Казанский (Приволжский) федеральный университет

Институт геологии и нефтегазовых технологий

Ежегодная международная стратиграфическая конференция Головкинского, 2014

Каменноугольная и пермская планетарные системы, стратиграфические события, эволюция биоты, седиментационные бассейны и полезные ископаемые

20–23 октября 2014 года

Сборник тезисов

Научный редактор

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УДК 55
ББК 26
К 11

Научный редактор
Данис К. Нургалиев

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К 11 **Ежегодная международная стратиграфическая конференция** Головкинского «Каменноугольная и пермская планетарные системы, стратиграфические события, эволюция биоты, седиментационные бассейны и полезные ископаемые» (20–23 октября 2014 г.). Сборник тезисов. – Казань: Изд-во Казан. ун-та, 2014. – 104 с.

ISBN 978-5-00019-270-2

Международная конференция посвящена проблемам каменноугольной и пермской планетарных систем, стратиграфическим событиям, эволюции биоты, седиментационным бассейнам и полезным ископаемым.

УДК 55
ББК 26

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К 11 Proceeding of Kazan Golovkinsky Stratigraphoic Meeting «Carboniferous and Permian Earth systems, stratigraphic events, biotic evolution, sedimentary basins and resources» (October, 20–23 2014). – Kazan, 2014. – 104 p.

International Stratigraphic Meetinf is dedicated to the Carboniferous and Permian Earth systems, stratigraphic events, biotic evolution, sedimentary basins and resources.

ISBN 978-5-00019-270-2

Evolution of Late Paleozoic Fusulinoida in the ecological context

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Foraminifera of the superorder Fusulinoida is one of the most common groups of organisms among Late Paleozoic marine benthic communities. Evolutionary stages of Fusulinoida are studied in detail by many Russian and foreign micropaleontologists. Traditionally, questions of evolution and ecology were considering independently each from other. However, the interaction of biotic and abiotic events in the evolution of organisms nobody is denied. At the present time, in connection with close attention to environmental problems, interest in questions of paleoecology has increased. Since foraminifera are sensitive to changes of temperature, salinity, chemistry and dynamics of marine water, the analysis of their morphological parameters can give indirect information about local and global environmental changes at the present and the past time.

The formation of the superorder Fusulinoida had during Early Carboniferous (Visean and Serpukhovian ages), when representatives of the ancestral superorder Endothyroida were dominated in foraminifera communities. Distinguishability of Fusulinoida from Endothyroida resulted in the formation of their shells with a stable septation, which probably indicates the uneven growth rate of Fusulinoida. This morphological feature is not characteristic of the Early Carboniferous Endothyroida. The formation of the observed innovation occurred against the backdrop of abiotic changes of the World Ocean, which took place at the turn of Serpukhovian and Bashkirian ages. In the fossil record this event was reflected in the decrease of other marine invertebrates' diversity.

Superorder Fusulinoida existed from Early Carboniferous to Late Permian. During this time there were 6 orders, more than 150 genera and about 2500 species. General evolutionary regularities in the history of the development of Fusulinoida are showed up in the complexity of the morphology and spatial organization of the shell. The direction of this process was formed under influences of changing external environments.

One of significant biological events in the evolution of Fusulinoida was associated with the emergence of innovations in the structure of the shell's wall, marking the appearance of the order Schwagerinida. Phylogenetic transition from Fusulinida to Schwagerinida represented the transformation of the four-layer wall with diaphanotheca in to the two-layer keriotheka wall with extensive porosity. This process occurred in Late Moscovian – Early Kasimovian age when global warming was observed according to some of geological and paleontological data. Probably in those conditions for Fusulinoida the wall structure with keriotheka was significant adaptive trait that has improved the communication of the organism with the environment. Thus, climate change at the turn of Moscovian and Kasimovian ages proved to be a stabilizing factor in retention of the morphological innovations of Fusulinoida.

Morphometrics (the quantitative analysis of organism form) is the key to understanding evolutionary, physiological, ontogenetic and functional processes in organisms both past and present, as noted at the TMS Joint Foraminifera and Nannofossil Spring Meeting (the Netherlands, 2014). The question "Which morphological parameters are most sensitive to environmental change?" is the most important in the ecological context. Earlier studies by M. N. Solovieva also have dealt

with this problem. She introduced the concept of integrative foraminifera systems to analyze the structure of the shells from the point of view of their functioning. Integrative systems detect the presence of communication and ensure consistency between different structures and survival functions. There are three integrative systems: the gravity, the communication, and the generation one.

The gravitational system includes chomata, folded septa and axis deposits. These structures have functions both shell's weighting and its mechanical strengthening. Mentioned structures are adaptive devices for the existence of organisms in a moving water environment. Such qualitative characteristics of the Fusulinoida structure as a shell's shape and a chamber's height that reflects a volume of a living chamber should be also included to the gravitational system.

A communicative system includes such shell's structures, which are used by an organism to communicate with an external environment. These structures include apertures, septal pores and some features of wall structures. Communication system is needed to perform vital functions such as metabolism, nutrition, breathing, i.e. physiological processes.

General patterns of organisms' phylogeny, revealed in the classic scientific works of A. N. Severtsov and I. I. Schmalhausen, are indicated in the historical development of Fusulinoida. The study of the Fusulinoida evolution allowed us to identify periods of idioadaptation, and the periods of aromorphosis.

Changes in the structures of the gravitational system took place mainly during periods of idioadaptation. They were adaptive in nature to specific biocenotic conditions and determine a local distribution of Fusulinoida.

Morphological structure of the communication system was changing mainly in periods of aromorphosis. Evolutionary innovations of the communication systems were raising a level of general vital functions of organisms, thereby ensuring their evolution towards biological progress on the background of global environmental changes.

Thus, the evolution path of Fusulinoida can be used as some tracer of global environmental changes during Late Paleozoic.