

Late Ordovician Reefs and the Biological Crisis at the Ordovician–Silurian Boundary

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Received January 31, 2017; in final form, May 10, 2017

Abstract—Reef formation in the Late Ordovician was relatively widespread in the Sandbian and Katian times. In the late Katian, it gradually reduced and ended in the Hirnantian, before the end of the Ordovician. In parallel, reef-building skeleton frame-building biota disappeared and was replaced with algae and calcimicrobes.

Keywords: reef formation, biotic crisis, Ordovician–Silurian boundary, Upper Ordovician reefs

DOI: 10.1134/S0869593818030085

INTRODUCTION

The problem of reef formation and biotic crises accompanied by mass extinctions has been being studied for a long time, and the one at the Ordovician–Silurian boundary is one of them (Copper, 2001a, 2001b, 2002; Fluegel and Kiessling, 2002; Webby, 2002). The paleontological issues are mainly discussed, in particular, the change of reef-building communities, while the types of such reef buildings are rarely studied. The aim of the present work is to consider the correlation between the cease of reef formation and biotic extinction in the greatest possible detail. The object of study is the Ordovician–Silurian boundary, or, more precisely, Upper Ordovician reefs.

The long-term “biological pause” lasted for the entire second half of the Middle Cambrian, Late Cambrian, and beginning of the Ordovician. The Cambrian-formed skeleton biota, although certainly constrained in terms of taxonomy, existed through all this time. But then, explosive faunal evolution (great Ordovician biodiversification event) occurred in the Middle Ordovician (Dronov, 2016; *The Great Ordovician...*, 2004). In the Russian literature, the great Ordovician biodiversification event was discussed in detail by Kanygin (2001).

One of the consequences of this biodiversification was a renewal of reef formation. Of course, it began earlier in the Early Cambrian and almost ceased in the Middle Cambrian; but in the Middle Ordovician, it renewed at a new level.

Newly formed reefs of the end of the Early–Middle Ordovician were considered in quite good detail by A.V. Dronov (Dronov, 2016; Dronov and Fedorov, 1994; Dronov and Ivantsov, 1994; Dronov and Kushlina, 2016) and, for example, in fundamental works by

Copper (2001a, 2001b, 2002), Fluegel and Kiessling, (2002), and Webby (2002). After a small hiatus at the end of the Middle Ordovician, reef formation restarted in the Late Ordovician. Restart of reef formation, disappearance of reefs at the Ordovician–Silurian boundary, and the relationships of these phenomena to the coeval biotic crisis and mass extinction are the subject of the present work.

The present study considers mainly reefs proper as complex geologic units formed as a result of vital activity of organic communities (*Sovremennye...*, 1990, pp. 114–119) and also such simpler buildings as bioherms (*Sovremennye...*, 1990, pp. 18–20).

STRATIGRAPHIC DISTRIBUTION OF LATE ORDOVICIAN REEFS

To solve the stated problem, we need the very detailed stratigraphy and exact correlation between narrow stratigraphic units, including that between very distant regions, but this condition obviously cannot always be satisfied. Graptolite zone references are not always available, whereas interregional correlation on global euglaciostatic transgressions and regressions is complicated by (and often is impossible because of) the peculiarities of geological evolution of particular regions. For example, the Baltic Basin was marked by regression in the late Hirnantian documented by sandstone accumulation, whereas in the Pechora region and in the Northern Urals the same period was the time when open-shelf layered limestones (Yaptikshor Horizon) accumulated.

Another point complicating the correlation of distant regions is that reef formation is affected by both purely biological factors (evolution of organisms, including reef builders and their communities) and

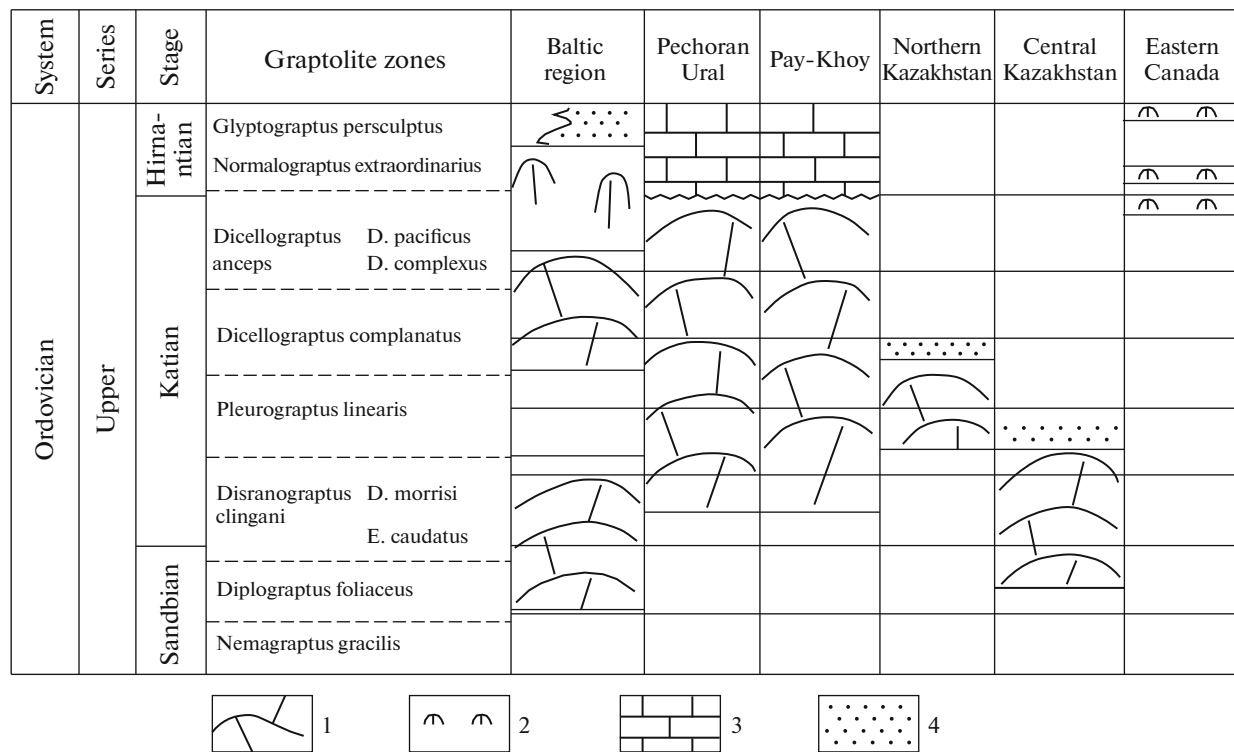


Fig. 1. Scheme of stratigraphic distribution of reefs and bioherms in the Upper Ordovician section. Legend: (1) reefs; (2) bioherms; (3) limestones; (4) detrital rocks.

local/regional purely geological ones (uplift and subsidence, as well as transgressions and regression induced by them, volcanism, supply of detrital and clay material, and others).

So we have to consider the evolution of Late Ordovician reefs in different regions taking all these points into consideration. The text and Fig. 1 provide only several examples, whereas a much larger volume of factual data can be found in the mentioned fundamental works. In addition to the general stratigraphic scheme (Bergstroem et al., 2008), the detailed stratigraphic scheme by Koren' (2002) was used in the analysis.

Additionally, the considered objects included those where reef structures have been studied in quite good detail and, as was mentioned above, for which a quite exact and detailed stratigraphic reference is available. Unfortunately, publications reviewed in such works as (*Rifogennye...*, 1997; *Rifovye...*, 2015) in most cases contain very general data; moreover, Ordovician and Silurian structures are mentioned and described together.

In the Baltic Basin, on the northwest East European Craton, reefs (*Vasalemma hemicosmite* reefs) appear in the Upper Ordovician, in the uppermost Keila Horizon, and can also be found in Oandu Horizon (Myannil', 1966; Myannil' and Einasto, 1968), generally corresponding to the uppermost *D. foliaceus* and *D. clingani* graptolite zones (upper Sandbian–lower Katian stage).

Individual buildings are massifs whose thickness exceeds that of host clays by a factor of two or more. They are composed of homogeneous fine-grained limestones with Siphoneae remains; there also are multiple “reefophyle organisms: corals, stromatopores, brachiopods” (Myannil', 1966, p. 126). Echinoderm cystoids play an important but not absolutely clear role (their evolutionary peak fell in the Ordovician).

Then the hiatus occurs, and reefs are absent in the Rakvere, Nabala, and Vormsi horizons (uppermost *D. clingani* Zone and *P. linearis* Zone).

Reef formation restarted in the Pirgu time (*D. complanatus* and *D. anceps* zones). The termination of reef formation occurred in a quite unordinary manner: in the Porkuni Horizon (Hirnantian Stage) finishing the Ordovician section, reefs do not reach the top part of the horizon. In some cases, they are covered by quartz sandstones of the Siuges Member, while in other cases the superimposing rocks are also sandstones of the Kamariku Member. The Porkuni Horizon proper is characterized by “development of relatively shallow reef (bioherm) bodies” (Myannil', 1966, p. 95).

Such distribution of reefs in the Upper Ordovician section is characteristic of the entire Baltoscandian region (Kroeger et al., 2016). In some areas, probably, lower Hirnantian buildings are less thick (less than 10 m).

Thus, reef formation in the region ceased before the end of the Ordovician and was caused by regression and sandstone accumulation; however, the intensity of reef formation gradually decreased during the Katian and Hirnantian ages up to the appearance of fine bioherms in the Porkuni Horizon.

Reefs in the northeastern margin of the East European Craton and in the Northern Urals were studied in detail by Antoshkina (1994, 2003).

The first reef building appeared here in the Late Ordovician. Bioherms about 10 m thick composed of bryozoans and tabulata remains are found in the upper Kozhim Formation (lower Katian). Virtually full-scale reefs referring to the uppermost Katian Stage are found and described in the areas of the Ilych, Bad'yashok, and Lek-Elets rivers. These isolated massifs formed in the transition zone from the shallow water shelf of the Bel'skoe-Elets structural-facial zone to the deep-water basin of the Sakmara-Lemva structural-facial zone; their thickness ranges from 110 to 500 m. They are composed of stromatoporoideas, corals (including Heliolitidae, Receptaculita, and sponge-like organisms), at permanent abundance of microbial-algae communities.

In the Pechora Ural region, reef formation occurred in a quite narrow time interval. Reef buildings are reported in the upper Lesser Tavra Formation, corresponding to the Sur'ya Horizon in the West Urals and to the upper Katian of the general stratigraphic scale.

In the vertical section, the change of biotic communities as a reflection of reef ecosystem succession was revealed; note that deposits of the finishing stage of reef formation are represented by carbonate detritus and, importantly, microbial (including stromatolite-related) buildings, in the absence of an abruptly reduced amount of frame organisms in their intravital positions.

In general, reef formation terminated by the end of the Hirnantian Age. In a number of cases, shallowing up to drainage of the reefs was revealed, followed by their subsequent rapid coverage by relatively deep-water open-shelf deposits of the Yaptikshor Formation closing the Ordovician section. Importantly, these deposits contain "remains of shelly and colonial fauna" (Antoshkina, 1994, p. 22). In other words, reef formation ended before the onset of mass extinction. And, we recall, microbial units clearly dominate in the top parts of the very reefs.

A similar pattern is revealed in Pay-Khoy, Vaigach, and Novaya Zemlya. Small reef buildings appear at the base of the upper part of the Yugra Horizon (lower Katian stage). In the middle Katian (Varnek Horizon), reefs up to 70–80 m thick are identified; they were built by colonial tabulata, rugose, stromatoporoidea, and bryozoans, in the permanent presence of cyanobacteria and algae. The tops of these

reefs are covered by bioclastic limestones with bryozoan detritus and bedded stromatolites.

Reef formation ended before the end of the Hirnantian; the climax marked by biodiversity and frame reef building ended even before this; top parts of the section are still ascribed to reefs and are represented by almost exclusively cyanobacterial products.

After this, despite the following subsidence and transgression, reef formation did not restart.

Ordovician reef buildings of Kazakhstan were described, in particular, in (Nikitin, 1973; Levina and L'vova, 1959; L'vova et al., 1964; Nikitin et al., 1974).

In Central Kazakhstan, the so-called Anderken bioherm range is developed (Nikitin et al., 1974). This is a series of bioherms and bioherm massifs up to 60–80 m thick. The main builders were various red and green algae, as well as cyanobacteria; rarely, frame-building organisms (corals, bryozoans, sponges) can be found. The age of the Anderken Formation, in whose middle part the buildings are developed, refers to the D. clingani Zone, or the beginning of the Katian Age.

In North Kazakhstan, in the Lake Mailisor area, reef buildings are thicker (up to 250–300 m, or even more) and quite clearly subdivide into facial zones (bioherm zone and the related shoal, zones of fore-reef slope and back-reef lagoon), generally creating an atoll character of this building.

The main builders were various algae, although bryozoans and, less commonly, corals were also found, as well as non-reef-building fauna (brachyopods, trilobites, crinoids, gastropods). These reefs are younger in age than those in Central Kazakhstan and are confined to the Angrenor Formation, correlating to the Pleurograptus linearis Zone and referring to the middle of the Katian Stage.

In the Altai-Salair region, large reefs formed in the early–middle Katian and early Hirnantian (Sennikov, 2011).

Small Upper Ordovician reef buildings and often the inheriting Silurian reefs were developed in the northern Canadian Cordillera, in the Arctic, and in the eastern provinces of Canada (Cecile, 1988).

The reefs buildings are studied in quite good detail, in particular, on Anticosti Island, eastern Canada (Copper, 2001a, 2001b). Small buildings 4–5 m thick and about 15 m wide were identified in the Mill Bay Formation dated to the end of the Katian Age (D. pacificus Zone). Generally, small sizes of reefs can probably be explained by geological and paleogeographic peculiarities of the particular locations where they formed: stable ancient platform, covered by a shallow sea basin, characterized by a slow downwarping rate. The absence of significant depths did not enable further growth to form reefs proper which would significantly rise above the basin bottom.

These buildings are composed chiefly of micritic limestones with rugose and, to a lesser degree, stro-

matopora; calcimicrobes (*Girvanella*, *Rothpletzella*, and others) are also abundant. At some levels in the overlying Elliz Bay Formation (Hirnantian; *N. extraordinarius* and *G. persculptus* zones), there are buildings characterized by the analogous biota. It was noted that buildings of the uppermost Katian are characterized by the clear domination of corals above stromatopora, which are in turn the main reef builders in the Sandbian and lowermost Katian. Additionally, calcimicrobes and red solenoporid algae were the important Hirnantian reef builders. In this respect, Copper noticed that the “Hirnantian reefs are microbial mud-mounds with a sparse fauna of calcimicrobes, green algae, lithistid sponges, bryozoans, and brachiopods” (Copper, 2001b, p. 107).

Copper attributed the cyclicity of reef formation and periodic appearance and disappearance of reefs to glaciation, with generally small buildings formed during the interglacials.

The first extinction and cessation of reef formation occurred at the end of the Katian Age; the second one was less expressed and occurred by the middle of the Hirnantian (top of the *N. extraordinarius* graptolite zone); the third one occurred at the Upper Ordovician boundary (top of the *G. persculptus* Zone).

DISCUSSION

Generalizing the data presented above, we can state that maximal reef formation in the Late Ordovician took place in the Sandbian and in the first half of the Katian Age, but generally declined in the second half of the Katian. This is reflected both in the amount of areas where reefs developed and in the number and size of reefs in the areas of Sandbian and Katian reef formation. The analogous situation is reported for the very end of the Ordovician, when the main reef formation took place at the end of the Katian, whereas it was either absent or of very limited extent (as in the Baltic region and in eastern Canada) in the Hirnantian. During the cessation of reef formation, reef-building biota also changed: stromatoporoidea decreased in amount or completely disappeared, leading to the relative increase in the fraction of corals, algae, and calcimicrobes. Note that reef formation demonstrates a certain staged character: first frame-building skeleton fauna disappeared, but reef formation continued (although at slower rate) owing to activity of algae and calcimicrobes. However, this caused disappearance of frame reefs and their replacement with mud-mounds.

Copper (2001a, 2001b) considered the problem of reef formation at the Ordovician–Silurian boundary and unambiguously linked the development and disappearance of reefs to glaciations that occurred in this period. He believed that glaciation had a two-way effect: it caused the decrease in water temperature, on one hand, and this negatively affected reef builders; on the other hand, global sea level drop due to partial

water-to-ice transition led to the fact that considerable shelf areas became surfaced and, hence, lithotopes favorable for reef builders declined. To a certain degree, Dronov (2013) also shares this point of view.

However, the real situation seems to be even more complicated. Indeed, the mass extinction at the Ordovician–Silurian boundary simultaneously to the development of glaciations makes the conclusion that the latter caused the former (in particular, cessation of reef formation) seemingly natural and quite obvious.

Nevertheless, the logical and apparently convincing explanation provided by Copper for the concrete objects he studied turns out to be much less validated and reliable upon the wider view of the problem. For example, the Gondwana glaciation in the Late Paleozoic was much greater in extent, but did not impede quite intense reef formation in the Late Carboniferous–Permian. On the other hand, the Kellwasser and Frasnian–Famennian boundary extinction events were not related to glaciations at all.

The cessation of reef formation in many particular cases can be explained by purely geological causes: drainage, supply and accumulation of detrital material, and so on. It is important to note, however, a clear trend toward reduction of reef formation by the very end of the Ordovician. Additionally, among the considered objects, there is one example—northeastern European part of Russia—illustrating that carbonate deposits could have formed in the presence of potential reef builders, but without formation of reefs proper. As was mentioned above, reefs in this region are developed in the Sur’ya Formation of the upper Katian; after drainage and subsequent transgression, despite the quite favorable paleogeographic conditions that existed in the Kyr’ya (Yaptikoshor) Basin, which had a larger depth than the basin before it, reef formation did not restart.

On the contrary, an essentially different (so to say “internal”) cause of stoppage of reef formation seems to be much more probable. As was shown by Kanygin, proceeding from the theory of open system development, these systems undergo constant punctuated changes through crises owing to coordinated internal (emergent) and external factors, so “crisis states of the biosphere should be considered as regular events in the developed system, with the unavoidable consequences after attaining a more stable state at each evolutionary stage” (Kanygin, 2001, p. 633).

The reef ecosystem is a more closed, self-contained one and appears to be less stable and more vulnerable, while more changeable (it starts to change before the organic world on the whole begins to change); development of reefs stops before an overwhelming biological crisis. This is probably caused by the trophic structure of a reef community; this structure is formed as a result of succession of a reef biocenosis to the climax stage when the system is stable and nearly self-contained. Trophic links are stable, so the system requires

only sunlight for photosynthetic organisms to accumulate energy which is supplied to maintain the system. But the system can remain stable only under these particular environmental conditions: once they change, even insignificantly, trophic and mediatopic links break and the reef-building biocenosis destructs. Particular groups of organisms, including reef builders, may continue their existence, but not as part of a reef ecosystem anymore. In fact, Copper said almost the same: “reef abundance and scale, the “health of the ecosystem,” may be a better predictor of global mass extinction events than diversity decline or flux” (Copper, 2001a, p. 165).

In light of the aforesaid, we can understand better the Hirnantian reef formation in eastern Canada. Reefs proper are absent there as complex ecosystems. Multiple trophic relationships characteristic of “self-contained systems” of reefs did not form within these small buildings. As was noted above, buildings are virtually of microbial origin, with a very small contribution of frame-building organisms. This is one example of how reef formation is affected by both biological factors and the general geological environment.

We can also distinguish several stages in how reef formation stopped: first, frame-building skeleton organisms disappeared, but reefs continued to be formed (although at slower rate) owing to activity of algae and calcimicrobes.

CONCLUSIONS

In broad sense, Late Ordovician reef formation developed in cycles and reached its peak in the middle of the Katian Age. To certain degree, this corresponds to the abrupt depletion in biological diversity of benthic organisms at the Katian–Hirnantian boundary (Alekseev, 2000). Hirnantian reef formation is much more limited and usually represented by bioherms and also, importantly, it finished before the end of the Ordovician, accompanied by the simultaneous decrease in number and then by the complete disappearance of frame-building organisms.

It seems that termination of reef formation by frame-building organisms before the end of the biotic crisis with replacement of the respective buildings by simpler algal and bacterial ones (with the simultaneous existence of frame-building organisms) was at least a widespread, if not ubiquitous, phenomenon. The similar situation with reef formation is characteristic of the Frasnian–Famennian boundary. In this period, it either completely finished (for example, in the Western Canadian Sedimentary Basin) or reef formation by frame-building organisms involving various biota was replaced by incomparably poorer, simple microbial buildings; the latter was reported in many Frasnian reefs in the framings of the Caspian Basin and Pechora syncline (southeastern and northeastern East European Craton, respectively), in Harz (Ger-

many), in Guilin (South China), and in other regions (Kuznetsov, 2003; Zhuravleva, 2017; Shen et al., 2010).

ACKNOWLEDGMENTS

I am grateful to A.V. Dronov for the provision of important data on the topic and fruitful constructive discussions of the content of the manuscript and to A.S. Alekseev for valuable critical remarks.

Reviewers: A.S. Alekseev and A.V. Dronov

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Translated by N. Astafiev