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Geological and Biological Reasons for the Cessation of Reef Formation: Evidence from the Paleozoic

V. G. Kuznetsov[a], * **and L. M. Zhuravleva**[a], **
[a]*Gubkin Russian State University of Oil and Gas, Leninskii pr. 65/1, Moscow, 119991 Russia*
**e-mail: vgkuz@yandex.ru*
***e-mail: zhurawlewa.lilia@yandex.ru*

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Abstract—The Paleozoic reef formation was a cyclic process, and its global-scale cessation was related to biological reasons: biotic crises and large-scale extinctions near the Early—Middle Cambrian, Ordovician—Silurian, Frasnian—Famennian, Serpukhovian—Bashkirian, and Permian—Triassic boundaries. The Early Cambrian stage of reef formation terminated simultaneously with the disappearance of Archaeocyatha. At the subsequent stages marked by much more complicated ecosystems, the reefs ceased to grow before the complete extinction of reef-builder communities. Hiatuses in the reef formation within separate stages were related to the geological and paleogeographical reasons (manifestations of volcanism, regressions, climate aridization, and others).

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INTRODUCTION

Reefal buildups are an important element of the sedimentary cover. They have a very high geological significance as a proxy for studying the biogenic carbonate formation and the subsequent transformations of rocks, as well as the mutual influence of biological and geological processes.

The reefal biocoenotic system represents one of the most complicated biological objects in our planet in terms of not only the composition and diversity of organisms involved therein, but also the mechanism of their functioning and interrelations because of their long-term evolution.

On the whole, evolution of life (biocoenosis make up by organisms included) in the geological time was marked by a nonlinear pattern: the geological history includes both periods of a vigorous bloom, but also periods of a higher or lower attenuation of the gradual or abrupt decrease in the development of organisms up to the point of their large-scale extinctions. Despite such irregularity, however, the process of development, on the whole, follows a path to sophistication.

FORMULATION OF THE ISSUE AND RESEARCH OBJECT

The geological and biological processes are marked by close interrelations during the formation of reefal buildups. In the majority of reefs, organisms in the composition of biocoenoses are represented by the skeletal varieties (framework species included). However, one can also see buildups made up by the bacterial—algal communities that are often defined by the generalized term “mud mounds.”

From the geological point of view, reef is a carbonate massif completely or partly composed of remains of organisms and their decomposition products. During the formation of the massif, it was rising above the surrounding seafloor. Since the reef growth rate exceeds the accumulation rate of the surrounding sediments, it is significantly thicker than the host synchronous sediments.

From the biological point of view, reefs are products of the activity of organisms making up an intricate biocoenosis, which is characterized by a marked diversity of the functionally different organisms: active and passive reef-builders or reef-lovers. This intricate ecosystem functions under certain conditions and evolves in accordance with the general evolution of the organic world.

The Earth’s geological history included epochs of a wide development of reefs and, on the contrary, epochs of a drastic attenuation of reef formation and even absence of reefs. In particular, the Paleozoic history includes five stages of the active development of reefs: Early Cambrian, Middle—Late Ordovician, Silurian—Frasnian, late Visean—Serpukhovian, and Permian.

Cessation of reef formation is attributed usually to paleogeographical variations, climate oscillations, regressions, and some geological factors. However, biological reasons for this phenomenon have also been

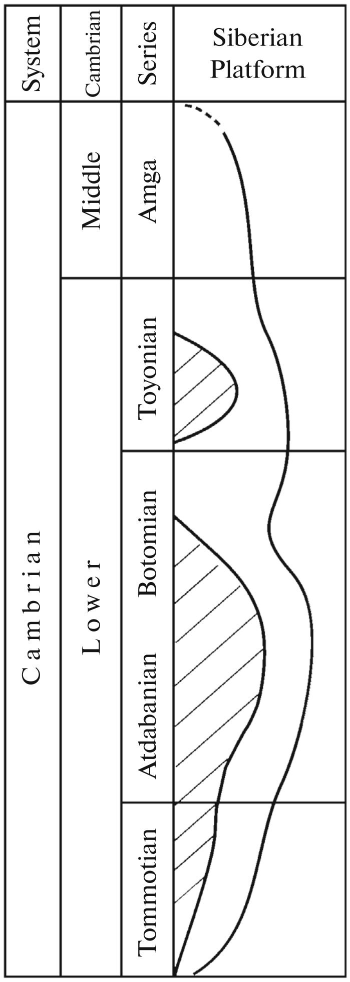

Fig. 1. Schematic stratigraphic distribution of reefs in the Cambrian in the Siberian Platform. Intervals of the development of Archaeocyatha reefs are hatched.

established. The present paper is based the analysis of relationships of the biological and geological impact as reasons for the cessation of reef development with the Paleozoic stage of the geological history as example.

DEVELOPMENT OF REEFS IN THE PALEOZOIC

To examine the given issue in historical perspective, it is necessary to provide an overview of the Paleozoic reef formation and its relationship with the greatest biotic events: large-scale extinctions recorded near the Early–Middle Cambrian, Ordovician–Silurian, Frasnian–Famennian, Serpukhovian–Bashkirian, and Permian–Triassic boundaries.

In general, the Vendian history included diverse soft-bodied (nonskeletal) multicellular organisms that lacked the capacity to make up rigid (the more so framework) bodies. Modes of the existence of bacteria (Cyanophyta included) were represented by biofilms and biomats that promoted the formation of layered stromatolites. As shown by I.K. Korolyuk (1960), V.P. Maslov (1960), and V.G. Kuznetsov (2008), columnar stromatolites rose above the basin floor only by a few centimeters and did not foster the formation of large seafloor topographies.

Appearance of reefs in the strict sense was related to the origination and development of calcareous skeleton organisms in the Cambrian that could make up a framework.

Cambrian reefs are widespread and best studied in the Siberian Platform and Altai–Sayany fold region.

Bioherms and bioherm massifs (made up by Archaeocyatha included) appeared in the Siberian Platform almost since the beginning of the Cambrian, whereas reefs only appeared since the mid-Tommotian. The bioherms were microbial–algal structures, whereas reefs were related to the appearance of cubiform Archaeocyatha and individualized organisms identified by V.A. Luchinina (1989) as a specific group of calcibionts or, according to another terminology, as calcimicrobes (Renalcis, Chabakoviaceae, branching and vertically growing epiphytons). Ultrafine brittle twigs of the epiphytons were not very firm, but they grew upward and detained the carbonate sediment.

The development of Archaeocyatha–algal reefs ceased with the extinction of Archaeocyatha by the onset of Middle Cambrian. These reefs made up, in particular, the West Yakutian barrier-reef complex that separated the Yudoma–Olenek deep-water basin with black shales from the Turukhansk–Irkutsk–Olekma shelf basin. Another reef group framed the shoals located in the shelf basin, such as Nepa–Botuoba, Baikit, Daldyn–Markha, and Turukhansk (Kuznetsov et al., 2000; *Stratigrafiya* ..., 2016). At the beginning of the Middle Cambrian, reef formation was related completely to the microbial–algal organisms (Fig. 1).

In the Altai–Sayany region, Archaeocyatha appeared later, and reefs began to form since the Atdabanian (Bazaikha superunit of the regional stratigraphic scale). In general, their development ceased in the Botomian but continued in some places in the Obruchevian, which is comparable with the Toyonian of the General Stratigraphic Scale (Fig. 2). Cessation of the Archaeocyatha-bearing reef formation in the Early Cambrian and continuation of the microbial–algal reef formation in the Middle Cambrian are noted in the global scale (Zhuravlev, 2001). The situation changed appreciably when the Great Ordovician Biodiversification promoted a significant expansion of the spectrum of reef-builders and included Tabulata, Rugosa, Stromatoporoidea, and Bryozoa at a constant presence of the microbial–algal communities. Reefs formed by these communities are sufficiently widespread in the Middle Ordovician (Sandobian) and Upper Ordovician (lower Katian). Reefs of this age are known in northern and central Kazakhstan, Pai-Khoi, Pechora Urals, and Baltic region (Antoshkina, 1994, 2003; Copper, 2001a, 2001b; L'vova et al., 1964; Myannil and Einasto, 1968; Nikitin et al., 1974; Webby, 2002).

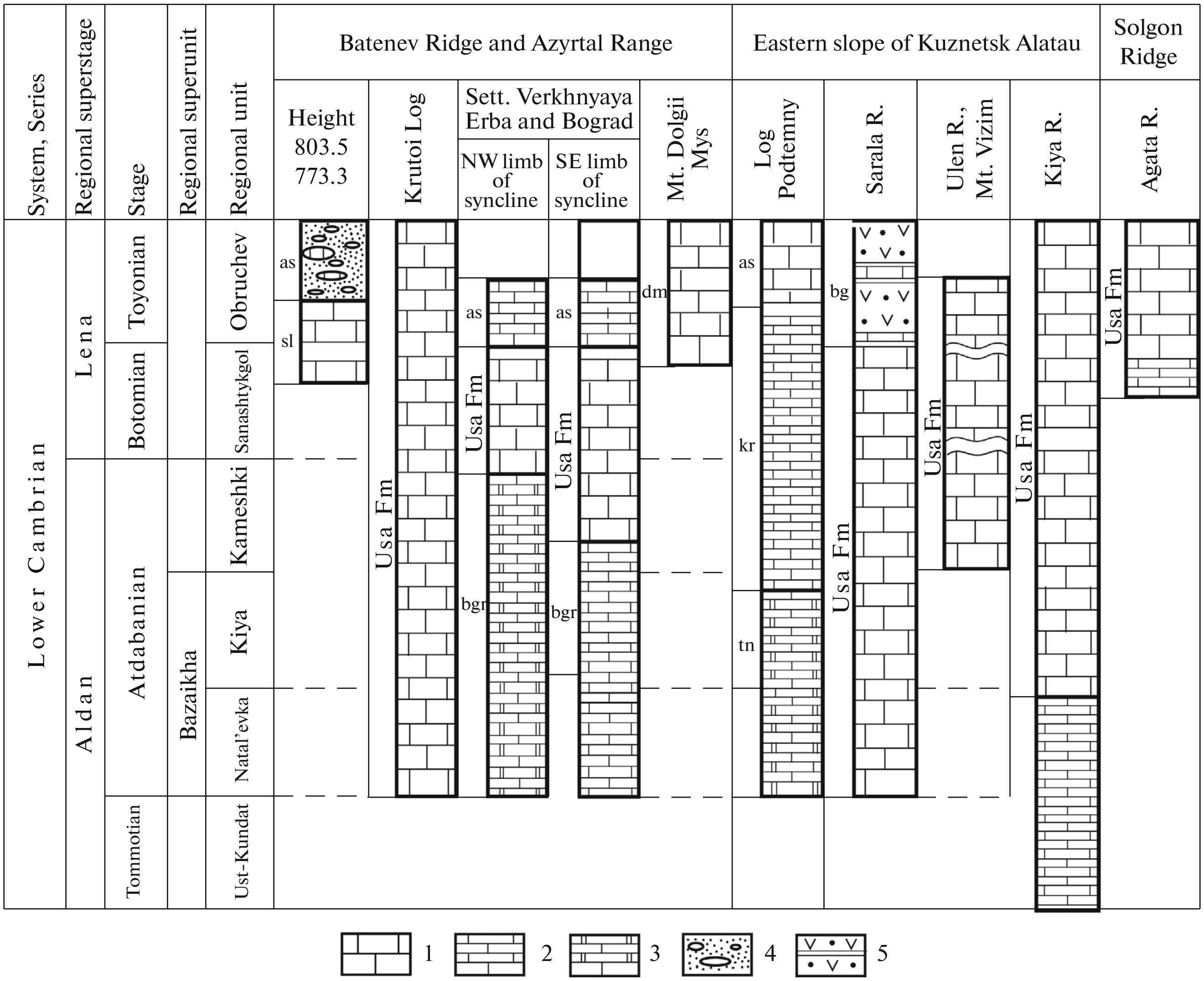

Fig. 2. Schematic stratigraphic distribution of reefs in the Cambrian in the Altai–Sayany region (Zadorozhnaya, 1986). (1) Usa Formation (massive Archaeocyatha-algal limestones); (2) laminated black limestones; (3) laminated black limestones and dolomites; (4) gritstones and conglomerates with bioherms; (5) effusives, tuffs with interlayers of limestones and siltstones. Formations: (as) Asertal, (sl) Solontsi, (bgr) Bagrad, (dm) Dolgomas, (kr) Kureninsk, (tn) Tunguzhul, (bg) Bogoyul.

Ordovician (upper Katian) reefs are studied in the northern and Polar Urals. They are overlain successively by the lower Hirnantian rocks (sedimentary-diagenetic breccias of the Bad'yashor Formation) and the shallow-water carbonates of the Kamennaya Baba Formation (Antoshkina et al., 2015). Thus, carbonate deposition continued in the Hirnantian, but reefs were not formed. At the same time, small bryozoan–algal bioherms were formed in the Hirnantian in some regions (Baltic region, eastern Canada). The framework (potential reef-building) organisms still existed but beyond the reefal biocoenosis (Fig. 3).

After the biotic crisis and large-scale extinction at the Ordovician–Silurian boundary, reef formation resumed rather rapidly and continued with certain variations until the end-Frasnian, i.e., the next Frasnian–Famennian crisis (Kellwasser Event). On the whole, the Devonian Period was marked by one of the reef building maximums not only in the Paleozoic, but also in the Earth's whole geological history. The set of reef-builders remained constant at least at the level of large taxa: Stromatoproidea, Rugosa, Tabulata, diverse algae and, to a lesser extent, Bryozoa.

As at the preceding stage, reefs disappeared until the end-Frasnian marked by the deposition of clayey beds that record the Kellwasser Event. At the same time, the potential reef-building stromatoporoids still existed at the base of the Famennian, but they did not play a significant role in reef building at this time. Such situation is observed in the Devonian framing of the Caspian Basin, Timan–Pechora Syneclise, Western Canada Basin, Canning Basin (West Australia), South China, and Garz area (Germany) (Fig. 4) (Geldzetzer, 1991; Kuznetsov and Zhuravleva, 2018a,

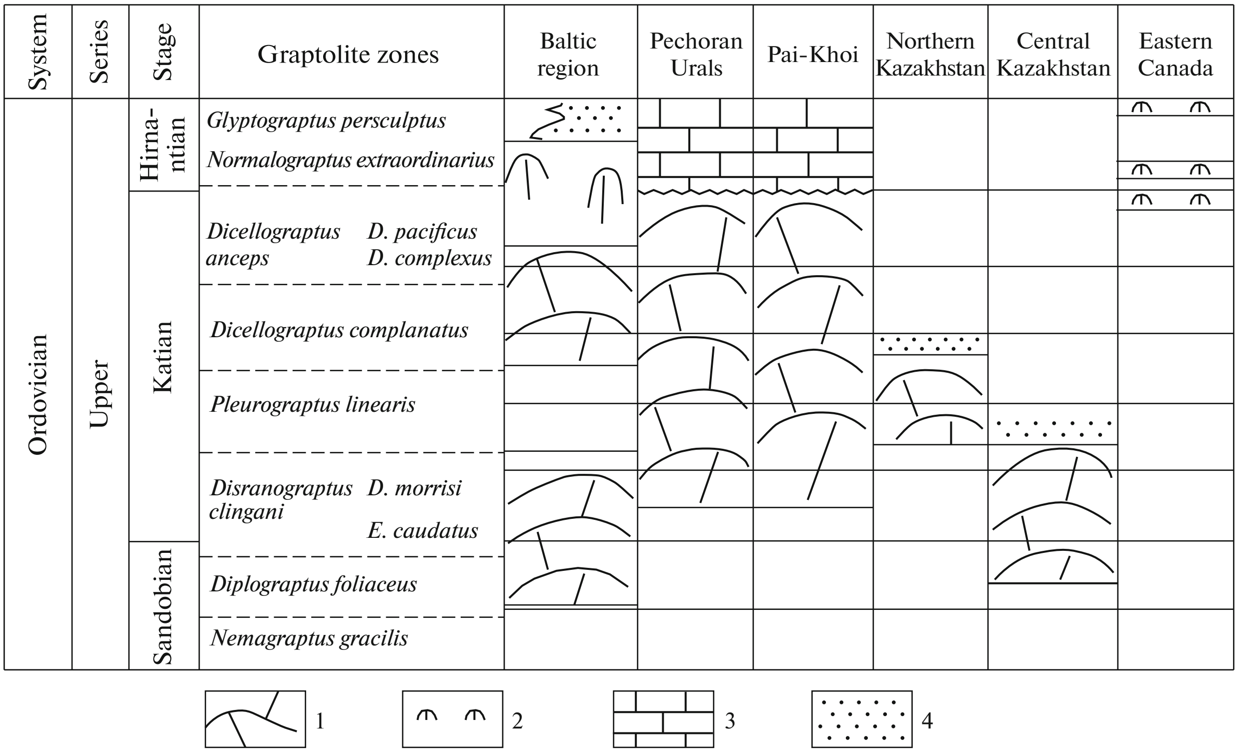

Fig. 3. Schematic stratigraphic distribution of reefs and bioherms in the Upper Ordovician. (1) Reefs; (2) bioherms overlying the reefal sediments; (3) limestones; (4) clastic rocks.

2018b; Playford et al., 1989; Shen et al., 2010; Veevers and Wells, 1961; Weller, 1991; Zhuravleva, 2017).

This period was marked by the existence of long-evolving reefs, for example, “Herzynian limestones” (Urals) that represent the Silurian–Lower Devonian complex. However, the reefs were developed more often in the course of narrower time intervals and overlapped by salts or clays rather than carbonate sediments, e.g., saliferous sequences of the Upper Silurian Saline Formation (Michigan Basin, United States), Muskeg, Black Creek, and their Devonian analogs in the Western Canada Basin or clays of the Ireton Formation in the same basin, as well as the Vorob’evian, Mullinian, Sargaevian, Mendymian, and Volgogradian clays of the Devonian in the lower Volga region, Caspian Basin, and other areas.

The Famennian Age was marked by the onset of a long-term development of the bryozoan–algal mud mounds that continued during the whole Famennian, Tournaisian, and a significant Visean interval.

The next (late Visean–Serpukhovian) stage of intense reef formation was characterized by a relatively limited set of reef-building organisms: bryozoans, algae, calcibionts along with foraminifers, corals, and crinoids (Kuznetsov and Antoshkina, 2005). This stage terminated because of the Serpukhovian–Bashkirian biotic crisis.

The Permian reef formation was confined to two paleogeographical zones: continental block of northern Pangea and the Paleotethys region. In the Pangean block, reefs were formed in the Early (eastern Russian Platform) and Middle Permian and, possibly, at the beginning of the Late Permian (Permian Basin, United States; Zechstein, Europe). The main reef-builders were bryozoans, tubiphytes, and, to a lesser extent, sponges and various algae. The biocoenosis included numerous and diverse foraminifers, brachiopods, and other organisms. In all cases, the cessation of reef formation was provoked by paleogeographical reasons—the carbonate accumulation gave way to the deposition of saliferous sequences at the end of the Artinskian and Kungurian (Early Permian), as well as salts of the Ochoa Formation (United States) and Verra Group (Europe)—and was unrelated to biotic events.

The situation is different in the Tethyan region. The Middle Permian reefs were developed in Pamir, Primorye, and southern China. The Late Permian reef formation was relatively less intense. Reefs of this age are known in the Caucasus (Urushan Unit) and southern China (Yangtze Platform). The reefal biocoenosis included a wider range of organisms: numerous and diverse Sphinctozoa, Inozoa, Bryozoa, algae, calcimicrobes including nonframework species: brachiopods, molluscs, foraminifers, and echinoderms.

Data on several scrutinized reefs in this region revealed that their development ceased before the end-Permian (Fig. 5), but potential reef-building organisms still existed at this time both in reef formation zones, such as southern China (Enos, 1995; Fan et al.,

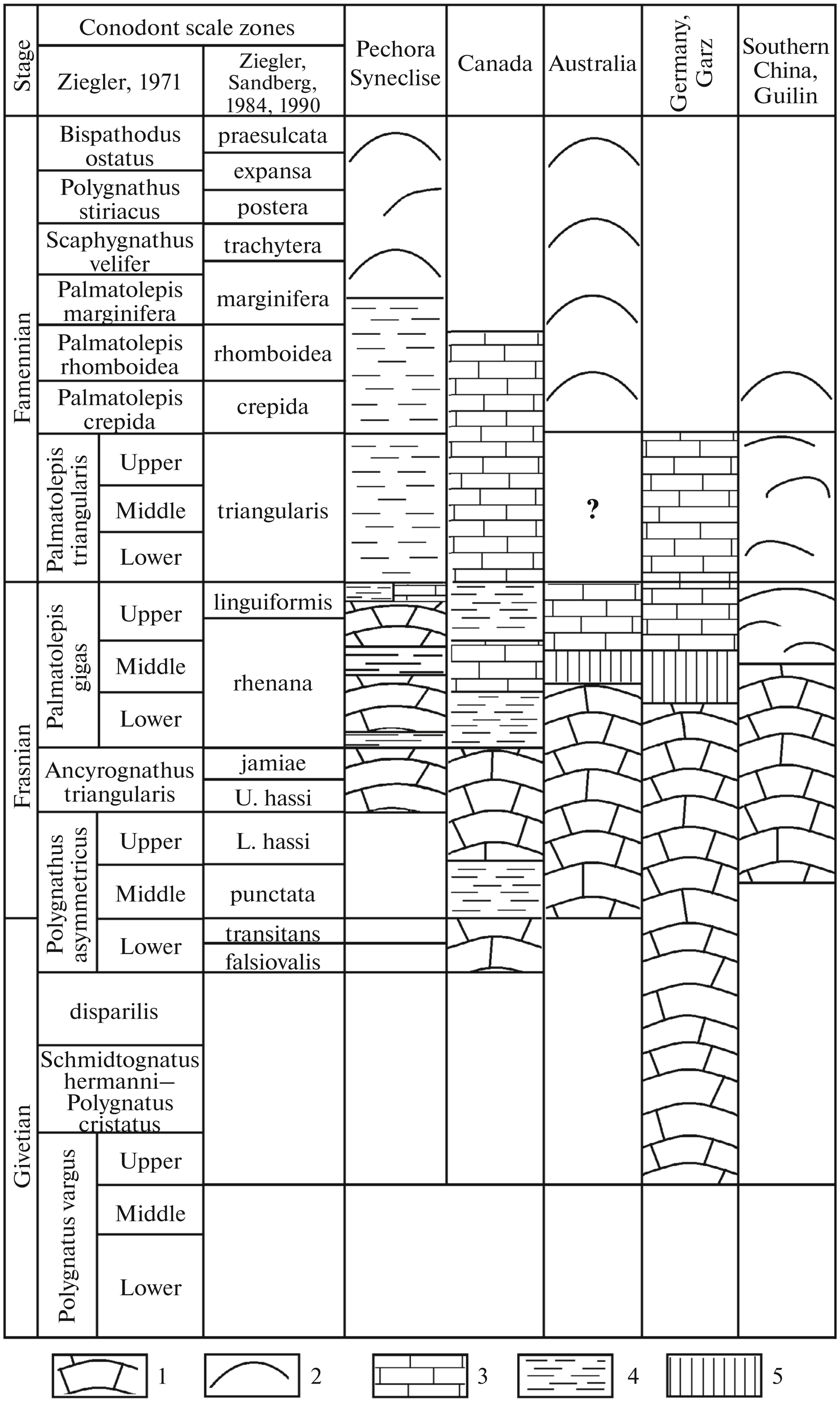

Fig. 4. Schematic stratigraphic distribution of reefs and mud mounds near the Frasnian–Famennian boundary. (1) Framework reefs; (2) mud mounds; (3) nonreefal carbonate rocks; (4) clayey sequences; (5) stratigraphic hiatuses.

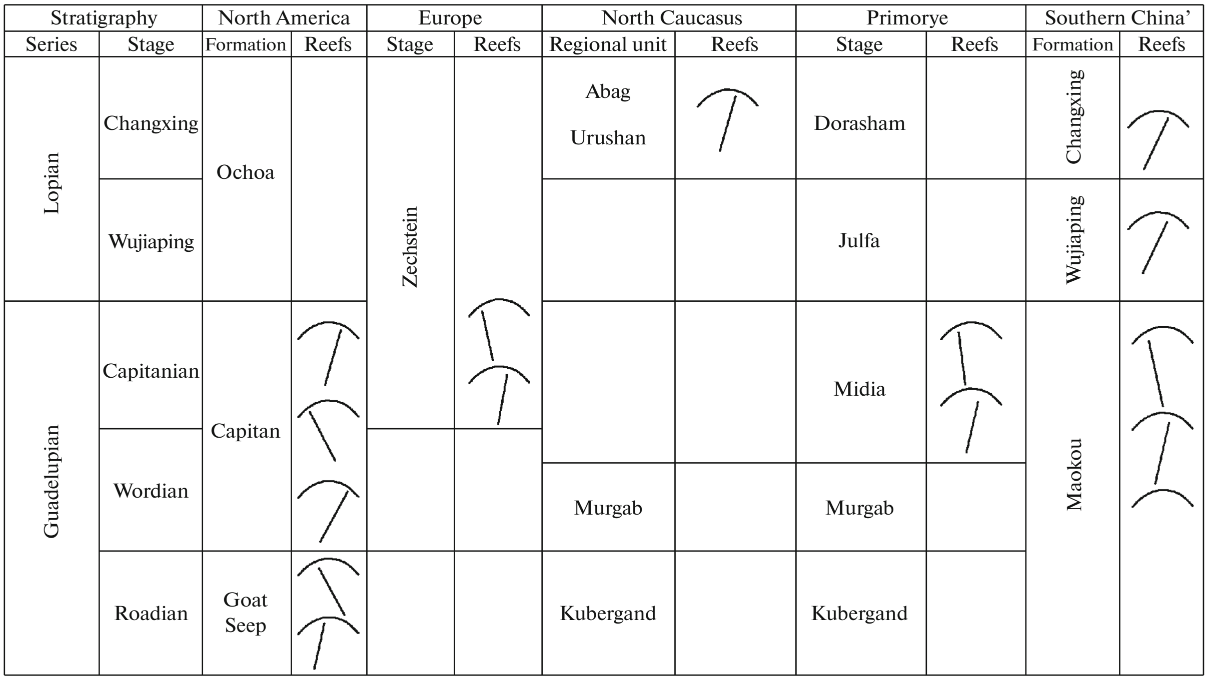

Fig. 5. Schematic stratigraphic distribution of reefs in the Middle and Upper Permian.

1982; Huaibo et al., 1991; Li et al., 1985; Wu Xichin et al., 1990), and in extra-reef settings, e.g., the Transcaucasus (*Razvitie* ..., 1965).

DISCUSSION

Data presented above show that the global-scale cessation of reef formation at the boundary of large stages of the Paleozoic reef formation was caused by biological reasons: large-scale extinctions of biota (reef-builders included) during the biotic crises recorded at the Early–Middle Cambrian, Ordovician–Silurian, Frasnian–Famennian, Serpukhovian–Bashkirian, and Permian–Triassic boundaries.

Dynamics in the attenuation of reef development varied during different stages. In the Cambrian, existence of the framework reefs ceased simultaneously with the disappearance of Archaeocyatha, the sole skeletal organisms of this epoch. At the Frasnian–Famennian and Permian–Triassic boundaries, reefs ceased to form even before the termination of the biotic crisis, i.e., when the potential framework-forming reef-builders still existed. The Serpukhovian–Bashkirian interval lacks reef-including sections with stratigraphic subdivisions. Therefore, exact timing of the cessation of reef formation has not been established so far.

Specifics of the cessation of reef formation during different biotic crisis intervals can likely be attributed to special characteristics of the reefal ecosystems at different Paleozoic stages. In the course of existence, the reefs attained the climax stage by certain time with the most complete development of an intricate biocoenosis. The latter was distinguished by a diversity of both reef-building and reef-dwelling organisms that also delivered the carbonate building material. These organisms had not only cross-media topic but also numerous mutually beneficial links that supported the vital activity and development of the system under specific facies-paleogeographic and geochemical environments. If the environment changed, the well-balanced closed system became unstable and rapidly degraded, resulting in cessation of the reef formation. In this case, some components of the system (potential reef-building taxa) continued to exist but beyond the reefal biocoenosis. Actually, extinction and change of taxa took place later and terminated the gradual evolution of this phenomenon, which was a rather fast process in the geological time scale but not an instantaneous event. In this process, the most organized biota (framework-forming stromatoporoids, corals, bryozoans, and calcite sponges) disappeared at a relatively early stage but the algae and, particularly, bacterial communities, which are tolerant and stable to paleoecological variations, still existed and could make up prominent buildups (biostromes and bioherms).

After such crises, microbial–algal structures (mud mounds) were formed for some time when the potential reef-building organisms also likely existed and evolved but beyond the reefal ecosystem.

Exception in the Cambrian Period, when the reef formation ceased together with the disappearance of Archaeocyatha, only supports the above assumption. The point is that the biocoenosis and biota in the Cambrian were still very primitive, and an intricate ecosystem of the later period was not yet developed at that time.

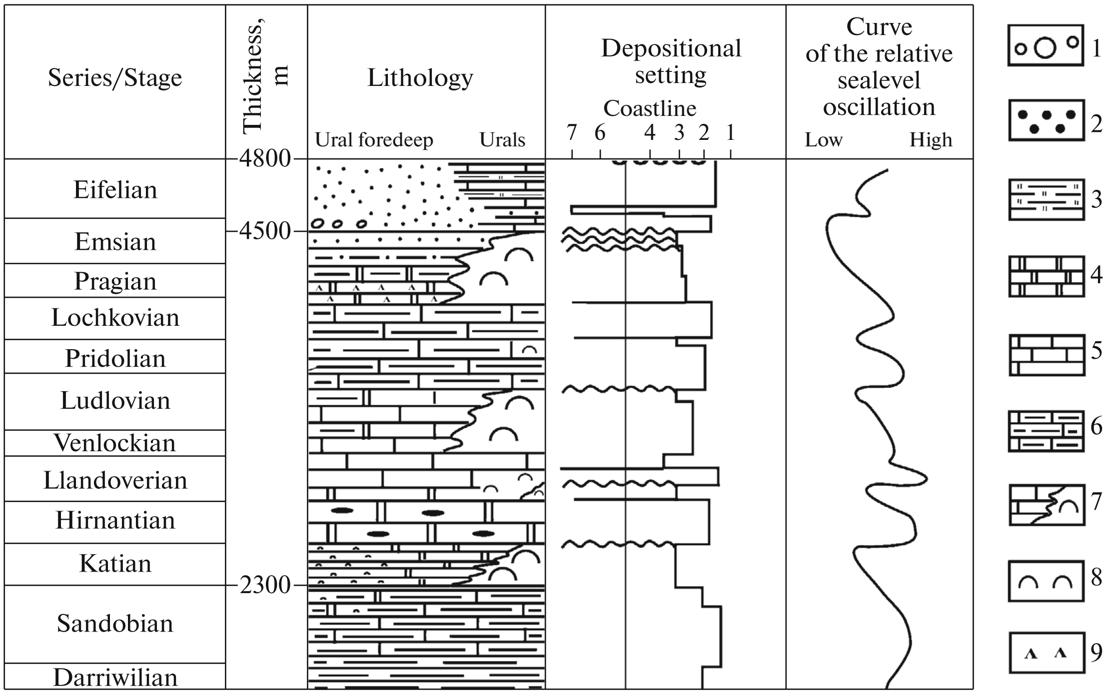

Fig. 6. Cyclic development of reefs in the Upper Ordovician–Middle Devonian in the North Urals, modified after (Antoshkina, 2003) taking the modern stratigraphic scheme into account. (1) Conglomerates; (2) sandstones and siltstones; (3) siliceous shales; (4) dolomites; (5) limestones; (6) clayey limestones; (7) reefs; (8) bioherms and biostromes; (9) evaporites.

Without describing the reasons for biotic crises, let us note the following point: our data presented above do not support the assumption that all large-scale extinctions in the Earth's history took place as one-act events provoked by catastrophic phenomena (e.g., impact processes). Though instantaneous in the geological sense, the processes of extinction nevertheless embraced certain short intervals when the intricate reefal ecosystem could respond to a negative influence more rapidly than the biota in general. The catastrophic events were likely markers rather than causes for the cessation of extinctions.

Being not experts in biology, we do not dare to scrutinize the tropic structure and links with the reefal biocoenosis. However, such analysis carried out by G.A. Zavarzin and S.V. Rozhnov (2011) provides some insight into the issue under consideration. They demonstrated that the Recent and, probably, Mesozoic and Cenozoic reefal ecosystems have and had a "double trophic loop" that guarantied the marvelous stability of system. Consequently, the reefs became virtually autonomous, and their existence and evolution only needed energy as solar light. This assumption was suggested for the present-day reefs by E. Odum (1972).

The Paleozoic reefal ecosystem was less developed, less isolated, and less "autonomous." Therefore, changes in external conditions provoked, first of all, a breakdown of the reef-building system and, consequently, disappearance of reefs. One cannot rule out that their formation continued virtually until the end of biotic crises because of the more stable ecosystem of Mesozoic and Cenozoic reefs. This fact suggests the lack of their preemptive disappearance, but this assumption requires special scrutinization.

Resumption of reef formation after the biotic crisis followed a slightly different scenario.

In the Middle and partly Late Cambrian as well, algal buildups (mud mounds) could be formed after the disappearance of Archaeocyatha at the Early–Middle Cambrian boundary.

After the Ordovician–Silurian boundary crisis, the framework reef building was resumed rather rapidly without any significant pause.

The scenario is different after the Frasnian–Famennian and Permian–Triassic extinctions.

After the Kellwasser Event, the Frasnian–Famennian boundary was only marked by the formation of microbial–algal buildups (classic mud mounds) over a very long period extending from the Famennian–Tournaisian to the early Visean. Such mounds are studied and described in England, Belgium, Ireland, and other regions (Lees and Miller, 1995).

The Bashkirian Age along with the Middle and partly Late Carboniferous represented a pause in reef building. In some places, the bioclastic limestones overlap the Serpukhovian reefs as, for example, in the Caspian Basin.

At a lower (regional) level of the formation and development of reefs, the cessation scenario is different: it is dominated by geological processes, such as volcanism, regressions, and climatic and paleogeo-

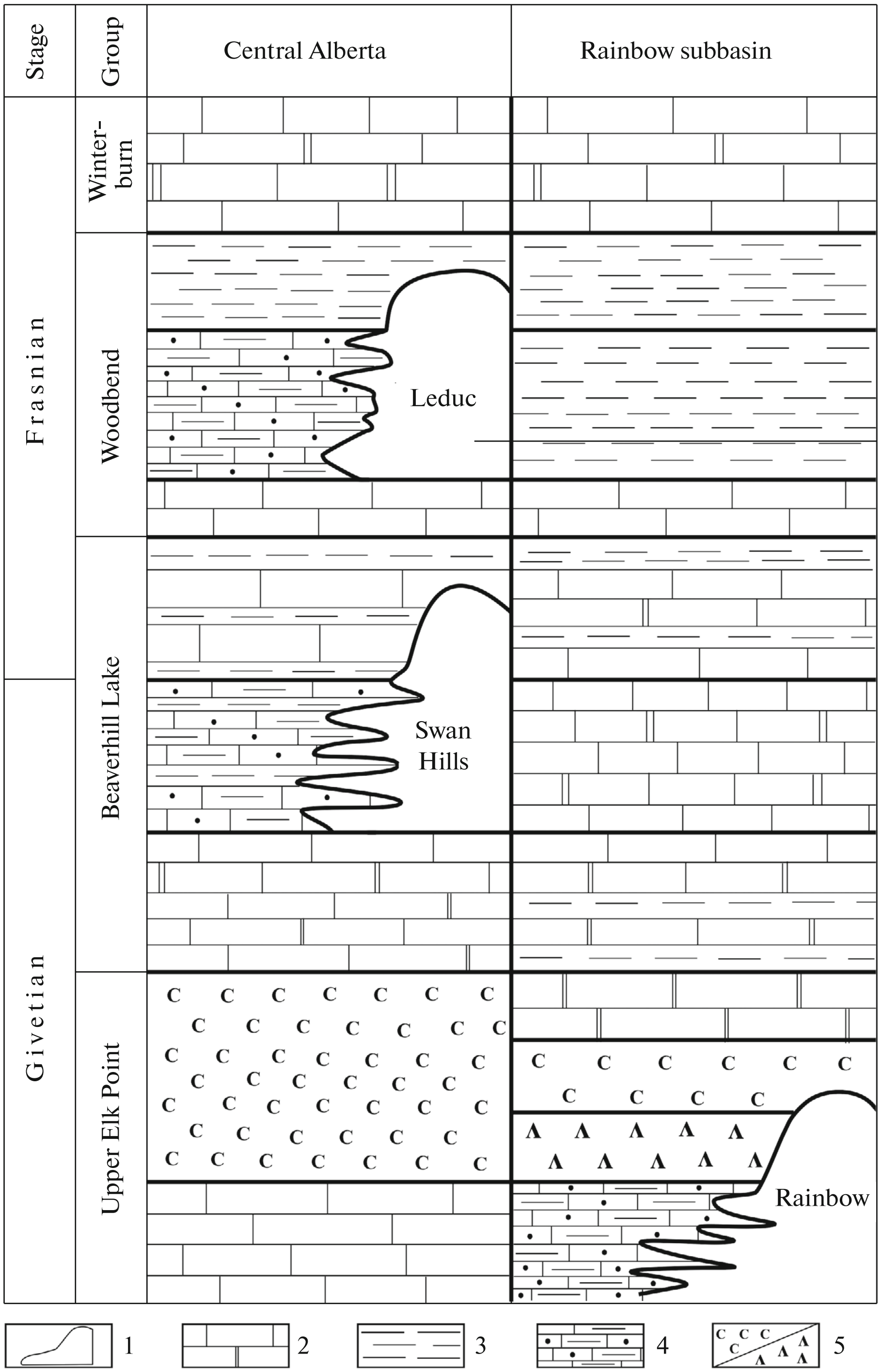

Fig. 7. Cyclic development of Middle and Upper Devonian reefs in the Western Canada Basin. (1) Reefs; (2) shallow-water limestones and dolomites; (3) clays and shales; (4) bituminous–clayey limestones; (5) evaporites: (s) rock salt, (ʌ) anhydrite.

graphic changes leading to a partial isolation of basins and change in the formation of rock types, and so on.

In the course of regional regressions, the carbonate deposition gave way to the formation of clayey sequences that overlapped the reefs and filled up the reef formation basins. The basins were filled up with evaporites during the climate aridization and partial isolation. The overlying sequences are represented by: sandy–clayey members in the Silurian–Lower Devonian section, northern Urals (Fig. 6); Silurian Saline saliferous formation, Michigan and Illinois basins, United States; Prairie, Muskeg, and Ireton Clay, Western Canada Basin (Fig. 7); clayey and sandy–clayey rocks of the Vorob’evian, Mullinian, Pashiiskian, Sargaevian, Petinian units that overlie reefs in the lower Volga region and Caspian Basin framing; salts of the Verra and Stassfurt Group, Zechstein Formation, Germany; and others. The cessation of reef formation is also recorded in volcanic regions, for example, Dedebulak bioherm range in Kirgizia (Teslenko et al., 1983).

Given that the cessation of reef formation is governed by geological processes near the boundary of extinctions, reef is not formed even after the subsequent transgression and the development of paleogeomorphological conditions and the resumption of carbonate sedimentation. For example, reef formation is not resumed after the Ireton Clay deposition in the Western Canada basin, and reefs are missing in the Nisku carbonate formation that terminated the Frasnian Stage.

CONCLUSIONS

The Earth's Paleozoic history includes five stages of framework reef formation: Early Cambrian, Middle–Late Ordovician, Silurian–Frasnian, late Visean–Serpukhovian, and Permian.

The global-scale cessation of reef building at the boundaries of these stages was provoked by biological reasons, such as biotic crises and large-scale extinction of organisms (reef-builders included).

Intervals between the reef-building stages were marked by the formation of microbial–algal mud mounds. Their widest and most prolonged development is typical of the Frasnian–Tournaisian and initial Visean periods.

In the Early Cambrian, the formation of reefs ceased simultaneously with the disappearance of Archaeocyatha. At other stages, the cessation took place before the complete extinction of the major framework-forming reef-builders, because the intricate multicomponent and well-balanced ecosystem at the climax stage of reef development responded to unfavorable environmental changes leading to biotic crises and cessation of the framework reef formation. Nevertheless, potential reef-builders continued to exist beyond the reefal ecosystem until their complete extinction. Such phenomenon is lacking in the much more primitive Cambrian ecosystems.

Hiatuses in reef formation in the course of large stages were provoked by paleogeographical reasons, such as marine regression leading to the accumulation of clayey sequences and climate aridization that promoted the formation of evaporites.

After the biotic crises and periods of mud mound formation, the process of reef formation was resumed with a quite different reef-builder community. The reef-building biota did not change basically when the reef formation was resumed after hiatuses related to regional paleogeographical reasons.

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