern has been documented at the species level when comparing global and North American foraminiferal diversity (Groves and Wang, 2009). Those parallel trends suggest that paleoclimatic events in the North American province were controlled primarily by global factors. Of course, this suggestion must be taken with great caution and evaluated further with different approaches and methods.

## 7. Conclusions

The North American shelves during Pennsylvanian and Permian time were paleogeographically located in tropical paleolatitude, but appear to have had temperate paleoclimates as indicated by significantly lower foraminiferal diversity than correlative warm-water Tethyan faunas. The episodic appearances of Tethyan faunal elements on the North American shelves are interpreted to indicate paleoclimatic warming events, rising sea levels, and interregional migrations of taxa. Several warming and cooling events are identified. The magnitude of taxonomic changes in each event could potentially be used for provisionally estimating paleoclimatic variations. The occurrences of forms exotic to North America during warming episodes are always delayed in regards of their first appearances in Tethys. The duration of these delays was dependent the magnitude and intensity of the warming episodes.

The cooling events are associated with increasing provincialism, decreasing taxonomic diversity and appearances of endemic forms characteristic of temperate water provinces only. The occurrence of these forms in Boreal and North American provinces appears to be isochronous, probably because their environments were uniform. The patterns of global and North American province diversity at generic and species levels are very similar. A strong link between biotic and climatic events in North American province and the similarity of biotic changes in the North American and other provinces suggests that paleoclimatic events in North American province were controlled by global factors.

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