

Early recovery of sponge framework reefs after Cambrian archaeocyath extinction: Zhangxia Formation (early Cambrian Series 3), Shandong, North China

Jeong-Hyun Lee^a, Jongsun Hong^b, Suk-Joo Choh^b, Dong-Jin Lee^{c,d}, Jusun Woo^{e,*}, Robert Riding^f

^a Department of Geology and Earth Environmental Sciences, Chungnam National University, Daejeon 34134, Republic of Korea

^b Department of Earth and Environmental Sciences, Korea University, Seoul 02841, Republic of Korea

^c Department of Earth and Environmental Sciences, Andong National University, Andong 36729, Republic of Korea

^d College of Earth Science, Jilin University, Changchun 130061, People's Republic of China

^e Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon 21990, Republic of Korea

^f Department of Earth and Planetary Sciences, University of Tennessee, Knoxville 37996, USA

ARTICLE INFO

Article history:

Received 15 March 2016

Received in revised form 7 June 2016

Accepted 9 June 2016

Available online 11 June 2016

Keywords:

Cambrian

Metazoan-microbial reef

Sponge

Rankenella

Reef framework

ABSTRACT

Reefs dominated by the anthaspidellid sponge *Rankenella zhangxianensis*, the calcimicrobe *Epiphyton* and the stem-group cnidarian *Cambroctoconus orientalis*, together with encrusting microstromatolites occur early in the middle Cambrian (Series 3, late Stage 5) of Shandong, eastern China. In the Zhangxia Formation, these in situ components created a tight framework, with centimeter-scale growth cavities mainly filled by fine-grained matrix. Among them, *R. zhangxianensis* and *C. orientalis* mutually attached and locally formed metazoan-dominated frameworks. These metazoan-microbial reefs form thin lenses <2 m wide within microbial mounds, and probably developed at least a few centimeters of synoptic relief above these surrounding structures. With an age of >505 Ma, these *Rankenella* reefs indicate recovery of framework-building metazoans within ~5 million years of the archaeocyath reef decline. In structure, they resemble archaeocyath reefs as well as Early Ordovician lithistid sponge-microbial reefs, having conjoined conical macroskeletons thickly veneered by calcimicrobes and microbial carbonate with largely matrix-filled intervening cavities. In combination with other sponge-microbial reefs reported from Australia, Iran, Korea and the USA, they demonstrate that an anthaspidellid sponge-microbial reef consortium was widespread throughout the mid-late Cambrian.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

In contrast to microbial reefs of the Precambrian, Phanerozoic reef frameworks were often constructed by calcified metazoans and algae. Early Paleozoic reefs show that this change in reef character was gradational and prolonged. In the early Cambrian (Terreneuvian and Series 2), archaeocyath sponges locally formed reef frameworks (Rowland, 1984; Riding and Zhuravlev, 1995; Gandin and Debrenne, 2010), and were commonly subordinate components of microbial reefs (Fagerstrom, 1987; Wood et al., 1992; Kruse et al., 1995; Gandin and Debrenne, 2010; Pruss et al., 2012; Zhuravlev et al., 2015). It was widely thought that, following the late early Cambrian disappearance of reef-building archaeocyaths, microbes resumed their dominant

reef-building role (Zhuravlev, 1996; Wood, 1999; Rowland and Shapiro, 2002; Lee et al., 2015) until lithistid sponges such as the anthaspidellid sponge *Archaeoscyphia* began to form reefs together with microbialites and calathiids in the Early Ordovician (Riding and Toomey, 1972; Pratt and James, 1982; Cañas and Carrera, 1993; Adachi et al., 2011; Li et al., 2014; Hong et al., 2015). Subsequently, from the mid-Ordovician, calcified metazoans and algae dominated global reef ecosystems throughout the Phanerozoic, only disappearing temporarily in mass extinction aftermaths (Schubert and Bottjer, 1992; Webby, 2002; Riding, 2006; James and Wood, 2010).

However, the view that reef-building metazoans were absent from middle-late Cambrian reefs has been revised following recognition of late Cambrian anthaspidellid sponge-microbial reefs in Iran (Hamdi et al., 1995) and additional subsequent reports of middle-late Cambrian sponge-microbial reefs (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Hong et al., 2012, 2016; Kruse and Reitner, 2014; Lee et al., 2014a; Adachi et al., 2015). These lithistid sponge-microbial reefs not only broadly resemble their counterparts in the Early Ordovician but, as we show here, have

* Corresponding author.

E-mail addresses: jeonghyunlee@cnu.ac.kr (J.-H. Lee), bulgeun@korea.ac.kr (J. Hong), sjchoh@korea.ac.kr (S.-J. Choh), djlee@andong.ac.kr (D.-J. Lee), jusunwoo@kopri.re.kr (J. Woo), rriding@utk.edu (R. Riding).

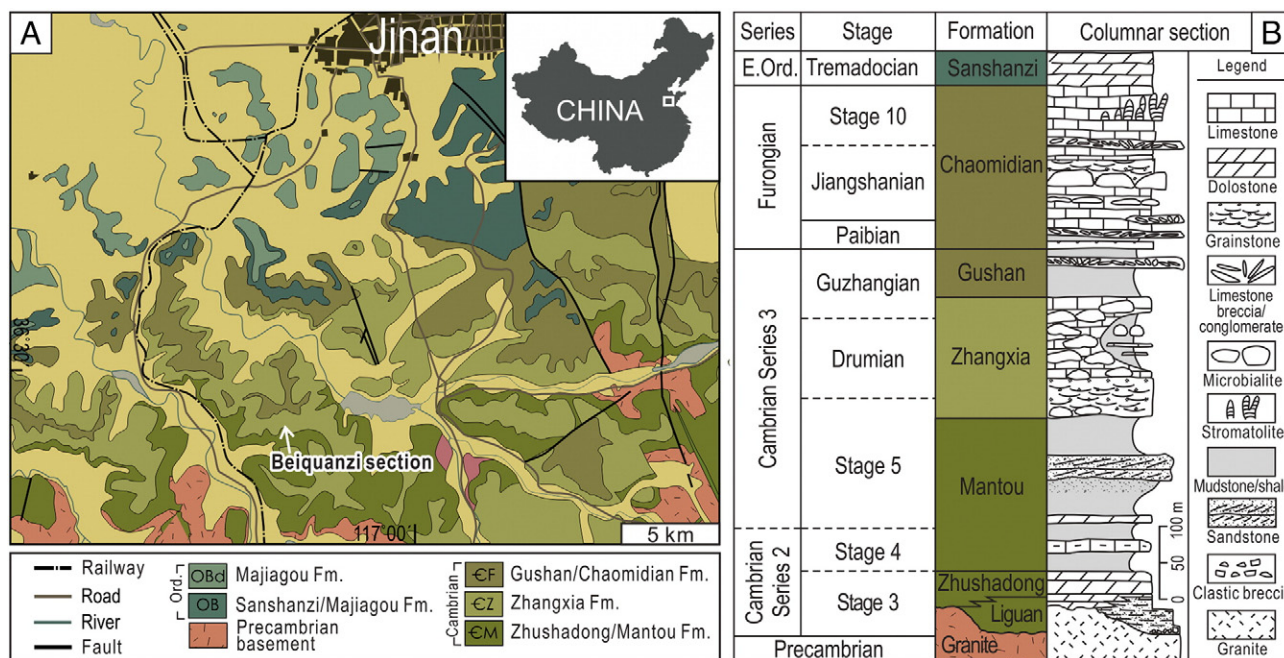


Fig. 1. (A) Geological map with the study area (Beiquanzi section; 36°28'47"N, 116°55'28"E) marked by an arrow. (B) Summary of the Cambrian succession in Shandong Province, China. (A, after Ma and Qiao, 2002; B, after Chough et al., 2010.)

structural similarities with archaeocyath reefs. Despite their often relatively small size, middle–late Cambrian sponge–microbial reefs represent an important stage in early metazoan reef development during the prolonged interval between the late early Cambrian

archaeocyath extinction event and the Early Ordovician emergence of diverse metazoan reefs.

The middle Cambrian Zhangxia Formation in Shandong Province, China contains several horizons of metazoan–microbial reefs which



Fig. 2. Outcrop of the Zhangxia reefs near Beiquanzi. (A) The metazoan–microbial reefs (shaded) occur as lenses within large microbial reefs. Hammer is 28 cm in length. (B) Close-up, showing the anthaspidellid sponge *R. zhangxianensis* (white arrows) associated with microbialite. Scale in centimeters. (C) Debris of *R. zhangxianensis* (white arrows) in inter-mound sediment. Scale in centimeters.

are among the earliest that developed after the archaeocyath decline (Woo, 2009). These reefs are composed of anthaspidellid sponges, calcified microbes such as *Epiphyton*, microstromatolites, and ‘stem-group’ cnidarians (Adachi et al., 2015; Lee et al., 2016). Since the discovery of Zhangxia metazoan-microbial reefs (Woo, 2009), the paleontology of the stem-group cnidarians and sponges has been documented in detail (Park et al., 2011; Lee et al., 2016). However, the reef-structure remains poorly understood, although Adachi et al. (2015) examined the structure of these sponge-microbial reefs and suggested that lithistid sponges would have provided substrates for microbial growth. Here we focus on the metazoan-microbial reefs in the lowermost part of the Zhangxia Formation (Lioparia Zone; late Cambrian Stage 5). Their components and sedimentological roles provide insights into the development of reef-building by metazoans following the archaeocyath demise.

2. Geological setting and methods

The North China (Sino-Korean) Platform occupies an extensive area (1500 km east-west, 1000 km north-south) and comprises Cambrian–Ordovician successions mainly composed of shallow-marine carbonates and siliciclastics (Meng et al., 1997). The Cambrian succession in Shandong Province consists of the following formations in ascending order: Liguan, Zhushadong, Mantou, Zhangxia, Gushan, and Chaomidian (Fig. 1) (Chough et al., 2010). In the study area, near Beiquanzi village (Fig. 1A), 25 km south of Jinan city, the Zhangxia Formation is about 180 m thick and consists mainly of microbialite, oolitic/oncolitic packstone-grainstone, skeletal grainstone, and bioturbated lime mudstone-wackestone (Woo, 2009) (Fig. 1B). Microbialites include thrombolite, dendrolite, *Epiphyton* framestone, encrusting stromatolite, biostromal stromatolite, and leiolite (Woo et al., 2008; Woo and Chough, 2010; Howell et al., 2011). Trilobite biozones (*Lioparia*, *Crepicephalina*, *Amphoton-Taizuia*, and *Damesella-Yabeia*) (see Geyer and Shergold, 2000; Peng et al., 2012) indicate that the Zhangxia Formation ranges in age from late Stage 5 to the early Guzhangian Stage of Cambrian Series 3 (middle Cambrian).

Detailed sedimentological logging of the reefs at the Beiquanzi section documented the depositional environments, and mega- and macroscale morphologies of the reefs (Figs. 1 and 2). Four scales of microbialite description, mega-, macro-, meso-, and microscale (Shapiro, 2000; Chen and Lee, 2014), were used to describe Zhangxia reefs, and we also analyzed the associations of the reef-building components in terms of guild concept (Fagerstrom, 1988; Fagerstrom and Weidlich, 1999). More than 30 samples were slabbbed and over 200 thin sections were prepared to observe meso- and microstructure. To assess the distribution of reef-building components and their roles, large format thin sections (7.6 × 5.2 cm) were prepared from the slabs, and sets of serial thin sections were used to determine the three-dimensional structures and distributions of the reef components.

3. Zhangxia reefs

3.1. Reef occurrence and morphology

Reefs in the lowermost Zhangxia Formation are >7 m in height and 30 m in width, and sharply overlie skeletal and oolitic packstone-grainstone (Fig. 2A). They are overlain by oncolitic packstone-grainstone grading upward to oncolitic wackestone-packstone. The Zhangxia reefs can be divided into two parts. The lower part is characterized by large laterally coalesced meter-scale thrombolite mounds containing the numerous thin lensoid metazoan-microbial reefs, ~150 cm wide and ~30 cm thick (Fig. 2A, B) that are the focus of this study. Interspaces between the large thrombolite mounds are ~3 m wide, with sharp margins, and trend northwest-southeast. The interspaces contain bedded skeletal-oncolitic packstone-grainstone and bioturbated oncolitic wackestone, with bivalves, sponges, and

trilobites (Fig. 2C). The upper part of the reef is biostromal and consists of layered meter-scale thrombolite bioherms veneered by thin dolomitic mud-rich sediments (Fig. 2A).

3.2. Metazoan-microbial reef constituents

Six main components of the metazoan-microbial reefs are recognized: the anthaspidellid sponge *Rankenella zhangxianensis* Lee et al., 2016, an unidentified siliceous sponge, the ‘stem-group’ cnidarian *Cambroctoconus orientalis* Park et al., 2011, the calcified microbe *Epiphyton*, microstromatolite, and undifferentiated microbialite (Figs. 3–5). *R. zhangxianensis*, *Epiphyton* and microstromatolite are the dominant reef constituents, whereas the unidentified siliceous sponges and *C. orientalis* are rare. These metazoan-microbial reefs are individually small (~150 × 30 cm) and show no obvious vertical or lateral variation within themselves.

R. zhangxianensis is obconical, 3–21 mm in diameter and up to 610 mm in length, with smooth outlines (Lee et al., 2016). The rare domal morphology of a sponge reported by Adachi et al. (2015) from

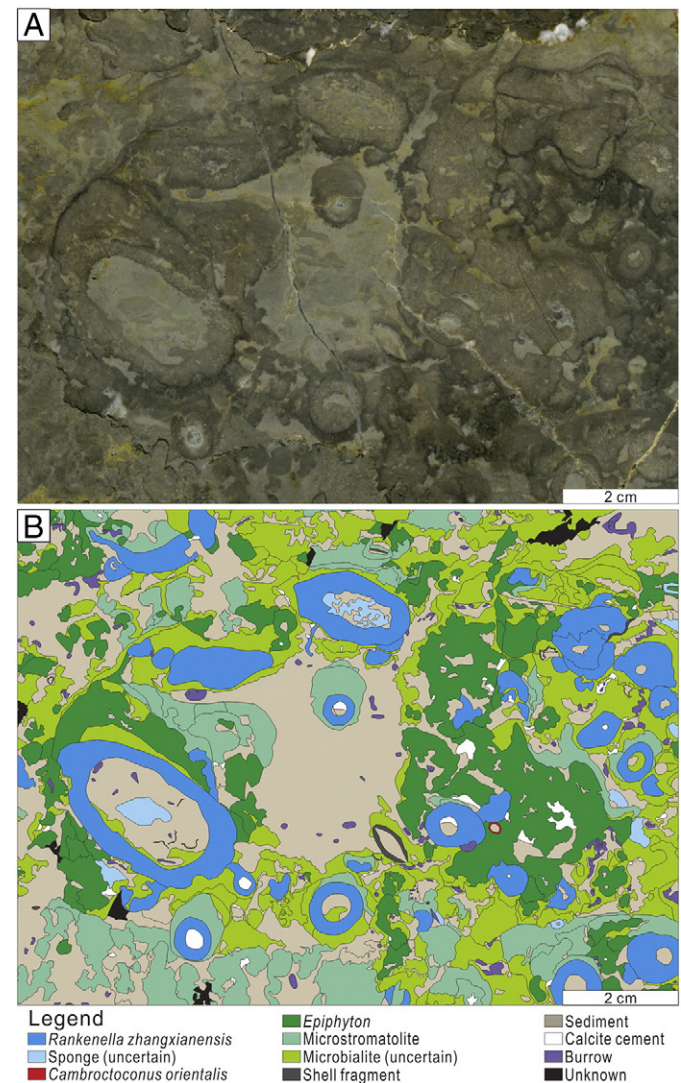


Fig. 3. Metazoan-microbial reef near Beiquanzi, showing photograph of a polished slab (A) and map (B) of centimeter-scale framework. The map is based on several sets of thin sections made from the slab. Framework of mutually attached *R. zhangxianensis* and *Epiphyton* is stabilized by encrusting microstromatolite and other microbialite. *C. orientalis* is a minor component within the reef. Unidentified siliceous sponges are present within the spongocoel of *R. zhangxianensis* and in growth spaces in the framework.

the Jiulongshan section appears to be a cross-section of a holdfast without the main body attached. The spongocoel of *R. zhangxianensis* accounts for about half of the total skeletal diameter (40–60%). *R. zhangxianensis* is characterized by anthaspidellid-type ladder-like spicule networks, with trabs parallel/subparallel to the gastral surface that diverge and then perpendicularly join the dermal surface. Many examples of *R. zhangxianensis* are diagenetically altered. As a result, their internal structure is often unclear and spicules have been merged by dissolution and re-precipitation of calcite (Fig. 4C). Spongocoels are filled with micrite and/or geopetal cement (Fig. 4). Macroborings that sharply cut the wall occur rarely (Fig. 5F). *R. zhangxianensis* (including spongocoel) occupies up to 20% or more of the reef volume and is commonly attached to hard substrates, such as other *R. zhangxianensis* individuals, *C. orientalis*, microbialite, or shell fragments (Figs. 3, 4, and 5A). Upward-growing *R. zhangxianensis* is rare; most examples show horizontal to downward growth (Fig. 4).

Unidentified siliceous sponges are a minor component within the reef (~1%), and mostly lack clear outlines (Fig. 4C). They are characterized by straight to partly curved spicules (~20 µm in diameter and ~100 µm in length) that form irregularly shaped networks (~13 mm long) of evenly spaced spicules within light-colored micrite. In some cases, these spicule networks gradually pass into peloidal fabrics. These features suggest spicule networks that elsewhere have been attributed to keratose sponges (Luo and Reitner, 2014), although their taxonomic affinities remain unknown. The unidentified siliceous sponges mainly occur within, but sometimes also outside, the spongocoel of *R. zhangxianensis* (Fig. 3).

C. orientalis is a 'stem-group' cnidarian characterized by an octagonal cone-shaped structure containing paired septa (Park et al., 2011). It widens gradually from the closed holdfast end to the open end, and is 1–1.5 cm in length and 5–7 mm in diameter. The walls are generally thin (ca. 0.7 mm) and perforated.

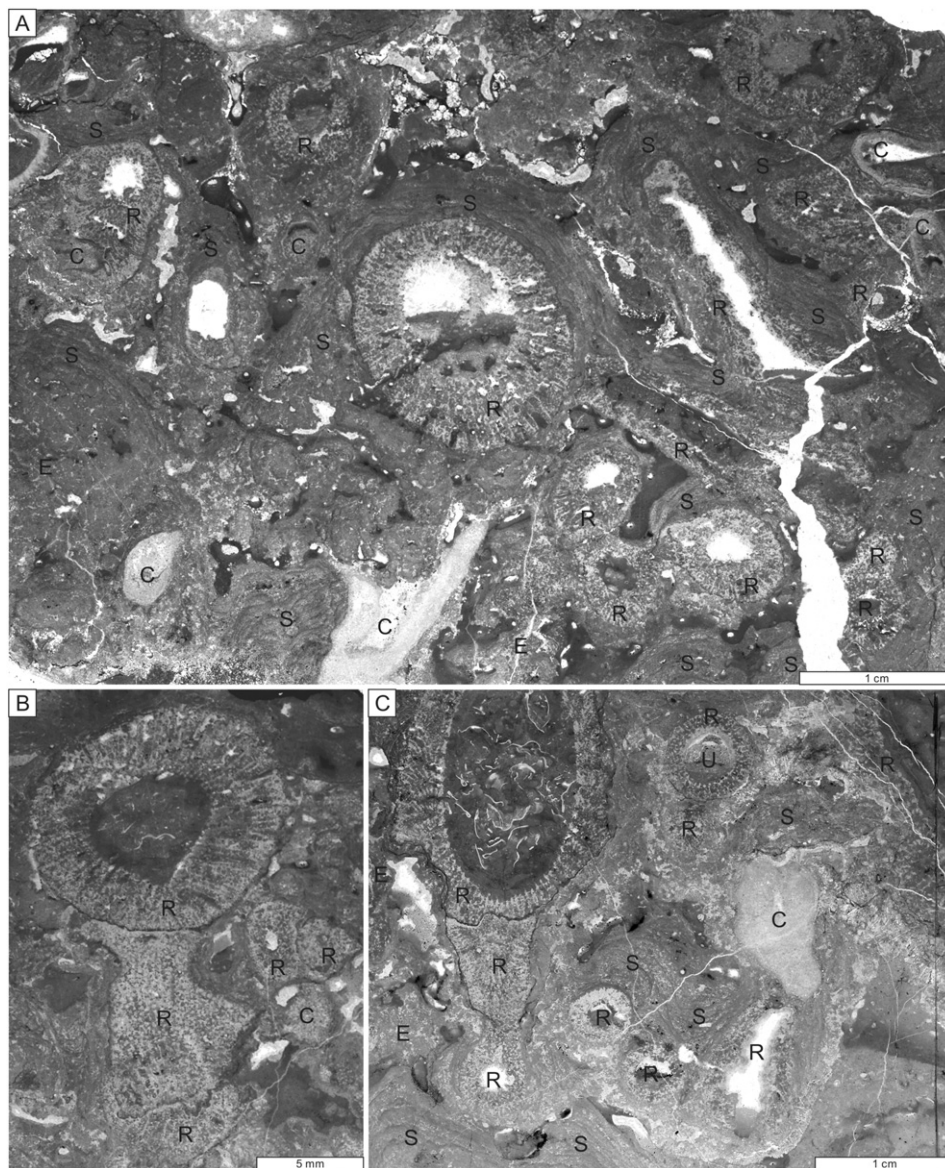


Fig. 4. Examples of metazoan-dominated frameworks within Zhangxia reefs near Beiquanzi. Epiphyton is rare to absent in these photomicrographs. R: *R. zhangxianensis*, C: *C. orientalis*, S: microstromatolite, E: Epiphyton, U: undifferentiated sponge. (A) *R. zhangxianensis* commonly attached to other *R. zhangxianensis* (center) or *C. orientalis* (upper left). Note occurrence of geopetal structures within spongocoels, indicating primary growth direction of sponges. (B) An example of downward-growing sponge. (C) A complex framework formed by *R. zhangxianensis* and *C. orientalis*, encrusted by microstromatolite. Note a poorly preserved example of *R. zhangxianensis* in the lower middle part of this photomicrograph. (B, modified after Lee et al., 2016.)

C. orientalis is a minor component of the reefs, occupying <3% of the volume, and usually attached to microbialite or *R. zhangxianensis* (Figs. 4 and 5A).

Epiphyton is a dendritic calcified microbe consisting of micritic filaments (Bornemann, 1886), that in our specimens are ~40 µm in diameter and up to ~300 µm in length and forms millimeter-scale fan-shaped masses (Woo et al., 2008; Woo and Chough, 2010). In addition, Zhangxia *Epiphyton* locally developed chambered forms 0.5–2 mm in diameter reminiscent of *Renalcis* (Woo et al., 2008). *Epiphyton* has variously been compared with cyanobacteria and red algae (Riding, 1991, 2001). *Epiphyton* thalli are commonly subvertical to horizontal, although some are oriented downward (Fig. 5D, E). They are commonly attached to microbialite, but also to *R. zhangxianensis* (Fig. 5C). Areas dominated by *Epiphyton* occupy up to 20% of the reef volume.

Microstromatolites are characterized by thin alternating laminae (~100 µm thick) of dark gray dense micrite and light gray peloidal micrite. Microstromatolites mainly have convex-up lamination with curved or undulose surfaces that often truncate underlying laminae. Their outer morphology ranges from single or branched columns,

~6 mm in diameter and ~7 mm in height, to thin crusts on substrates that include *R. zhangxianensis*, *Epiphyton*, and *C. orientalis* (Figs. 3, 4, and 5B). Their outlines are relatively clear, allowing them to be distinguished from surrounding materials.

Undifferentiated microbialite typically exhibits clotted-peloidal fabric with faint laminae and small areas separated by fenestrae. It is often dolomitized and grades into microstromatolite, suggesting it is probably poorly preserved microstromatolite. Like microstromatolite, undifferentiated microbialite encrusts associated reef-building constituents and has distinct outlines.

In addition to being mutually attached, *R. zhangxianensis*, *Epiphyton*, and *C. orientalis* also exhibit substrate preferences (Figs. 3 and 4). Among 16 identified holdfasts of *R. zhangxianensis*, 10 are attached to other individuals of *R. zhangxianensis*, 3 to *C. orientalis*, and 3 to undifferentiated microbialite. Neither *R. zhangxianensis* nor *C. orientalis* is attached to *Epiphyton* (Figs. 3–5). On the other hand, *Epiphyton* thalli are often either mutually attached, or are attached to *R. zhangxianensis* or *C. orientalis* (Figs. 3 and 5C–E). Interstitial spaces within the framework are up to 5 cm in size and are mainly filled by micrite or,

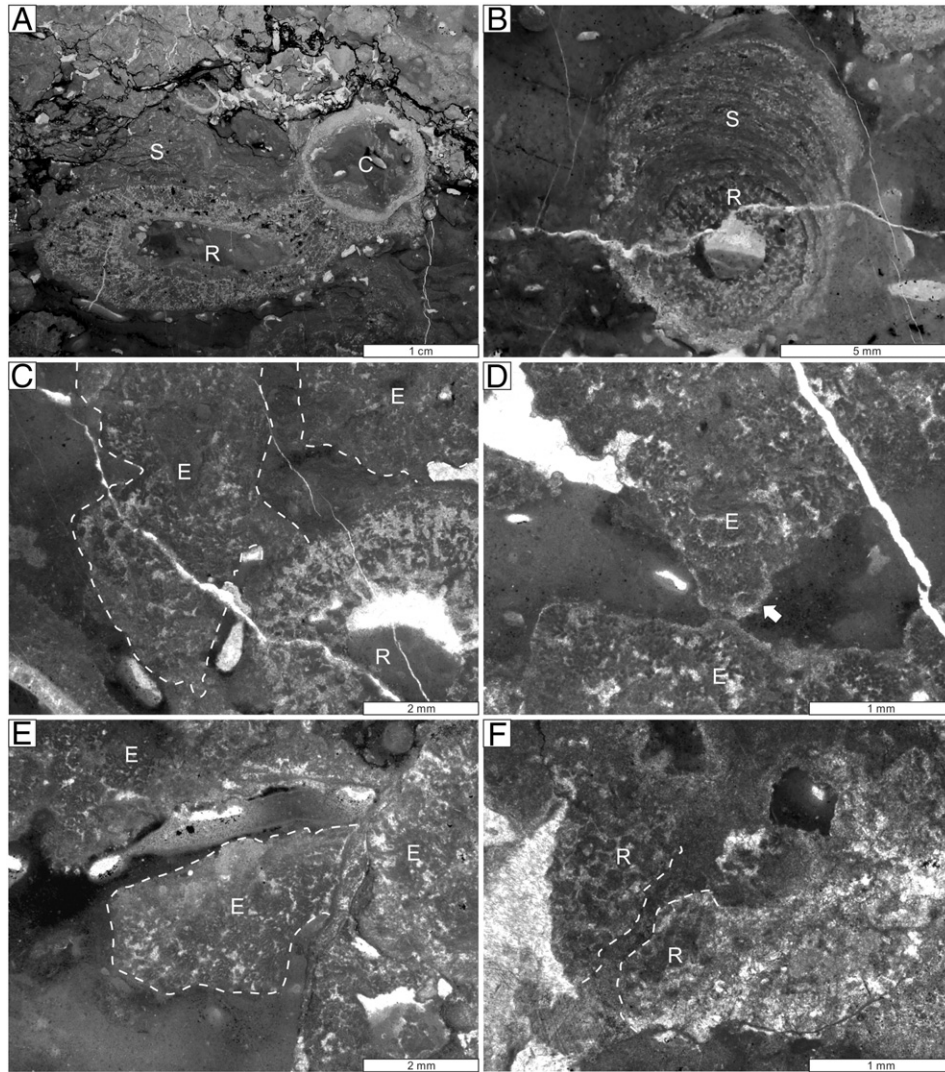


Fig. 5. Photomicrograph showing relationships between the Zhangxia reef-building components. R: *R. zhangxianensis*, C: *C. orientalis*, S: microstromatolite, E: *Epiphyton*. (A) *R. zhangxianensis* attached to the lower part of *C. orientalis*. (B) Columnar microstromatolite growing on an individual of *R. zhangxianensis*. (C) *Epiphyton* thalli attached to *R. zhangxianensis*. (D) *Epiphyton* thalli (arrow) attached to pre-existing *Epiphyton*, forming dendritic fabrics. (E) Downward growing *Epiphyton* thalli, attached to walls formed by other *Epiphyton* thalli. (F) Boring (white dotted line) in *R. zhangxianensis*.

locally, by microstromatolite and undifferentiated microbialite (Fig. 3). Sparitic cements commonly occur between framework components, e.g., beneath or in between *Epiphyton*. Spongocoel of *R. zhangxianensis* is also filled by micrite, microbialite, and unidentified sponge, as well as by sparite in some examples (Figs. 3 and 4). The micrite-fills often contain burrows which themselves are filled with cement and/or coarser micritic sediment and locally exhibit geopetal fabric. Minor amounts of bivalve and trilobite fragments are embedded within the micrite.

3.3. Metazoan-microbial reef structure

Zhangxia reefs formed in shallow subtidal environments, indicated by wavy-stratified, coarse-grained oolitic, oncolitic, and bioclastic carbonates that occur between the mounds (Woo, 2009). These reefs would have been formed by amalgamation of microbial-dominated reef mounds and partly by metazoan-microbial lenses, which are the focus of this study. The main constructors of the metazoan-microbial reef lenses are *R. zhangxianensis* and *Epiphyton*, with minor *C. orientalis*. Mutually attached *R. zhangxianensis* and *C. orientalis* formed stable framework that provided substrates for microstromatolites and *Epiphyton* (Figs. 3 and 4). Scarcity of attachment of either *R. zhangxianensis* or *C. orientalis* to *Epiphyton* suggests preference of these framework-building metazoans for using other metazoans as substrates.

The presence of numerous downward-growing sponges and laterally or subvertically oriented *Epiphyton* thalli suggest synoptic relief of at least a few centimeters during reef growth. This relief was primarily due to the framework-building organisms: *R. zhangxianensis*, *Epiphyton*, and *C. orientalis*. The metazoan-microbial frameworks were encrusted and

stabilized by microstromatolite (Adachi et al., 2015) and undifferentiated microbialite, and contain centimeter-scale growth cavities. Macroboring was unimportant and bored or topped sponges are rare within the reefs. Disarticulated shells of bivalves and trilobites within the reefs are interpreted as remains of dwellers. Locally these fragments provided substrates for microbialite (Fig. 3). Unidentified siliceous sponges together with microbialites occupied framework, shelter and intraskeletal cavities. Soft-bodied burrowers inhabited the interstitial spaces filled with micrite.

4. Significance of Zhangxia metazoan-microbial reefs

A widely held generalization has been that following the archaeocyath demise in Cambrian Series 2, reefs were dominated by microbialites until the cosmopolitan Early Ordovician appearance of lithistid sponge (*Archaeoscyphia*)–calathiid–microbialite reefs (Fagerstrom, 1987; Zhuravlev, 1996; Wood, 1999; Pratt et al., 2001; Rowland and Shapiro, 2002; Webby, 2002; James and Wood, 2010). However, late Cambrian (early Furongian) reefs with abundant *Rankenella* as well as microbialites have long been known from Iran (Hamdi et al., 1995). This occurrence was regarded as exceptional (Rowland and Shapiro, 2002), but other examples of reefal lithistids have since been described from the late Cambrian of the USA (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007), and middle Cambrian of Korea (Hong et al., 2012, 2016), Australia (Kruse and Reitner, 2014) and China (Adachi et al., 2015) (Fig. 6). In many of these late Cambrian examples, sponges appear to have had a significant frame-building role (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008). In contrast, doubts have remained concerning the framework-building ability of sponges in many middle Cambrian reefs (Hong et al., 2012; Kruse and Reitner, 2014; Adachi et al., 2015), although they would have been important in terms of sediment production in carbonate platform (Hong et al., 2016). An exception is the Zhangxia reefs. In reefs from localities near to those that we describe here, Adachi et al. (2015) reported sponge abundances up to 14% without mutual attachments of metazoans. We can now confirm that metazoan abundances in these reefs are commonly up to 20% or more, and that mutual attachment of *Rankenella* and *Cambroctoconus* created frameworks that provided substrates for *Epiphyton* and stromatolites.

Thus, these Zhangxia metazoan-microbial reefs are the earliest lithistid sponge reefs so far reported (Adachi et al., 2015; Lee et al., 2016). They are constructed by framework-building metazoans and *Epiphyton*, and are comparable with those of the Furongian and Early Ordovician, where lithistid sponges locally formed reef frameworks together with microbialites (Kruse and Zhuravlev, 2008; Hong et al., 2015). Zhangxia reefs are broadly similar to early Cambrian reefs, in which archaeocyaths were typically subordinate to microbial components but locally were mutually attached, forming metazoan frameworks (Rowland, 1984; Riding and Zhuravlev, 1995). It therefore appears that, following the archaeocyath demise, the metazoan frame-building niche was occupied by lithistid sponges (Hong et al., 2012). In contrast, mid-Cambrian calcified microbes maintained their previous reef-building roles and changed less, although their diversity may have decreased as archaeocyaths declined (Zhuravlev, 1996; Riding, 2001; Lee et al., 2014b). Overall, this indicates a varied but continuous pattern of reef-building by metazoans and microbial carbonates throughout the Cambrian and Early Ordovician, even though the specific components differed in detail.

5. Conclusions

In middle Cambrian (Series 3, late Stage 5) reefs in the lowermost Zhangxia Formation of Shandong Province, China, the anthaspidellid sponge *R. zhangxianensis*, abundant *Epiphyton* and the stem-group cnidarian *C. orientalis*, formed frameworks encrusted and stabilized by

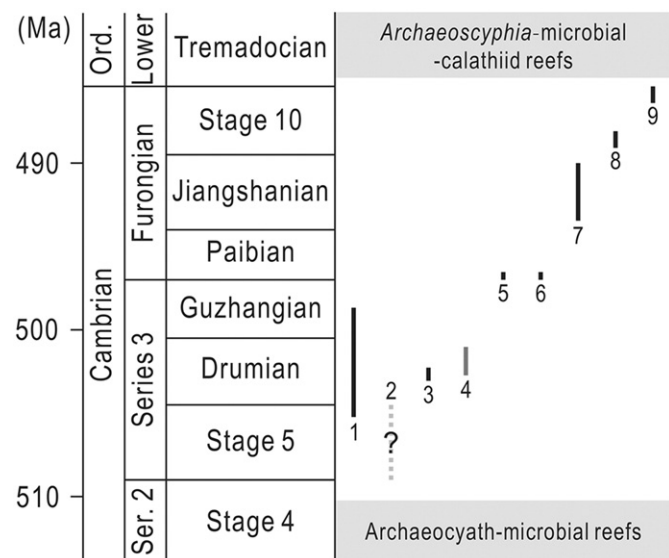


Fig. 6. Occurrence of lithistid sponge-microbial reefs during Cambrian Series 3 and the Furongian. Dotted light gray line: age, occurrence, and reef-building role of sponges uncertain. Dark gray line: dwelling sponges. Black line: framework-building sponges (or constructor). 1. *Rankenella zhangxianensis*-*Epiphyton*-*Cambroctoconus orientalis* reef, Zhangxia Formation, Shandong Province, China (this study). 2. *Orlinocyathus*-*Epiphyton* reef, Dedebulak Formation, Kyrgyzstan (Teslenko et al., 1983). 3. Siliceous sponge (possible anthaspidellid)-*Epiphyton* reef, Daegi Formation, Taebaeksan Basin, Korea (Hong et al., 2012; Lee et al., 2015). 4. *Angulocellularia*-*Taninia*-*Rankenella mors* reef, Ranken Limestone (Undilla Sub-Basin, Georgina Basin), Australia (Kruse and Reitner, 2014). 5. *Rankenella hamdii*-*Girvanella* reef, Mila Formation, Iran (Hamdi et al., 1995; Kruse and Zhuravlev, 2008). 6. *Gallatinospongia conica*-dendrolite reef, Bonanza King Formation, Nevada and California, USA (Shapiro and Rigby, 2004). 7. *Wilbernicyathus donegani*-*Girvanella-Tarthinia* reef, Wilberns Formation, Texas, USA (Johns et al., 2007). 8. Anthaspidellid sponge-microbial reef, Desert Valley Formation, Nevada, USA (Mrozek et al., 2003). 9. *Wilbernicyathus donegani*-*Girvanella-Tarthinia* reef, Dotsero Formation, Colorado, USA (Johns et al., 2007). (Time-scale from Peng et al., 2012.)

microstromatolites and other microbialites. These reefs also contained bivalves, trilobites, and soft-bodied burrowers in inter-framework spaces, and unidentified cryptic siliceous sponges. This relatively complex reef ecosystem appeared within ~5 million years of the decline of archaeocyath-microbial reefs, indicating that mutually attached framework-building metazoans recovered faster in the mid-Cambrian than previously recognized.

Acknowledgements

We thank reviewer Katherine Marenco for detailed suggestions that helped improve the final manuscript. This study was supported by the National Research Foundation of Korea (2015R1A6A3A03019727 to JHL, 2015R1A2A2A01007063 to SJC, and 2013R1A2A2A01067612 to DJL), and by a Korea University Grant to JHL and JH. This paper forms a part of a KOPRI arctic research project (PE16030). This study is a contribution to the IGCP Project 653 'The onset of the Great Ordovician Biodiversity Event'.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in online version, at doi: <http://dx.doi.org/10.1016/j.palaeo.2016.06.018>. These data include the Google map of the most important areas described in this article.

References

- Adachi, N., Ezaki, Y., Liu, J., 2011. Early Ordovician shift in reef construction from microbial to metazoan reefs. *PALAIOS* 26, 106–114. <http://dx.doi.org/10.2110/palo.2010.p10-097r>.
- Adachi, N., Kotani, A., Ezaki, Y., Liu, J., 2015. Cambrian Series 3 lithistid sponge-microbial reefs in Shandong Province, North China: reef development after the disappearance of archaeocyaths. *Lethaia* 48, 405–416. <http://dx.doi.org/10.1111/let.12118>.
- Bornemann, J.G., 1886. *Die Versteinerungen des cambrischen Schichtensystems der Insel Sardinien nebst vergleichenden Untersuchungen über analoge Vorkommnisse aus anderen Ländern*. Verh. Kais. Leopoldinisch-Carolinischen-Dtschen. Akad. Naturforscher 51, 1–148 (in Dutch).
- Cañas, F., Carrera, M., 1993. Early Ordovician microbial-sponge-receptaculitid bioherms of the Precordillera, Western Argentina. *Facies* 29, 169–178. <http://dx.doi.org/10.1007/BF02536927>.
- Chen, J., Lee, J.-H., 2014. Current progress on the geological record of microbialites and microbial carbonates. *Acta Geol. Sin.* 88, 260–275. <http://dx.doi.org/10.1111/1755-6724.12196>.
- Chough, S.K., Lee, H.S., Woo, J., Chen, J., Choi, D.K., Lee, S.-b., Kang, I., Park, T.-y., Han, Z., 2010. Cambrian stratigraphy of the North China platform: revisiting principal sections in Shandong Province, China. *Geosci. J.* 14, 235–268. <http://dx.doi.org/10.1007/s12303-010-0029-x>.
- Fagerstrom, J.A., 1987. *The Evolution of Reef Communities*. John Wiley and Sons, New York (600 pp.).
- Fagerstrom, J.A., 1988. A structural model for reef communities. *PALAIOS* 3, 217–220. <http://dx.doi.org/10.2307/3514531>.
- Fagerstrom, J.A., Weidlich, O., 1999. Strengths and weaknesses of the reef guild concept and quantitative data: application to the Upper Capitan-Massive Community (Permian), Guadalupe Mountains, New Mexico-Texas. *Facies* 40, 131–156. <http://dx.doi.org/10.1007/BF02537472>.
- Gandin, A., Debrenne, F., 2010. Distribution of the archaeocyath-calcimicrobial bioconstructions on the Early Cambrian shelves. *Palaeoworld* 19, 222–241. <http://dx.doi.org/10.1016/j.palwor.2010.09.010>.
- Geyer, G., Shergold, J., 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes* 23, 188–195.
- Hamdi, B., Rozanov, A.Y., Zhuravlev, A.Y., 1995. Latest Middle Cambrian metazoan reef from northern Iran. *Geol. Mag.* 132, 367–373. <http://dx.doi.org/10.1017/S0016756800021439>.
- Hong, J., Cho, S.-H., Choh, S.-J., Woo, J., Lee, D.-J., 2012. Middle Cambrian siliceous sponge-calcimicrobial buildups (Daegi Formation, Korea): metazoan buildup constituents in the aftermath of the Early Cambrian extinction event. *Sediment. Geol.* 253–254, 47–57. <http://dx.doi.org/10.1016/j.sedgeo.2012.01.011>.
- Hong, J., Choh, S.-J., Lee, D.-J., 2015. Untangling intricate microbial-sponge frameworks: the contributions of sponges to Early Ordovician reefs. *Sediment. Geol.* 318, 75–84. <http://dx.doi.org/10.1016/j.sedgeo.2015.01.003>.
- Hong, J., Lee, J.H., Choh, S.J., Lee, D.J., 2016. Cambrian Series 3 carbonate platform of Korea dominated by microbial-sponge reefs. *Sedimentary Geology* 341, 58–69. <http://dx.doi.org/10.1016/j.sedgeo.2016.04.012>.
- Howell, J., Woo, J., Chough, S.K., 2011. Dendroid morphology and growth patterns: 3-D computed tomographic reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 335–347. <http://dx.doi.org/10.1016/j.palaeo.2010.11.013>.
- James, N.P., Wood, R., 2010. Reefs. In: James, N.P., Dalrymple, R.W. (Eds.), *Facies Models 4*. Geological Association of Canada, St. John's, pp. 421–447.
- Johns, R.A., Dattilo, B.F., Spincer, B., 2007. Neotype and redescription of the Upper Cambrian anthaspidellid sponge, *Wilberniacyathus donegani* Wilson, 1950. *J. Paleontol.* 81, 435–444. <http://dx.doi.org/10.1666/05028.1>.
- Kruse, P.D., Reitner, J.R., 2014. Northern Australian microbial-metazoan reefs after the mid-Cambrian mass extinction. *Assoc. Australas. Paleontol. Mem.* 45, 31–53.
- Kruse, P.D., Zhuravlev, A.Y., 2008. Middle-Late Cambrian *Rankenella-Girvanella* reefs of the Mila Formation, northern Iran. *Can. J. Earth Sci.* 45, 619–639. <http://dx.doi.org/10.1139/e08-016>.
- Kruse, P.D., Zhuravlev, A.Y., James, N.P., 1995. Primordial metazoan-calcimicrobial reefs; Tommotian (Early Cambrian) of the Siberian Platform. *PALAIOS* 10, 291–321. <http://dx.doi.org/10.2307/3515157>.
- Lee, J.-H., Chen, J., Choh, S.-J., Lee, D.-J., Han, Z., Chough, S.K., 2014a. Furongian (late Cambrian) sponge-microbial maze-like reefs in the North China Platform. *PALAIOS* 29, 27–37. <http://dx.doi.org/10.2110/palo.2013.050>.
- Lee, J.-H., Lee, H.S., Chen, J., Woo, J., Chough, S.K., 2014b. Calcified microbial reefs in the Cambrian Series 2 of the North China Platform: implications for the evolution of Cambrian calcified microbes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 403, 30–42. <http://dx.doi.org/10.1016/j.palaeo.2014.03.020>.
- Lee, J.-H., Chen, J., Chough, S.K., 2015. The middle-late Cambrian reef transition and related geological events: a review and new view. *Earth Sci. Rev.* 145, 66–84. <http://dx.doi.org/10.1016/j.earscirev.2015.03.002>.
- Lee, J.-H., Woo, J., Lee, D.-J., 2016. The earliest reef-building anthaspidellid sponge *Rankenella zhangxianensis* n. sp. from the Zhangxia Formation (Cambrian Series 3), Shandong Province, China. *J. Paleontol.* 90, 1–9. <http://dx.doi.org/10.1017/jpa.2015.53>.
- Li, Q., Li, Y., Kiessling, W., 2014. Early Ordovician sponge-*Calathium*-microbial reefs on the Yangtze Platform margin of the South China Block. *GFF* 136, 157–161. <http://dx.doi.org/10.1080/11035897.2013.862852>.
- Luo, C., Reitner, J., 2014. First report of fossil "keratose" demosponges in Phanerozoic carbonates: preservation and 3-D reconstruction. *Naturwissenschaften* 101, 467–477. <http://dx.doi.org/10.1007/s00114-014-1176-0>.
- Ma, L., Qiao, X., 2002. *Geological Atlas of China*. Geological Publishing House, Beijing, pp. 222–223.
- Meng, X., Ge, M., Tucker, M.E., 1997. Sequence stratigraphy, sea-level changes and depositional systems in the Cambro-Ordovician of the North China carbonate platform. *Sediment. Geol.* 114, 189–222. [http://dx.doi.org/10.1016/S0037-0738\(97\)00073-0](http://dx.doi.org/10.1016/S0037-0738(97)00073-0).
- Mrozek, S., Dattilo, B.F., Hicks, M., Miller, J.F., 2003. Metazoan reefs from the Upper Cambrian of the Arrow Canyon Range, Clark County, Nevada. *Geol. Soc. Am. Abstr. Programs* 35, 500.
- Park, T.-y., Woo, J., Lee, D.-J., Lee, D.-C., Lee, S.-b., Han, Z., Chough, S.K., Choi, D.K., 2011. A stem-group cnidarian described from the mid-Cambrian of China and its significance for cnidarian evolution. *Nat. Commun.* 2, 442. <http://dx.doi.org/10.1038/ncomms1457>.
- Peng, S., Babcock, L.E., Cooper, R.A., 2012. The Cambrian Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G. (Eds.), *The Geologic Time Scale 2012*. Elsevier, pp. 437–488. <http://dx.doi.org/10.1016/B978-0-444-59425-9.00019-6>.
- Pratt, B.R., James, N.P., 1982. Cryptalgal-metazoan bioherms of early Ordovician age in the St George Group, western Newfoundland. *Sedimentology* 29, 543–569. <http://dx.doi.org/10.1111/j.1365-3091.1982.tb01733.x>.
- Pratt, B.R., Spincer, B.R., Wood, R.A., Zhuravlev, A.Y., 2001. Ecology and evolution of Cambrian reefs. In: Zhuravlev, A.Y., Riding, R. (Eds.), *Ecology of the Cambrian Radiation*. Columbia University Press, New York, pp. 254–274.
- Pruss, S.B., Clemente, H., Laflamme, M., 2012. Early (Series 2) Cambrian archaeocyathan reefs of southern Labrador as a locus for skeletal carbonate production. *Lethaia* 45, 401–410. <http://dx.doi.org/10.1111/j.1502-3931.2011.00299.x>.
- Riding, R., 1991. Calcified cyanobacteria. In: Riding, R. (Ed.), *Calcareous Algae and Stromatolites*. Springer-Verlag, Berlin, pp. 55–87.
- Riding, R., 2001. Calcified algae and bacteria. In: Zhuravlev, A.Y., Riding, R. (Eds.), *Ecology of the Cambrian Radiation*. Columbia University Press, New York, pp. 445–473.
- Riding, R., 2006. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sediment. Geol.* 185, 229–238. <http://dx.doi.org/10.1016/j.sedgeo.2005.12.015>.
- Riding, R., Toomey, D.F., 1972. The sedimentological role of *Epiphyton* and *Renalcis* in Lower Ordovician mounds, Southern Oklahoma. *J. Paleontol.* 46, 509–519.
- Riding, R., Zhuravlev, A.Y., 1995. Structure and diversity of oldest sponge-microbe reefs: Lower Cambrian, Aldan River, Siberia. *Geology* 23, 649–652. [http://dx.doi.org/10.1130/0091-7613\(1995\)023<0649:SADOOS>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1995)023<0649:SADOOS>2.3.CO;2).
- Rowland, S.M., 1984. Were there framework reefs in the Cambrian? *Geology* 12, 181–183. [http://dx.doi.org/10.1130/0091-7613\(1984\)12<181:wtfrit>2.0.co;2](http://dx.doi.org/10.1130/0091-7613(1984)12<181:wtfrit>2.0.co;2).
- Rowland, S.M., Shapiro, R.S., 2002. Reef patterns and environmental influences in the Cambrian and earliest Ordovician. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. SEPM Special Publication Vol. 72. SEPM, Tulsa, pp. 95–128. <http://dx.doi.org/10.2110/pec.02.72.0095>.
- Schubert, J.K., Bottjer, D.J., 1992. Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* 20, 883–886. [http://dx.doi.org/10.1130/0091-7613\(1992\)020<0883:etsapm>2.3.co;2](http://dx.doi.org/10.1130/0091-7613(1992)020<0883:etsapm>2.3.co;2).
- Shapiro, R.S., 2000. A comment on the systematic confusion of thrombolites. *PALAIOS* 15, 166–169. [http://dx.doi.org/10.1669/0883-1351\(2000\)015<0166:ACOTSC>2.0.CO;2](http://dx.doi.org/10.1669/0883-1351(2000)015<0166:ACOTSC>2.0.CO;2).
- Shapiro, R.S., Rigby, J.K., 2004. First occurrence of an *in situ* anthaspidellid sponge in a dendrolite mound (Upper Cambrian; Great Basin, USA). *J. Paleontol.* 78, 645–650. [http://dx.doi.org/10.1666/0022-3360\(2004\)078<0645:FOOALS>2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2004)078<0645:FOOALS>2.0.CO;2).

- Teslenko, I.L., Mambetov, A.M., Zhuravleva, I.T., Myagkova, Y.I., Meshkova, N.P., 1983. The Dedebulak bioherm belt and the history of its development. Tr. Inst. Geol. Geofiz. Sibirskoye Otd. 569, 124–138 (in Russian).
- Webby, B.D., 2002. Patterns of Ordovician reef development. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. SEPM Special Publication Vol. 72. SEPM, Tulsa, pp. 129–179. <http://dx.doi.org/10.2110/pec.02.72.0095>.
- Woo, J., 2009. The Middle Cambrian Zhangxia Formation, Shandong Province, China: Depositional Environments and Microbial Sedimentation (Ph.D. Thesis) Seoul National University, Seoul (243 pp.).
- Woo, J., Chough, S.K., 2010. Growth patterns of the Cambrian microbialite: phototropism and speciation of *Epiphyton*. Sediment. Geol. 229, 1–8. <http://dx.doi.org/10.1016/j.sedgeo.2010.05.006>.
- Woo, J., Chough, S.K., Han, Z., 2008. Chambers of *Epiphyton* thalli in microbial buildups, Zhangxia Formation (Middle Cambrian), Shandong Province, China. PALAIOS 23, 55–64. <http://dx.doi.org/10.2110/palo.2006.p06-103r>.
- Wood, R., 1999. Reef Evolution. Oxford University Press, Oxford (414 pp.).
- Wood, R., Zhuravlev, A.Y., Debrenne, F., 1992. Functional biology and ecology of Archaeocyatha. PALAIOS 7, 131–156. <http://dx.doi.org/10.2307/3514925>.
- Zhuravlev, A.Y., 1996. Reef ecosystem recovery after the Early Cambrian extinction. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events. Geological Society of London Special Publications Vol. 102. Geological Society of London, Oxford, pp. 79–96. <http://dx.doi.org/10.1144/GSL.SP.1996.001.01.06>.
- Zhuravlev, A.Y., Naimark, E.B., Wood, R.A., 2015. Controls on the diversity and structure of earliest metazoan communities: Early Cambrian reefs from Siberia. Earth Sci. Rev. 147, 18–29. <http://dx.doi.org/10.1016/j.earscirev.2015.04.008>.