



Controls on the diversity and structure of earliest metazoan communities: Early Cambrian reefs from Siberia



Andrey Yu. Zhuravlev ^{a,*}, Elena B. Naimark ^b, Rachel A. Wood ^c

^a Department of Biological Evolution, Faculty of Biology, Moscow State University named after M.V. Lomonosov, Moscow GSP-1, 119991, Russia

^b Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow 117997, Russia

^c School of GeoSciences, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JW, UK

ARTICLE INFO

Article history:

Received 19 December 2014

Accepted 27 April 2015

Available online 14 May 2015

Keywords:

Cambrian

Reefs

Communities

Diversity

Niche-assembly

Neutral models

ABSTRACT

Understanding the mechanisms that sustain high biodiversity and regulate community structure remains a major challenge as past ecological interactions cannot be reconstructed with precision. Here we reveal the dynamics of the earliest diverse skeletal metazoan communities known, the early Cambrian (Tommotian–Atdabanian) archaeocyathan sponge reefs, over a period of 20 million years from their first appearance ~535 million years ago (Ma) until the first mass extinction event ~512 Ma. Archaeocyaths were restricted to the Siberian Platform until ~520 Ma, and so these data provide unique insight into a single, evolving isolated species pool. Systematic and statistical analyses, including α -diversity, evenness, Jaccard similarity, species abundance distributions, and Spearman statistics coefficient were undertaken for 58 sampling units representing 6121 individuals of 84 archaeocyath species from the Siberian Platform. These statistical results indicate an overall similarity to analyses of species co-occurrence in modern tropical coral reefs and rainforest communities. We show a prevalence of niche-assembly mechanisms throughout the entire Tommotian–Atdabanian interval. By the late Atdabanian, however, these earliest metazoan reefs showed the addition of community assembly processes, which can be attributed to neutral behaviour.

© 2015 Elsevier B.V. All rights reserved.

Contents

1. Introduction	18
2. Dataset	20
2.1. Geological setting and age constraints	20
2.2. Localities and sampling	20
2.3. Reef facies	21
2.4. Methods	23
3. Results	24
4. Nature of early Cambrian reefal communities	25
5. Conclusions	27
Acknowledgements	28
Appendix A. Supplementary data	28
References	28

1. Introduction

Two principal views persist as to the controls on the distribution and abundance of species in space and time. Niche-assembly theories

suggest that communities are highly integrated entities of inter-dependent and strongly interacting species where each species occupies a unique niche (Elton, 1927; Hutchinson, 1959; Gause, 1984; Silvertown, 2004). By contrast, neutral models based on predictions of Gleason (1926) and Ramenskiy (1935) define communities as casual aggregations of individuals representing different species. This view was formalised by Hubbell (2001) whereby individuals representing

* Corresponding author.

E-mail address: ayzhur@mail.ru (A.Y. Zhuravlev).

the same ecological guild are demographically identical regardless of species: all species within the same ecological guild are assumed to be equal in their per capita random probability to originate, speciate, become extinct, or found new communities. Neutral models therefore consider species-specific traits unimportant and rely upon demographic traits only. By contrast, niche models consider interactions between species, individuals, and environments the dominant factors and, thus, rely upon species-specific (deterministic) traits.

Deterministic species-level traits such as resource partitioning, physiological tolerances, habitat preferences, and reproductive strategies are all ignored by neutral models because communities are considered to be assembled by stochastic processes only within saturated ecological systems (Gaston and Chown, 2005; Clark, 2012). Neutral models also suggest a substantial redundancy of species and a weak species interaction within highly diverse communities such as tropical rain forests and coral reefs (e.g., Hubbell, 2001; Volkov et al., 2007). Some have suggested, however, that niche-assembled and dispersal-assembled models of community integrity may not be mutually exclusive but are either extremes of a continuum, or may operate at different scales where neutral models are merely ideal statements for a further building of more complex assumptions (Chesson, 2000; Tilman, 2004; Alonso et al., 2006; Gravel et al., 2006; Adler et al., 2007; Chisholm and Pacala, 2010; Rosindell et al., 2011; Beckage et al., 2012; Cheng et al., 2012).

In order to test the quantitative and qualitative dynamics of initial community assembly, we have considered the earliest biodiverse metazoan communities known: early Cambrian archaeocyathan sponge reefs. Archaeocyaths are an extinct group of calcified aspiculate sponges (Debrenne et al., 2015), which appeared on the isolated Siberian Platform about 535 Ma and remained indigenous there until approximately 520 Ma. They therefore represent the evolution of an endemic species pool. These species are preserved in situ as closely-interacting metazoans over a period of some 15 million years (Myr) without the influence of any input of any propagules from other regions. We have also

included data from the following 8 Myr up until the extinction of most archaeocyaths ~512 Ma. The archaeocyath species pool here, therefore, persistently grew by a balance of speciation/extinction processes from its first origination (zero-point). Thus, these reefs offer a good dataset to test predictions of niche-assembly or neutral theory in deep time and to trace community dynamics in a single metacommunity of ancient reefs through their evolution.

Archaeocyaths grew as either clonal, modular reef-builders that were able to gain secure attachment to substrate, or solitary reef-dwellers, the largest of which were able to stabilise muddy substrates in dense settlements (mud-stickers), or as small oblique encrusting cryptobionts from their first appearance at the beginning of the Cambrian Stage 2 (Wood et al., 1992; Zhuravlev and Wood, 1995; Fig. 1D). All archaeocyathan species were sessile organisms limited by space, and relied upon broadcasting propagules into the environment where the eventual site of growth was strongly dependent on the initial larval settlement site. Excellent preservation, rapid lithification, high community diversity, and multiple localities of reefal fauna allow for detailed palaeoecological studies of the earliest metazoan reefal biota which are not strongly time-averaged and were free of allochthonous species from other regions (Kruse et al., 1995; Riding and Zhuravlev, 1995; Fig. 1).

A number of features, such as mutual integrowth, encrustation, regeneration, and dwarfing by neighbouring species is indicative of approximately comparable growth rates (Zhuravlev, 2001a). Noteworthy is that while gregarious modular species were prone to mutual overgrowths with conspecific and even other species individuals, solitary species display acute rejection and allogenic incompatibility manifested in avoidance behaviour, partial skeletal atrophy of less aggressive individuals, or precipitation of excess skeletal tissue at the species boundary space (Wood et al., 1992; Debrenne and Zhuravlev, 1994; Figs. 1A–C). This set of reactions is indicative of negative intraspecific rather than interspecific effects (Chesson, 2000). Such interactions resemble tree species self-limitation in tropical rain forests that is controlled by tree

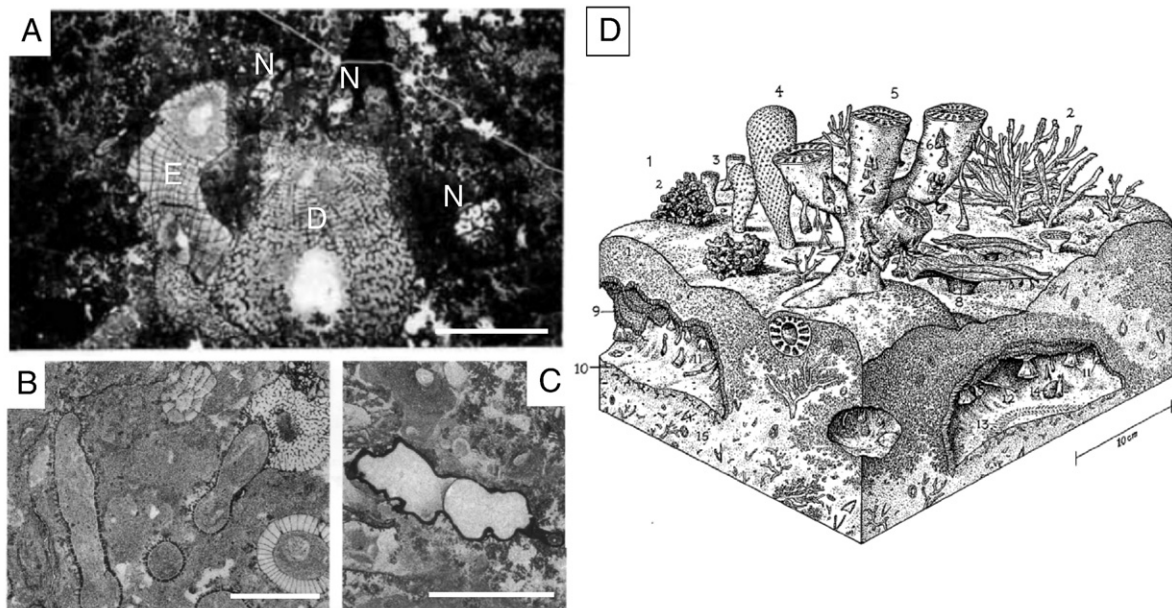


Fig. 1. Archaeocyath interactions in early Cambrian red mud mounds (reefal microfacies 4). A–C, Scale bars = 5 mm. (A) Branching modular *Dictyosyon gravis* (white D) encrusts and suppresses branching modular *Neolucicyathus sibiricus* (N) and solitary *Erismacoscinus oymuranensis* (E) within cryptic cavity created by clotted renalcid matrix. Oy-Muran, Atdabanian stage, *Retecoscinus zegebarti* Zone, sampling unit A128 (modified after Zhuravlev and Wood, 1995). (B) Branching modular *Archaeolynthus polaris* 1 (left and centre) encrusted by branching modular *Spinosocyathus maslennikovae* (top right), solitary *Nochoroicyathus anabarensis* (top centre) and *N. mirabilis* (bottom right) are present also. (C) Branching modular coralomorph *Cysticyathus tunicatus* (centre) encrusts solitary *N. anabarensis* (top left). Zhurinskiy Mys, Tommotian stage, *Dokidocyathus regularis* zone, sampling unit T211; microphotographs of thin sections by P. Kruse. (D) Reconstruction of middle Tommotian (T2) reef of mud mound type: 1 – *Renalcis*, 2 – branching modular *Archaeolynthus polaris* 1, 3 – solitary *Nochoroicyathus* spp., 4 – cancelloriid, 5 – branching modular *Cambrocyathellus tschuranicus*, 6 – pendant *Tumuliolynthus primigenius*, 7 – pendant *A. polaris* 2, 8 – solitary *Okulitchicyathus discoformis*, 9 – primary marine cement, 10 – cryptic microscopic burrowing, 11 – cryptic coralomorph *Cysticyathus tunicatus*, 12 – cryptic *A. polaris* 2, 13 – cryptic trace fossil, 14 – cryptic mollusc, 15 – calcareous micrite (copyright John Sibbick, modified from Wood, 1999).

Download English Version:

<https://daneshyari.com/en/article/4725707>

Download Persian Version:

<https://daneshyari.com/article/4725707>

[Daneshyari.com](https://daneshyari.com)