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The middle–late Cambrian reef transition and related geological events: A review and new view

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ABSTRACT

The reefs of the middle–late Cambrian (Cambrian Epoch 3–Furongian) have long been simply considered as microbialites that flourished in the aftermath of the archaeocyath extinction. Thorough review of the reefs in these periods shows, however, that the Cambrian Epoch 3 and the Furongian actually yield different types of reefs. The Cambrian Epoch 3 reefs are dominated by thrombolites and dendrolites, largely constructed by the calcified microbes *Epiphyton* and *Renalcis*. On the other hand, the Furongian reefs consist mainly of maze-like maceriate reefs and columnar stromatolites. The maceriate reefs most likely formed by siliceous sponges and calcified microbes including *Girvanella* and *Tarthinia*, whereas the columnar stromatolites were mainly constructed by *Girvanella*, *Tarthinia*, and minor siliceous sponges. Other microbial reefs (e.g., non-columnar stromatolites) persisted during the Cambrian Epoch 3 and the Furongian, mainly as small patch reefs or reefal crusts. Lithistid sponge-microbial reefs initially formed in the Cambrian Epoch 3 and occurred throughout the Furongian, but occupied only a minor portion during these periods.

Several geological events occurred across the boundary between the Cambrian Epoch 3 and the Furongian, including positive carbon and sulfur isotope excursions, a eustatic sea-level drop, major faunal turnover of trilobites, and diversification of new organisms. The coincidence of these events and the transition in reefal fabrics suggest that reef ecosystems were significantly influenced by at least some of these events. Among the events, it is likely that sea-level change would have affected reefs, although further studies are required in order to test whether and how the other events influenced the reef transition. *Epiphyton* and *Renalcis* (and thrombolites and dendrolites formed by them) declined greatly most likely due to sea-level fall and thus decreased in shallow marine habitat at the end of Cambrian Epoch 3. The Cambrian Epoch 3 thrombolites and dendrolites were gradually replaced by a sponge-microbial association of the maze-like, maceriate reefs and the columnar stromatolites in the Furongian, coincident with a sea-level rise.

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1. Introduction

Reef components change along with the evolution of life during the Earth history (Wood, 1999; James and Wood, 2010). The earliest reef-builders were cyanobacteria, which dominantly formed the reefs during the Precambrian. As various metazoans including corals, sponges, stromatoporoids, pelmatozoans, and bryozoans emerged in the Phanerozoic, they became the major reef builders. On the other hand, microbes flourished during certain periods of the Phanerozoic, such as shortly after mass extinctions when metazoans declined greatly (Schubert and Bottjer, 1992; Riding, 2006b). Among these periods, the longest metazoan "reef gap" in the Phanerozoic was thought to be the middle–late Cambrian (Boucot, 1990; Kiessling, 2009). During the early Cambrian (Terreneuvian and Epoch 2), archaeocyaths built reefs together with cyanobacteria (Rowland and Shapiro, 2002). Followed by the decline of archaeocyaths at the end of Cambrian Epoch 2, the middle–late Cambrian (Cambrian Epoch 3 and Furongian) was supposedly dominated by microbialites prior to the resurgence of metazoan reef-builders during the Early Ordovician (e.g., Sheehan, 1985; Wood, 1999; Riding, 2006b; James and Wood, 2010).

However, there are certain differences between the reefs of the Cambrian Epoch 3 and the Furongian (e.g., Zhuravlev, 1996). The Cambrian Epoch 3 was dominated by thrombolites and dendrolites (Zhuravlev, 1996; Woo et al., 2008; Woo and Chough, 2010), whereas maze-like maceriate reefs (most likely sponge-microbial reefs) (Shapiro and Awramik, 2006; Lee et al., 2010, 2014a) and columnar stromatolites (Campbell, 1976; Chen et al., 2014) flourished during the Furongian (cf. Zhuravlev, 1996). At the same time, several geological events are known to occur across the Cambrian Epoch 3–Furongian boundary, including a positive excursion of δ^{13}C (Steptoean Positive Carbon Isotope Excursion: SPICE) and a major trilobite faunal turnover (Saltzman et al., 2000; Peng et al., 2004).

The primary purpose of this study is to re-examine the characteristics of Cambrian Epoch 3 and Furongian reefs, and the related geological events. There are a number of unanswered questions with regard to the relationship between the evolution of reefs and the geological events during these periods. What are the differences between the reefs of Cambrian Epoch 3 and those of the Furongian? What caused these differences? How did the geological events affect the reef ecosystem? In order to answer these questions, the present study summarizes the current views on the reefs and geological events during the Cambrian Epoch 3 and the Furongian. It provides insight into the paleoecology of early Paleozoic reefs and its relationship to global paleoenvironmental changes.

2. Geological setting

Four major paleocontinents existed during the middle–late Cambrian, including Gondwana (Africa, Antarctica, Australia, India, South America, South China Block, Sino-Korean Block, and other peri-Gondwana terranes), Laurentia (North America, Greenland, and the Argentine Precordillera), Siberia, and Baltica (northern Europe) (Fig. 1) (Golonka, 2009; McKenzie et al., 2011). Most of these paleocontinents were submerged under shallow and extensive epeiric seas during the Cambrian due to the second-order eustatic sea-level rise that lasted until the Early Ordovician (Miller et al., 2005; Haq and Schutter, 2008). As a result, vast carbonate platforms formed in the tropical regions with shallow and warm waters where reefs flourished (Walker et al., 2002; Kiessling et al., 2003).

Detailed biostratigraphic studies, mainly based on trilobites, were carried out in the Cambrian strata (Peng et al., 2012). Although there are still debates in terms of stage boundary determination, trilobite biostratigraphy has enabled regional and global stratigraphic correlations. The Cambrian period has been subdivided into four epochs, which consist of ten stages: Terreneuvian (Fortunian and Stage 2), Epoch 2 (Stages 3 and 4), Epoch 3 (Stage 5, Drumian, and Guzhangian), and Furongian (Paibian, Jiangshanian, and Stage 10) (Peng et al., 2012). Among these, the Terreneuvian and the Cambrian Stage 2 approximately correspond to the previous Early Cambrian, the Cambrian Epoch 3 to the middle Cambrian, and the Furongian to the late Cambrian. In this paper, we follow this refined stratigraphic scheme.

3. Terminology

Reef is a controversial term, commonly used to describe "a discrete carbonate structure formed by in-situ or bound organic components that develops topographic relief upon the sea floor" (Wood, 1999), or "calcareous deposits created by essentially in place sessile organisms"

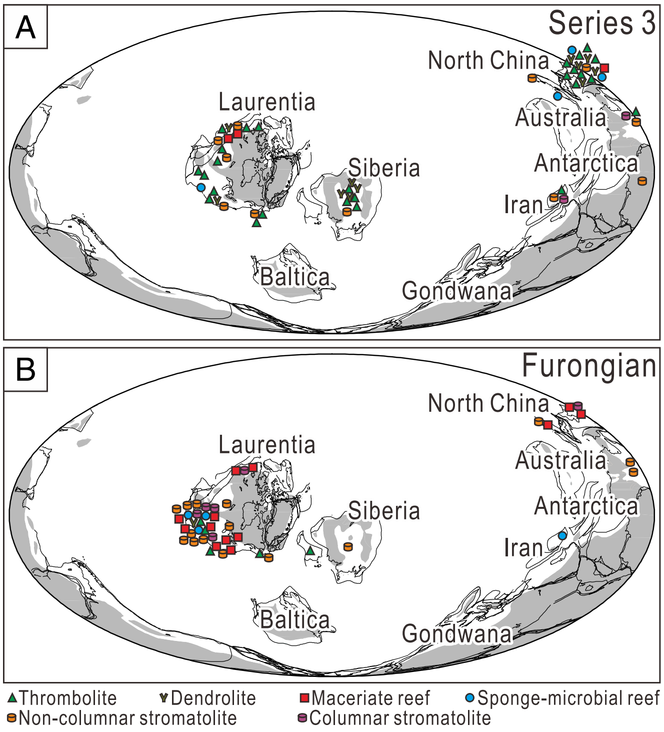

Fig. 1. Paleogeographical occurrences of reefs during the middle–late Cambrian (paleogeographical map modified after Golonka, 2009). A. Cambrian Epoch 3. B. Furongian. For raw data, see Table 1.

(Riding, 2002). In this paper, we follow the terms summarized by Riding (2002). *Bioherm* and *biostrome* are the terms that characterize the geometry of reefs. Bioherm indicates a dome- or lens-like reef, whereas biostrome indicates a distinctly bedded reef. *Mound* is a reef with topographic relief, which is mainly domal in shape. The terms *boundstone* and *framestone* refer to the texture of the reef rocks (Dunham, 1962; Embry and Klovan, 1971). *Boundstone* indicates carbonate rocks in which their "original components were bound together during deposition" (Dunham, 1962), which includes framestone, bindstone, and bafflestone (Embry and Klovan, 1971). *Framestone* describes reefs formed by framework-building organisms.

Microbialites are "organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation" (Burne and Moore, 1987). There have been several attempts to clarify the terminology of microbialites (e.g., Burne and Moore, 1987; Riding, 2000; Shapiro, 2000; Chen and Lee, 2014). In this study, we follow terminology proposed by Riding (2000) for microbialite texture, with modifications of Shapiro (2000) and Chen and Lee (2014). Stromatolites are "laminated benthic microbial deposits" (Riding, 2000), whereas thrombolites are "microbialite composed of a clotted mesostructure (mesoclots)" that are mostly centimeter-scale (Shapiro, 2000). Dendrolites are similar to thrombolites, but they consist of bush-like mesoclots (Riding, 1991b, 2000). Leiolite, defined by Braga et al. (1995), indicates microbialite with structureless, aphanitic fabric. The reefs in this study are described according to the four scales of microbialite observation proposed by Shapiro (2000): megastructure for the geometry of microbialite beds, macrostructure for the gross form of microbialite bodies, mesostructure for the textures of microbialites, and microstructure for the features that can be observed under a microscope. Also, the term maze-like "maceriate reef" is used to indicate reefs that are characterized by centimeter- to decimeter-scale branching maze-like structures (maceria structure) that occur from the late Cambrian Epoch 3 to the Early Ordovician (Shapiro and Awramik, 2006; Lee et al., 2010). Different macro- and mesostructures of Cambrian Series 3 and Furongian reefs are summarized in this study in order to interpret their implications in Earth history.

Not only macro- and mesostructures, but also microstructures bear critical information for the formational processes of reefs. Morphologies of calcified microbes would have been influenced by several factors, including organic assemblages responsible for their formation, growth conditions (e.g., sea-water chemistry, water temperature, and energy conditions), and diagenesis (Riding, 2000). As discussed by many previous researchers, generic names for calcified microbes are given to indicate morphologically distinct groups (e.g., dendritic, chambered, or filamentous structures), not phylogenetically distinct groups (Pratt, 1984; Woo et al., 2008; Luchinina, 2009), so caution is required to interpret their role in Earth history (Riding, 2000). On the other hand, it has been known that expansion and decline of certain calcified microbes (or structures) reflect changes in the environmental condition inducing their formation (Zhuravlev, 1996; Riding, 2000, 2001, 2006a; Săsăran et al., 2014). This study focuses on the relative abundance of calcified microbe "genera" in order to track changes in environmental conditions. Mainly three groups of calcified microbes are considered in this study,

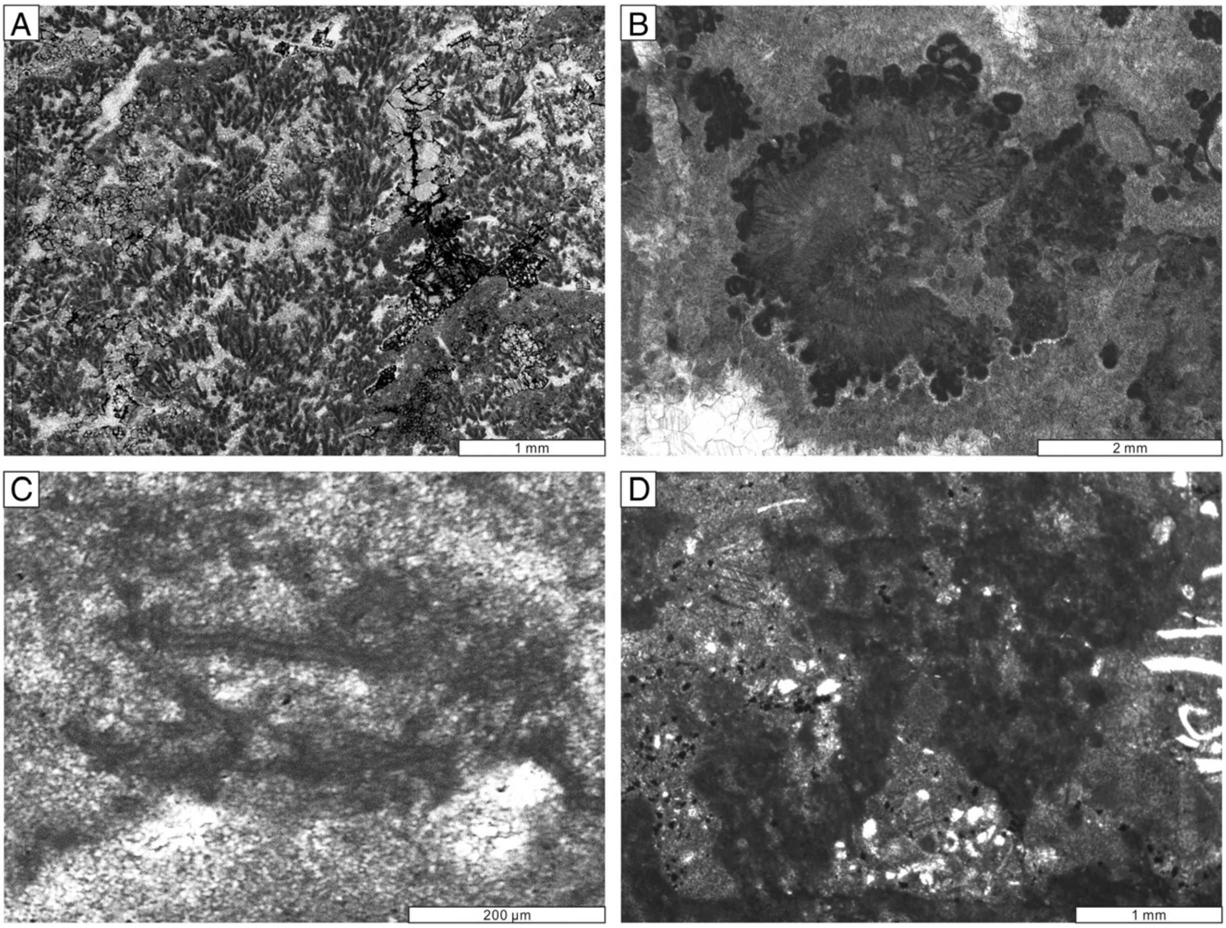

Fig. 2. Typical calcified microbes. A. *Epiphyton* (Cambrian Epoch 3, Shandong Province, China). B. *Renalcis* encrusting *Botomaella* (middle Ordovician, Shaanxi Province, China). C. *Girvanella* (Furongian, Shandong Province, China). D. *Angulocellularia* (Furongian, Taebaeksan Basin, Korea).
D. Courtesy of J. Woo.

Table 1

Summary of the Cambrian Series 3-Furongian reefs. Reef types are described and classified according to scheme of Riding (2000), Shapiro (2000), Shapiro and Awramik (2006), and Chen and Lee (2014). Reef structures are identified based on the text description and figures provided in the original references. Reefs redefined by Shapiro and Awramik (2006) or this study according to the photograph and description within the original references are marked by *. Reefs with only text description within the original references are marked by $^{?}$. Age of the reefs is corrected based on Peng et al. (2012).

Ancient location	Present location	Formation	Age	Depositional environment	Macrostructure	Mesostructure	Microstructure	Reference
Laurentia$^{?}$	Canadian Rockies, Canada	Cathedral Fm.	Stage 5	Platform margin	Mound	Thrombolite	*Epiphyton*, *Renalcis*	McIlreath (1977), Aitken (1989)
Siberia$^{?}$	Russia	Amga Fm.	Stage 5	No data	No data	Thrombolite, dendrolite	*Epiphyton*, *Renalcis*	Zhuravlev (1996, 2001), and references therein
Siberia$^{?}$	Russia	Nel'gaka Fm.	Stage 5	No data	No data	Thrombolite, dendrolite	No data	Zhuravlev (1996) and references therein
Siberia$^{?}$	Russia	Udachny Fm.	Stage 5	No data	No data	Thrombolite, dendrolite	No data	Zhuravlev (1996) and references therein
Siberia$^{?}$	Kyrgyzstan	Dedebulak Fm.	Stage 5	No data	No data	No data	Streptosolenid (?) sponge (*Orlinocyathus*), *Epiphyton*	Teslenko et al. (1983)
Laurentia	Canadian Rockies, Canada	Stephen Fm.	Stage 5	No data	Mound	SH-C stromatolite	*Girvanella*	Aitken (1967)
Laurentia	California, USA	Cararra Fm.	Stage 5	No data	Patch reef	Thrombolite	No data	Shapiro (2004)
Sino-Korea	Shandong Province, China	Mantou Fm.	Stage 5	Shallow subtidal with tidal effect	Patch reef	Thrombolite	No data	Lee and Chough (2011)
Laurentia	Virginia, USA	Upper Shady Dolomite	Stage 5	Platform margin	Mound, breccia	Thrombolite, dendrolite	*Epiphyton*, *Renalcis*, *Girvanella*	Pfeil and Read (1980), Read and Pfeil (1983), Kobluk (1985)
Laurentia	Wyoming, USA	Death Canyon Limestone	Stage 5	Shallow subtidal–lower intertidal	Mound	Thrombolite	Unclear lamination	Middleton (2001)
Laurentia	Pennsylvania, USA	Ledger Fm.	Stage 5	Platform margin	Biostrome	Thrombolite, stromatolite	*Renalcis*-like microbe, *Gordonophyton*, *Tarthinia*	de Wet et al. (1999, 2004)
Gondwana$^{?}$	Flinders Ranges, Australia	Wirrealpa and Aroona Creek Limestones	Stage 5 — Drumian	Channel within lagoon	Mound, branching column	Stromatolite	No data	Youngs (1978)
Gondwana	Ellsworth Mountains, Antarctica	Drake Icefall Fm.	Stage 5 — Drumian?	Carbonate platform	No data	Stromatolite	No data	Buggisch and Webers (1992)
Laurentia	Great Basin, USA	Bonanza King Fm.	Stage 5 — Guzhangian	Platform margin	Mound, biostrome	Thrombolite	*Epiphyton*	Kepper (1981), Rees (1986), Osleger and Montañez (1996)
Gondwana	Iran	Deh-Sulfiyan Fm.	Stage 5 — Guzhangian	Shallow subtidal to lower intertidal	Lamina, domal, column	Stromatolite	No data	Bayet-Goll et al. (2014)
Gondwana	Iran	Deh-Sulfiyan Fm.	Stage 5 — Guzhangian	Shallow subtidal	Mound	Thrombolite	Dolomitized	Bayet-Goll et al. (2014)
Sino-Korea	Shandong Province, China	Zhangxia Fm.	Stage 5 — Guzhangian	Shallow subtidal	Mound	*Epiphyton* framestone, thrombolite, dendrolite	*Epiphyton*, *Renalcis*, *Girvanella*, anthaspidellid sponge (*Rankenella zhangxianensis*), stem-group cnidarian (*Cambroctoconus orientalis*)	Woo et al. (2008), Woo (2009), Woo and Chough (2010), Howell et al. (2011), Lee et al. (in press)
Laurentia	Northwest Territories, Canada	Rockslide Fm.	Drumian	Continental slope near or below storm wave base	Mound	Thrombolite	*Girvanella*, *Epiphyton*, minor *Renalcis*	Pratt (1989, 1995)
Siberia$^{?}$	Aldan River, Russia	Ust'mil' Fm.	Drumian	No data	No data	Thrombolite	No data	Zhuravlev (2001), and references therein
Sino-Korea	Inner Mongolia, China	Zhangxia Fm.	Drumian	Subtidal, relatively deep	Patch reef	Thrombolite	Microstromatolite	Lee et al., submitted for publication-b
Gondwana	Georgina Basin, Australia	Ranken Limestone	Drumian	Bioclast-rich ramp debris	Unknown	Thrombolitic?	Microstromatolite, *Angulocellularia*, *Taninia*, anthaspidellid sponge (*Rankenella mors*)	Kruse and Reitner (2014)
Sino-Korea	Taebaeksan Basin, Korea	Daegi Fm.	Drumian–Guzhangian	Subtidal	Mound	Thrombolite	*Epiphyton*, siliceous sponge, stem-group cnidarian (*Cambroctoconus*)	Hong et al. (2012)
Sino-Korea	Shandong Province, China	Zhangxia Fm.	Drumian–Guzhangian	Shallow subtidal	Patch reef, crust	Stromatolite	Micritic/carbonate grain	Woo (2009)
Sino-Korea	Shanxi Province, China	Zhangxia Fm.	Drumian–Guzhangian	Subtidal	Mound	Thrombolite, dendrolite	*Epiphyton*	Zhang et al. (1985), Gao and Zhu, 1998, Mu et al. (2003)
Sino-Korea	Beijing, China	Zhangxia Fm.	Drumian–Guzhangian	Shallow subtidal	Mound	Thrombolite, dendrolite	*Epiphyton*	Zhang et al. (1985), Mu et al. (2003)

(continued on next page)

Table 1 (*continued*)

Ancient location	Present location	Formation	Age	Depositional environment	Macrostructure	Mesostructure	Microstructure	Reference
Sino-Korea	Liaoning Province, China	Zhangxia Fm.	Drumian–Guzhangian	Subtidal	Mound	Thrombolite, dendrolite	*Epiphyton*	Zhang et al. (1985), Mu et al. (2003)
Sino-Korea	Anhui Province, China	Zhangxia Fm.	Drumian–Guzhangian	Subtidal	Mound	Thrombolite, dendrolite	*Epiphyton*	Zhang et al. (1985), Mu et al. (2003)
Laurentia	Tennessee, USA	Maryville Limestone Fm.	Drumian–Guzhangian	Shelf margin	Mound	Centimeter-scale clots	*Renalcis*, *Girvanella*, sponge spicules	Srinivasan and Walker (1993), Rankey et al. (1994)
Gondwana	Amadeus Basin, Australia	Shannon Fm., Jay Creek limestone	Drumian–Guzhangian	Subtidal to intertidal	Patch reef, crust	Stromatolite	crystalline/vermiform	Kennard (1994)
Gondwana	Amadeus Basin, Australia	Shannon Fm., Jay Creek limestone	Drumian–Guzhangian	Subtidal to intertidal	Mound	Thrombolite	Massive/lobate lobe	Shergold et al. (1985), Kennard (1994)
Siberia?	Amga River, Russia	Tangha Fm.	Drumian–Guzhangian	No data	No data	Thrombolite	*Epiphyton*, *Renalcis*	Zhuravlev (2001), and references therein
Tarim?	Keping, China	Awatage Fm.	Drumian–Guzhangian	Intertidal	No data	Stromatolite	No data	Yu et al., 2001
Laurentia	Newfoundland, Canada	Petit Jardin Fm.	Drumian–Guzhangian	Very shallow subtidal to intertidal shelf	Mound	Stromatolite	Stromatoids	Kennard and James (1986), Kennard et al. (1989)
Laurentia	Newfoundland, Canada	Petit Jardin Fm.	Drumian–Guzhangian	Low-energy subtidal shelf	Mound	Thrombolite	Mesoclots	Kennard and James (1986), Kennard et al. (1989)
Laurentia	Great Basin (Utah), USA	Orr Fm.	Guzhangian	Shallow subtidal to intertidal	Mound	Thrombolite	*Epiphyton*, *Renalcis*	Lohmann (1976), Widiarti (2011)
Laurentia*	Canadian Rockies, Canada	Sullivan Fm.	Guzhangian	Shallow subtidal	No data	Maceriate reef	Recrystallized and dolomitized	Aitken (1967)
Laurentia*	Canadian Rockies, Canada	Waterfowl Fm.	Guzhangian	Shallow subtidal	No data	Maceriate reef	Recrystallized and dolomitized	Aitken (1967)
Laurentia	Canadian Rockies, Canada	Waterfowl Fm.	Guzhangian	Intertidal	Dome	LLH-C stromatolite	Microcrystalline, peloids, some filamentous alga	Aitken (1967)
Laurentia	Canadian Rockies, Canada	Waterfowl Fm.	Guzhangian	Shallow subtidal to intertidal	Mound, biostrome	Thrombolite, dendrolite	*Renalcis*, *Girvanella*	Waters (1989)
Sino-Korea*	Inner Mongolia, China	Abuqiehai Fm.	Guzhangian	Subtidal, relatively deep	Patch reef	Maceriate reef	Siliceous sponge, microstromatolite	Myrow et al. (in press), Lee et al., submitted for publication-b
Sino-Korea	Beijing, China	Gushan Fm.	Guzhangian	Subtidal	Dome	Thrombolite	*Epiphyton*	Mei et al. (2005), Chen et al. (2014).
Siberia?	Russia	Diringde Reef Massif	Guzhangian	No data	No data	Dendrolite	*Proaulopora*, *Amgaella*, *Gordonophyton*	Zhuravlev (2001), and references therein
Siberia?	Russia	Diringde Reef Massif	Guzhangian	No data	No data	Stromatolite	*Razumovskia*	Zhuravlev (2001), and references therein
Laurentia?	Idaho, USA	Nounan Fm.	Guzhangian	Subtidal	Biostrome	Thrombolite	No data	Saltzman et al. (2004)
Laurentia	Newfoundland, Canada	Cow Head Group	Guzhangian — Stage 10	Platform margin	Breccia	Thrombolite	*Girvanella*, *Epiphyton*, *Renalcis*	James (1981)
Laurentia?	Idaho, USA	Nounan Fm.	Paibian	Subtidal	No data	Stromatolite	No data	Saltzman et al. (2004)
Gondwana	Iran	Deh-Molla Fm.	Paibian	Subtidal	Patch reef	Sponges and bioclasts with encrustation	Anthaspidellid sponge (*Rankenella hamdii*), *Girvanella*	Hamdi et al. (1995), Kruse and Zhuravlev (2008)
Laurentia	Great Basin, USA	Bonanza King Fm.	Paibian	Shallow subtidal	Mound, biostrome	Dendrolite	?*Renalcis*, anthaspidellid sponge (*Gallatinospongia conica*)	Shapiro and Rigby (2004)
Laurentia	Tennessee, USA	Maynardville Limestone	Paibian	Shallow subtidal to lower intertidal	Mound	Thrombolite	*Renalcis*, *Epiphyton*, *Girvanella*	Markello and Read (1981, 1982), Glumac and Walker (1997)
Laurentia	Tennessee, USA	Maynardville Limestone	Paibian	Intertidal to supratidal	Column, SH, LLH, stratiform	Stromatolite	Crystalline	Markello and Read (1981, 1982), Glumac and Walker (1997)
Laurentia	Newfoundland, Canada	Petit Jardin Fm.	Paibian	Subtidal	Mound	Stromatolite	No data	Kennard et al. (1989), Saltzman et al. (2004)
Gondwana?	Queensland, Australia	Arrinthrunga Fm.	Paibian	No data	Mound	Stromatolite	No data	Shergold et al. (1985), Kennard and James (1986)
Laurentia*	Maryland, USA	Conococheague Limestone	Paibian–Jiangshanian	Lagoon	Mound, biostrome	Maceriate reef	*Renalcis* or *Renalcis*-like forms, *Girvanella*	Demicco (1985)
Laurentia	Maryland, USA	Frederick Limestone	Paibian–Jiangshanian	Platform margin	Breccia	Massive	*Epiphyton*, *Girvanella*	Demicco (1985)
Laurentia*	Precordillera, Argentina	La Flecha Fm.	Paibian — Stage 10	Shallow to deep subtidal	Tabular, mound, cone, ellipsoidal	Maceriate reef	Peloid, clotted micrite, *Nuia*	Armella (1994), Raviolo et al. (2010)
Laurentia	Precordillera, Argentina	La Flecha Fm.	Paibian — Stage 10	Intertidal to supratidal	Mound, LLH	Stromatolite	Micrite	Armella (1994)
Laurentia	Great Basin, USA	Nopah Fm.	Paibian — Stage 10	Shallow subtidal	Column, mound	Stromatolite	No data	Shapiro and Awramik (2000)
Laurentia	Great Basin, USA	Nopah Fm.	Paibian — Stage 10	Shallow subtidal	Column, mound	Thrombolite, dendrolite	No data	Shapiro and Awramik (2000)
Laurentia*	Missouri, USA	Bonneterre, Derby-doerun,	Paibian — Stage 10	Intertidal?	Mound, biostrome	Maceriate reef	No data	Howe (1966)

		Potosi, Eminence, Gasconade, Roubidoux, Jefferson City fms.						
Siberia?	Russia	No data	Paibian – Stage 10	No data	No data	Stromatolite	No data	Zhuravlev (1996), and references therein
Tarim	Xinjiang, China	Lower Qiulitag Group	Paibian – Stage 10	Intertidal	LLH	Stromatolite	Alternation of dark and light colored layers	Zhang et al. (2015)
Tarim*	Xinjiang, China	Lower Qiulitag Group	Paibian – Stage 10	Restricted to open marine subtidal	Stratiform, columnar	Maceriate reef	Micrite	Zhang et al. (2015)
Sino-Korea*	Shandong Province, China	Chaomidian Fm.	Jiangshanian	Near-below wave base subtidal	Mound, biostrome	Maceriate reef	Siliceous sponge, microstromatolite, *Girvanella*, *Tarthinia*	Lee et al. (2010, 2012, 2014a)
Laurentia	Texas, USA	Wilberns Fm.	Jiangshanian	Shallow marine	Mound	Thrombolite	Anthaspidellid sponge (*Wilbernicyathus donegani*), *Girvanella*, minor *Tarthinia*, *Epiphyton*, *Renalcis*	Johns et al. (2007)
Laurentia*	Canadian Rockies, Canada	Bison Creek Fm.	Jiangshanian	Shallow subtidal	Mound	Maceriate reef	No data	Aitken (1967)
Laurentia*	Pennsylvania, USA	Gatesburg Fm.	Jiangshanian	Shallow marine	Mound	Maceriate reef	No data	Taylor et al. (1999), Loch and Taylor (2004)
Laurentia	Canadian Rockies, Canada	Bison Creek Fm.	Jiangshanian	Shallow subtidal	Column	SH-C stromatolite	No data	Aitken (1967)
Sino-Korea*	Beijing, China	Chaomidian Fm.	Jiangshanian	Shallow subtidal	Mound	Maceriate reef	Siliceous sponge, *Girvanella*	Chen et al. (2014)
Laurentia?	Great Basin (Nevada), USA	Whipple Cave Fm.	Jiangshanian	Shallow marine	Column, mound	Stromatolite	No data	Cook and Taylor (1975)
Laurentia?	Oklahoma, USA	Fort Sill Limestone	Jiangshanian	Subtidal	Mound	Stromatolite	No data	Stitt (1976)
Kazakhstan	Kazakhstan	Maly Karatau	Jiangshanian	Ooid shoal (platform margin?)	Breccia	Thrombolite, dendrolite	*Girvanella*, *Epiphyton*, subordinate *Renalcis*, *Tharama* and *Gemma*	Cook et al. (1991), Pratt (1995)
Laurentia	Texas, USA	Wilberns Fm.	Jiangshanian – Stage 10	Intertidal to supratidal	Mound	Stromatolite	*Girvanella*, *Epiphyton*, *Renalcis*, *Nuia*	Ahr (1971), Chafetz (1973), Johns et al. (2007)
Laurentia*	Canadian Rockies, Canada	Mistaya Fm.	Jiangshanian – Stage 10	Shallow subtidal	Patch reef	Maceriate reef	No data	Aitken (1967)
Laurentia*	Great Basin, USA	Nopah Fm.	Jiangshanian – Stage 10	Restricted subtidal ramp	Mound	Maceriate reef	No data	Shapiro and Awramik (2006)
Laurentia*	Great Basin (Utah), USA	Notch Peak Fm.	Jiangshanian – Stage 10	No data	Column, mound	Maceriate reef	No data	Coulson et al. (2013)
Laurentia	Great Basin (Utah), USA	Notch Peak Fm.	Jiangshanian – Stage 10	No data	Column, mound	Stromatolite	No data	Coulson et al. (2013)
Laurentia*	Quebec, Canada	Strites Pond Fm.	Stage 10	Subtidal quite lagoon	Biostrome	Maceriate reef	*Renalcis*-like clusters, clotted fabric	Hersi et al. (2002)
Sino-Korea	Shandong Province, China	Chaomidian Fm.	Stage 10	Shallow subtidal with high energy	Biostrome, column	Stromatolite	*Girvanella*, minor *Tarthinia*, siliceous sponges	Chen et al. (2011, 2014)
Sino-Korea	Shandong Province, China	Sanshanzi Fm.	Stage 10	Shallow subtidal with high energy	Mound, biostrome	Maceriate reef	Dolomitized	Chen et al. (2014)
Sino-Korea	Taebaeksan Basin, Korea	Hwajeol Fm.	Stage 10	Deep subtidal	Mound	Dendrolite	*Angulocellularia*	Lee et al., submitted for publication-a
Laurentia	Colorado, USA	Dotsero Fm.	Stage 10	Shallow marine	Biostrome, column	Stromatolite	*Girvanella*, *Tarthinia*, anthaspidellid sponge (*Wilbernicyathus donegani*)	Campbell (1976), Myrow et al. (2003), Johns et al. (2007), Myrow and Chen (2015)
Laurentia?	Great Basin (Nevada), USA	Desert Valley Fm.	Stage 10	No data	No data	Stromatolite	Anthaspidellid sponge, *Renalcis*, *Epiphyton*	Mrozek et al. (2003), Dattilo et al. (2004)
Laurentia*	New York, USA	Little Falls Fm.	Stage 10	Restricted/normal marine, intertidal	Mound	Maceriate reef	No data	Mazzullo and Friedman (1977), Landing et al. (2003)
Laurentia	New York, USA	Hoyt Limestone	Stage 10	Shallow subtidal to intertidal	Column, mound	Stromatolite	Alternation of calcite and dolomite	Friedman (2000)
Australia?	Queensland, Australia	Ninmaroo Fm.	Stage 10	No data	No data	Stromatolite	No data	Shergold et al. (1985)
Laurentia?	Wisconsin, USA	St. Lawrence Fm.	Stage 10	Intertidal to shallow subtidal	Column	Stromatolite	No data	Runnegar et al. (1979)

Epiphyton (dendritic), *Renalcis* (chambered), and *Girvanella* (filamentous), together with genera described in previous studies (e.g., *Angulocellularia* and *Tarthinia*) (Riding, 1991a) (Fig. 2).

4. Cambrian Epoch 3–Furongian reefs

During the Cambrian Epoch 3, microbialites flourished in various regions including Laurentia, Siberia, Sino-Korean Block, Tarim, Iran, and Australia (Table 1; Fig. 1A). Many of the microbialites formed dm- to m-scale patch reefs, but some of them stacked and formed bioherms or biostromes of several tens of meters thick (Fig. 3) (Woo et al., 2008). Cambrian Epoch 3 reefs are mainly composed of thrombolites or dendrolites (Fig. 3B) (Zhuravlev, 1996; Seslavinsky and Maidanskaya, 2001). Thrombolites and dendrolites are both characterized by cm-scale mesoclots, which are surrounded by matrices (usually micrite or bioclasts) (Riding, 2000). These mesoclots often differ in color and/or texture from the surrounding matrix. Mesoclots of the thrombolites are usually rounded to irregular in shape, whereas those of the dendrolites are bush-like, dendritic in shape (Riding, 1991b, 2000; Shapiro, 2000; Woo et al., 2008). The bush-shaped branching calcified microbe *Epiphyton*, the chamber-shaped *Renalcis*, and other similar calcified microbes (i.e., those in the *Epiphyton* and *Renalcis* groups) are dominant within the thrombolites and dendrolites of the Cambrian Epoch 3 (Fig. 3D) (Riding, 1991a; Woo et al., 2008). Cambrian Epoch 3 thrombolites and dendrolites mainly flourished in shallow marine environments and on platform margins (Table 1).

Compared to thrombolites and dendrolites, stromatolites occupy a minor portion of Cambrian Epoch 3 reefs. These stromatolites usually formed small patch reefs (Youngs, 1978; Woo, 2009) or thin crusts on pre-existing surfaces including other microbial reefs (Kennard, 1994) in the shallow subtidal to intertidal environments (Table 1). Lithistid sponges (mainly anthaspidellids) existed within Cambrian Epoch 3 reefs of Sino-Korean Block (Woo, 2009; Hong et al., 2012; Lee et al., in press), in Kyrgyzstan (Teslenko et al., 1983), and in Australia (Kruse and Reitner, 2014). These sponges mainly acted as frame-builders within the reefs, but some were encrustors or dwellers (Fig. 3C) (Kruse and Reitner, 2014; Lee et al., in press). A few maceriate reefs began to occur in the late Cambrian Epoch 3 (Guzhangian), in the subtidal habitats of the Canadian Rockies and of Inner Mongolia (Table 1).

Furongian reefs have been recognized at numerous locations, including Laurentia, Sino-Korean Block, Siberia, Antarctica, Australia, Kazakhstan, and Tarim (Table 1; Fig. 1B). These reefs are usually meter-scale bioherms, but some extend over hundreds of kilometers, forming a relatively thin (~10 m) biostromes (Campbell, 1976; Lee et al., 2010; Chen et al., 2011; Myrow and Chen, 2015). Many of the Furongian reefs are maceriate reefs, which are characterized by maceria structures (cm- to dm-scale maze-like, branching structures) that mainly occurred during the Furongian and the Early Ordovician (Fig. 4A) (Shapiro and Awramik, 2006). Maceriate reefs formed within various environments, ranging from deep subtidal to intertidal (Table 1) (Shapiro and Awramik, 2006). Together with the maceriate reefs, crudely laminated columnar stromatolites flourished during the Furongian in shallow subtidal to intertidal environments (Fig. 4B; Table 1) (Campbell, 1976; Zhuravlev, 1996; Chen et al., 2011). These stromatolites are characterized by crude and thick (~1 mm) concave-upward laminations and dm-scale columnar structures. A few lithistid sponge (anthaspidellids)-microbial reefs are also recognized in Laurentia and Gondwana (Iran) (Hamdi et al., 1995; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008). On the other hand, thrombolites and dendrolites, which were abundant during the Cambrian Epoch 3, diminished greatly during the Furongian, but some remained in platform margin or shallow subtidal environments (Table 1) (James, 1981).

Many of the Furongian reefs have not been studied at microscale, partly due to dolomitization and recrystallization (Howe, 1966; Shapiro and Awramik, 2006). On the other hand, a recent study suggests that the maceriate reefs were formed by siliceous sponges of unknown affinity together with microbial components including microstromatolites, *Girvanella*, and *Tarthinia* (Fig. 4C) (Lee et al., 2014a). The temporally restricted occurrence of maceriate reefs (late Cambrian Epoch 3–Early Ordovician) supports their biogenic origin (Shapiro and Awramik, 2006; Lee et al., 2014a). Crudely laminated, columnar stromatolites mostly accompany *Girvanella* crusts together with minor *Tarthinia* along their layers (Fig. 4D) (Johns et al., 2007; Chen et al., 2011, 2014). Some poorly preserved siliceous sponges are also recognized among the columnar stromatolites (Johns et al., 2007; Chen et al., 2014).

In the following sections, the Cambrian Epoch 3 and Furongian reefs of Sino-Korean Block and Laurentia are reviewed, where detailed studies on these reefs were performed.

5. Cambrian Epoch 3–Furongian reefs in Sino-Korean Block

The Sino-Korean Block was a microcontinent located near Gondwana or part of Gondwana during the early Paleozoic (Golonka, 2009; McKenzie et al., 2011). The block yields a thick succession of mixed carbonate-siliciclastic deposits of the Cambrian Epoch 2–middle Ordovician, forming the North China Platform (Meng et al., 1997). Various microbialites flourished across the North China Platform, mainly during the Cambrian Epoch 3 and the Furongian (Zhang et al., 1985; Gao and Zhu, 1998; Mu et al., 2003; Woo et al., 2008; Woo, 2009; Chough et al., 2010; Lee et al., 2010, 2012, 2014a; Woo and Chough, 2010; Howell et al., 2011). Detailed observations on the reefs were mostly made in the eastern part of the platform (Shandong Province, China). In the following sections, we summarize the characteristics of the reefs in Shandong Province, together with occurrences in other areas of the platform.

5.1. Cambrian Epoch 3

The Cambrian Epoch 3 succession in Shandong Province (Zhangxia Formation) is represented by an ~180 m-thick, carbonate-dominated succession that consists mainly of oolitic/skeletal grainstones and microbialites, although a shale-dominated interval (ca. 100 m thick) locally exists in the middle part of the formation (Woo, 2009). Trilobite biozones including *Lioparia*, *Crepicephalina*, *Amphoton–Taitzuia*, and *Damesella–Yabeia* indicate that the formation formed during the late Cambrian Stage 5–early Guzhangian (Chough et al., 2010). The formation is overlain by a shale-dominated succession of the Gushan Formation (late Guzhangian) via a drowning unconformity (Chen et al., 2011). The grainstones and microbialites of the Zhangxia Formation were deposited on a shallow-water carbonate platform (Woo, 2009). The microbialites in the Zhangxia Formation contain *Epiphyton* framestone, thrombolite, dendrolite, stromatolite, and leiolite (Fig. 3A, B) (Woo et al., 2008; Woo and Chough, 2010). Metazoan reef-builders (anthaspidellid sponge *Rankenella zhangxianensis* Lee et al., in press and stem-group cnidarian *Cambroctoconus orientalis* Park et al., 2011) locally occur within the *Epiphyton* framestones, thrombolites, and leiolites (Fig. 3C) (Woo, 2009).

Thrombolites in the Zhangxia Formation are characterized by mm- to cm-scale dark-gray mesoclots in a light-gray lime mudstone matrix (Fig. 3B). These clots mainly consist of microsparitic calcites, *Girvanella*, and *Epiphyton*. Fossil fragments locally occur between the clots. The Zhangxia dendrolites are similar to thrombolites, except that the mesoclots display upward-widening dendritic shapes (Riding, 1991b, 2000; Howell et al., 2011). Coarse skeletal and peloidal grains occur between the dendritic mesoclots (Howell et al., 2011). Stromatolites either encrust other microbialites, forming thin crusts, or construct bioherms that are 3–30 cm thick. Leiolites form small domes ca. 50 cm in height, with aphanitic mesostructures (Woo, 2009). *Epiphyton* framestone lacks clear mesostructures, showing white, irregular masses composed of *Epiphyton* with cement of sparry calcite (Fig. 3A, D) (Woo and Chough, 2010). At least four different morphological variants of *Epiphyton* occur within the *Epiphyton* framestone,

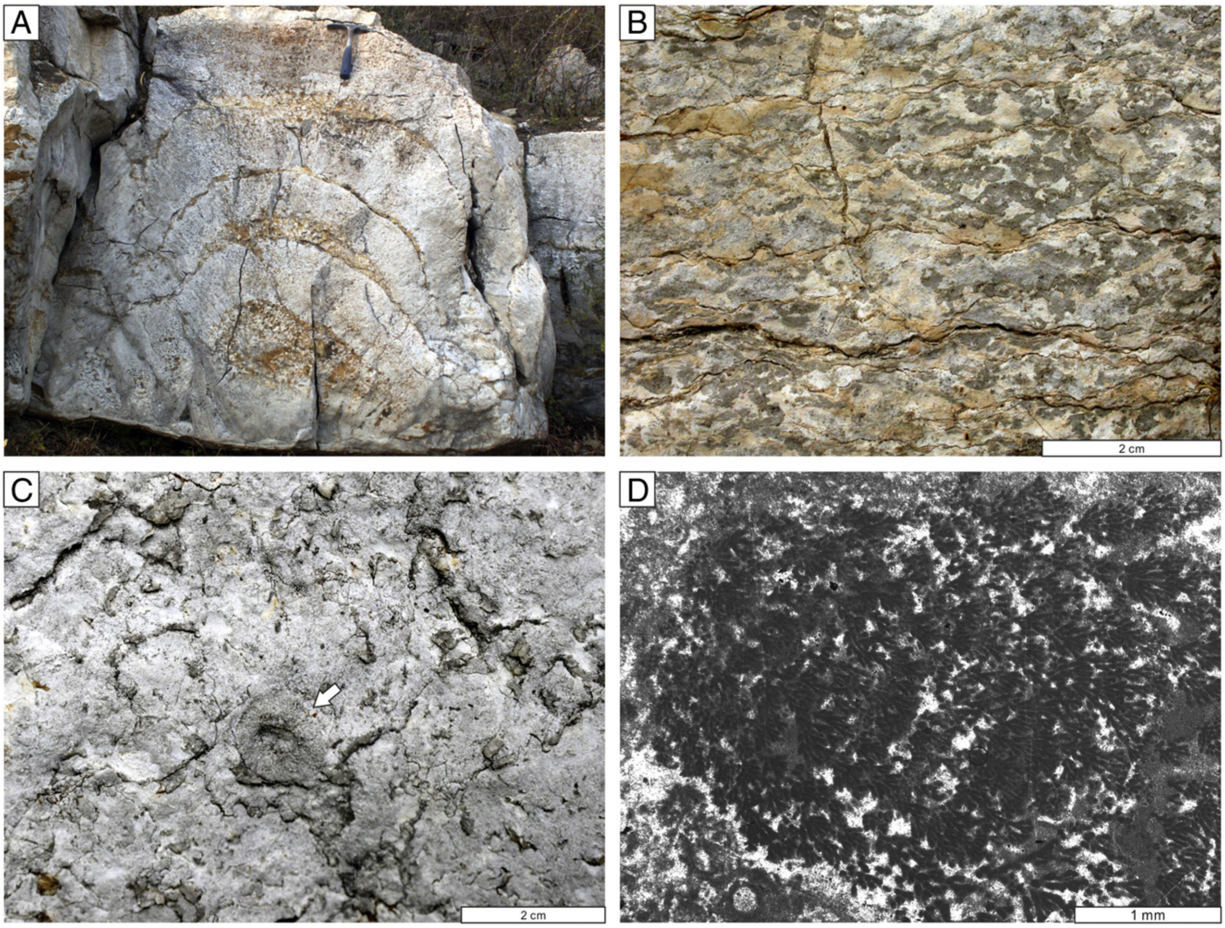

Fig. 3. Cambrian Epoch 3 reefs in Shandong Province, China (Drumian; Zhangxia Formation). For section locations, see Chough et al. (2010). A. *Epiphyton* framestone (Jiulongshan section). The bioherm displays an upward-widening fan shape. B. Thrombolite/dendrolite (Tangwangzhai section). Clots are a few mm in size. Some clots show an upward-widening dendritic shape. C. An anthaspidellid sponge *Rankenella zhangxianensis* (white arrow) within the *Epiphyton* framestone (Beiquanzi section). D. *Epiphyton*, showing branching structure.

which can be classified as different genera (e.g., *Gordonophyton* and *Tubomorphophyton*) (Woo et al., 2008; Lee et al., 2014b).

Although studied in less detail than the microbialites of Shandong Province, there are also some reports of microbialites from coeval successions elsewhere on the North China Platform. Thrombolites and dendrolites composed mainly of *Epiphyton* and *Renalcis* were reported from various localities: Liaoning, Jilin, Anhui, Shanxi, and Beijing (Zhang et al., 1985; Gao and Zhu, 1998; Mu et al., 2003). In addition, a recent study reveals that siliceous sponge–*Epiphyton* reef with minor *Cambroctoconus* occurs in the easternmost part of the platform (Drumian; Taebaeksan Basin, Korea) (Hong et al., 2012). These studies collectively demonstrate that *Epiphyton*-dominated thrombolites and dendrolites are widely distributed throughout the North China Platform. These *Epiphyton*-rich thrombolites and dendrolites were terminated by a platform-wide, diachronous drowning event that occurred during the middle Guzhangian, although some microbialites containing poorly preserved *Epiphyton* locally reappeared during the late Guzhangian (e.g., in the Beijing region) (Mei et al., 2005; Chen et al., 2014). The occurrence of *Epiphyton*-containing microbial reefs in the late Guzhangian suggests that the decline of *Epiphyton*-dominated thrombolites and dendrolites on the platform was not due to a platform-wide drowning event (Chen et al., 2014).

5.2. Furongian

The Furongian succession of the North China Platform commonly contains reefs, but they have only recently received attention (Lee et al., 2010, 2012, 2014a; Chen et al., 2014). The only detailed studies of the Furongian reefs were done in the eastern Sino-Korean Block (Shandong Province, China), in which the succession consists of a ca. 200-m-thick, carbonate-dominated unit (Chaomidian Formation) (Chough et al., 2010; Chen et al., 2011). The Chaomidian Formation formed during the Furongian, comprising the *Chuangia*, *Changshania–Irvingella*, *Kaolishania*, *Asioptychaspis–Tsinania*, *Quadraticephalus*, and *Mictosaukia* trilobite biozones (Chough et al., 2010). Deposition of the carbonate sediments mainly took place in shallow-water, storm-dominated subtidal environments (Chen et al., 2011, 2012; Lee et al., 2012). Two major types of reefs are recognized in this area: maceriate reefs and columnar stromatolites.

The maceriate reefs in the Chaomidian Formation are characterized by tabular, domal, or columnar macrostructures (Lee et al., 2010, 2012, 2014a). They are mainly present in the lower and middle parts of the formation (*Changshania–Irvingella* and *Kaolishania* zones, and partly within the *Asioptychaspis–Tsinania* Zone of the Jiangshanian Stage). Maceria structures are clearly distinguished in outcrops due to partial dolomitization along the boundary of maceria (Fig. 4A) (cf. Glumac and Walker, 1997). Each maceria is 0.5–3 cm in width and 3–20 cm in height, with inter-macerial detrital carbonate sediments (e.g., lime mud or grainstone). Detailed microfacies analysis revealed that the Chaomidian maceriate reefs consist of siliceous sponge spicule networks of unknown affinity and microbial components, including microstromatolites, *Girvanella*, and *Tarthinia* (described as a *Renalcis*-like form) (Fig. 4C) (Lee et al., 2014a). These siliceous sponges may represent non-spicular demosponges (e.g., “keratose” sponges), but further

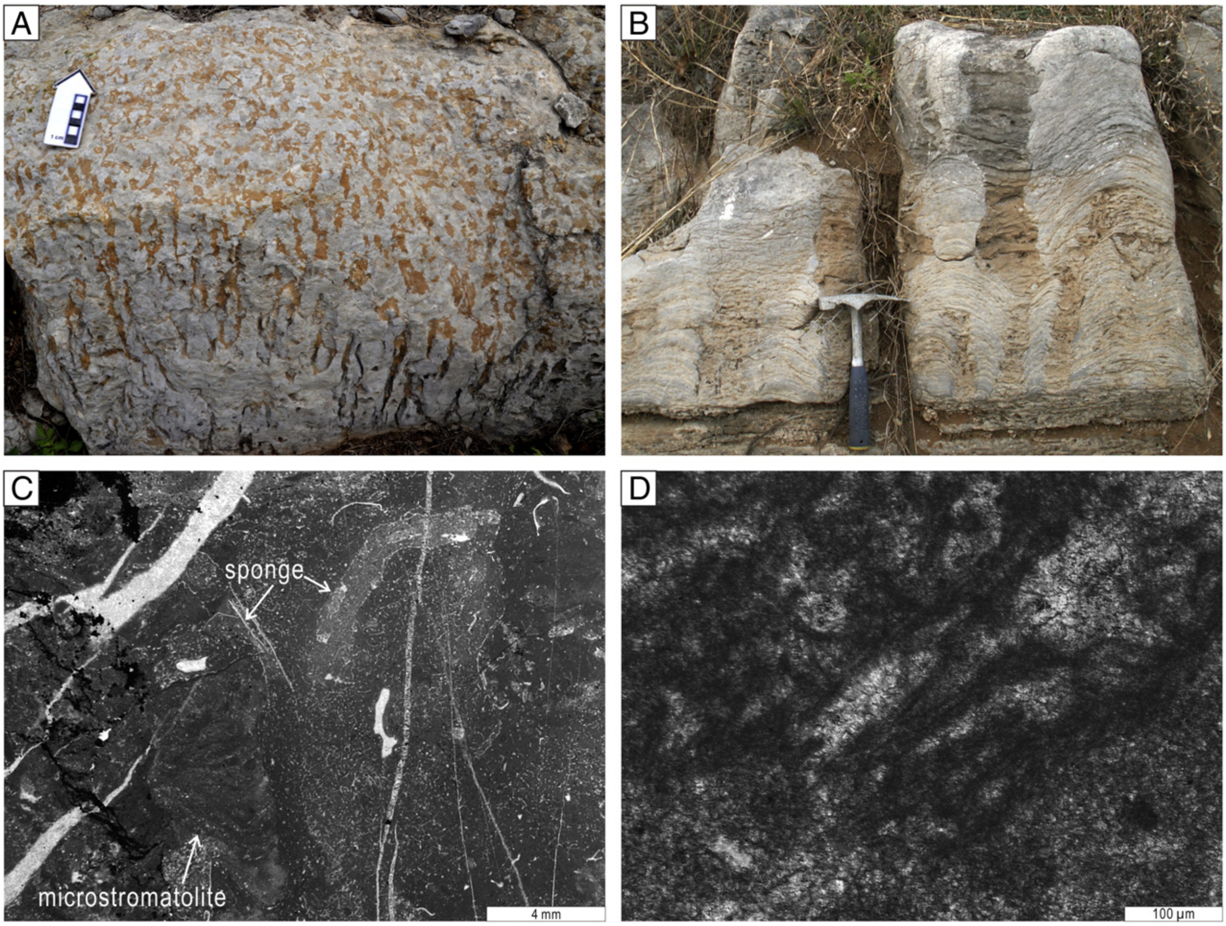

Fig. 4. Furongian reefs in Shandong Province, China (Jiangshanian–Stage 10; Chaomidian Formation). For section locations, see Chough et al. (2010). A. Maze-like maceriate reef (Tangwangzhai section). B. Columnar stromatolite, forming ca. 10 m thick biostrome (Jiulongshan section). Hammer for scale is 28 cm. C. Sponges and *Girvanella* within maceriate reef. D. *Girvanella* within columnar stromatolite.
A. From Chen et al. (2014). C. From Lee et al. (2014a).

studies are required in order to determine their taxonomy (Luo and Reitner, 2014). Dolomitized maceriate reefs also exist in the overlying Furongian–Early Ordovician Sanshanzi Formation (Chen et al., 2014).

The columnar stromatolites in the Chaomidian Formation are characterized by columns ca. 10 to 50 cm in width and 30 to 100 cm in height (Fig. 4B). They mainly occur in the upper part of the formation, within wackestone to packstone facies that formed in a protected lagoonal environment or in a relatively low-energy platform interior (Chen et al., 2011). They clearly display mm-thick, crudely convex-up laminations, characterized by alternation of light-gray, fine-grained laminae and dark-gray, coarse-grained laminae. Stylolites commonly exist along the laminations. In places, the stromatolites are extensively bioturbated. The columnar stromatolites mainly comprise the calcified microbes *Girvanella* and *Tarthinia*, and fossil fragments (trilobites, algae, cephalopods, and gastropods), together with minor poorly preserved siliceous sponge spicule networks, peloids, dolomite crystals, and calcite cement (Fig. 4D) (Chen et al., 2014).

6. Cambrian Epoch 3–Furongian reefs in Laurentia

Laurentia was a large paleocontinent located near the paleoequator during the Cambrian Epoch 3 and the Furongian (Fig. 1) (Thomas and Astini, 1996; Golonka, 2009). Overlying the basement rocks and the Precambrian strata, major deposition on the continent initiated in the early Cambrian, overlying the 'Great Unconformity' (Peters and Gaines, 2012). A thick Cambrian–Early Ordovician mixed siliciclastic-carbonate succession was deposited on Laurentia, resulting in the Great American Carbonate Bank (Palmer, 1981; Morgan, 2013). The second-order Sauk sequence, which is divided into four third-order sequences (Sauk I–IV), developed on the platform throughout the Cambrian and the Early Ordovician (Morgan, 2013). Various reefs developed on the continent during the Cambrian (Aitken, 1967; Lohmann, 1976; McIlreath, 1977; Pfeil and Read, 1980; Kepper, 1981; Read and Pfeil, 1983; Kobluk, 1985; Kennard and James, 1986; Rees, 1986; Aitken, 1989; Kennard et al., 1989; Pratt, 1989, 1995; Waters, 1989; Srinivasan and Walker, 1993; Rankey et al., 1994; Osleger and Montañez, 1996; de Wet et al., 1999, 2004; Middleton, 2001; Myrow et al., 2003; Saltzman et al., 2004; Widiarti, 2011; Myrow and Chen, 2015). The Cambrian Epoch 3 reefs mainly developed during the phase of the Sauk II sequence, whereas the Furongian reefs formed throughout the time of the Sauk III sequence. The Cambrian–Ordovician sedimentary rocks in Laurentia are separated by an old land, the Transcontinental Arch, into the eastern and western areas (southern and northern areas, respectively, during the early Paleozoic) (Derby et al., 2013). In the following sections, we summarize the reefs in these two different areas.

6.1. Cambrian Epoch 3

Cambrian Epoch 3 reefs are reported from various regions of Laurentia, including California, Virginia, Wyoming, Pennsylvania, the Great Basin (geographic term comprising most of Nevada and more than half of Utah, together with parts of California, Oregon, Idaho, and Wyoming), and Tennessee in the USA, and the Canadian Rockies, Northwest Territories, and Newfoundland in Canada (Table 1). These reefs generally developed in shallow subtidal environments (Kennard et al., 1989; Middleton, 2001; Widiarti, 2011) as well as on the shelf margin (Pfeil and Read, 1980; Srinivasan and Walker, 1993; Osleger and Montañez, 1996), with minor occurrence on the deep-water slope (Pratt, 1989, 1995). Regardless of the depositional environment, the Laurentian reefs generally represent typical thrombolites and dendrolites that mainly consist of *Epiphyton* and *Renalcis* with some *Girvanella* (Table 1; Fig. 5).

6.1.1. Eastern area

In the eastern area of Laurentia, reefs are reported from four different areas, including Virginia, Pennsylvania, Tennessee, and Newfoundland (Table 1). During Stage 5 and the Drumian, reefs mainly developed on the platform margin. These occurrences include the upper Shady Dolomite (Virginia; Stage 5) (Pfeil and Read, 1980; Read and Pfeil, 1983; Kobluk, 1985), the Ledger Formation (Pennsylvania; Stage 5) (de Wet et al., 1999, 2004), and the Maryville Limestone Formation (Tennessee; *Bolaspidella*–*Cedaria* zones, Drumian–Guzhangian) (Srinivasan and Walker, 1993; Rankey et al., 1994). These reefs on the platform margin are characterized by thrombolitic mounds with centimeter-scale mesoclots that consist mainly of *Epiphyton* and *Renalcis* in variable proportions.

The Shady Dolomite in Virginia comprises shelf edge, foreslope, and slope facies, constituting a carbonate platform margin (Pfeil and Read, 1980; Barnaby and Read, 1990; Read and Repetski, 2013). Several blocks and bioherms of microbial reefs were identified from the upper Shady Dolomite. The microbial reefs consist of *Epiphyton* and *Girvanella* boundstones, thrombolites, and stromatolites (Read and Pfeil, 1983). *Epiphyton* boundstone was mainly constructed by *Epiphyton*, together with minor *Girvanella* and *Renalcis* (Fig. 5B). *Girvanella* boundstone mainly consists of *Girvanella*, with minor *Epiphyton* and *Renalcis*. No calcified microbes were identified from thrombolites and stromatolites; thrombolites mainly consist of tiny digitate structures with wackestone/mudstone and pellet sediment, whereas stromatolites contain laminae of pellet sediment and mud. Some cryptic (cavity-dwelling) organisms occur in microcavities of *Epiphyton* boundstones (Kobluk, 1985). These include *Epiphyton* and various calcified microbes, possible inarticulate brachiopods, and sponges. In Pennsylvania, the reefs mainly show a biostromal megastructure, characterized by thrombolitic and stromatolitic textures (de Wet et al., 1999, 2004). *Renalcis*-like microbes, *Gordonophyton*, and *Tarthinia* are the main component of these reefs, together with meter-scale cavities filled with radiaxial fibrous calcite and herringbone calcite cements. The Tennessee thrombolites are the least studied and only briefly mentioned in some manuscripts (Srinivasan and Walker, 1993; Rankey et al., 1994). These thrombolites are characterized by centimeter-scale clots which consist of *Renalcis*, *Girvanella*, and some sponge spicules.

In Newfoundland, the Cape Ann Member of the Petit Jardin Formation, consisting of thrombolites and stromatolites, developed in shallow subtidal to supratidal settings during the late Drumian–early Guzhangian (*Bolaspidella* Zone) (Chow and James, 1987). A bioherm in the member is ca. 10 m thick and laterally continuous (Kennard et al., 1989). The following is summarized from Kennard et al. (1989). The bioherm comprises three zones: a basal thrombolite zone, a central stromatolitic thrombolite zone, and an upper stromatolite zone. The basal thrombolites comprise millimeter-scale lobate and pendant-shaped mesoclots surrounded by thin fibrous cement or stromatolitic laminae, with interstitial lime mud (Fig. 5A). The upper stromatolites are characterized by a laterally linked, hemispheroidal shape, 5–30 cm in diameter that consist of 1–10 mm thick, laterally discontinuous stromatolitic layers, with peloidal grainstones in between. The central zone shows a mixed occurrence of thrombolite and stromatolite. The bioherm generally developed in a low-energy, shallow subtidal environment, protected by an ooid shoal. The thrombolites were constructed by calcified coccoidal microbial colonies under quiet conditions, whereas the stromatolites were formed by sediment-trapping microbes, probably of filamentous shape, forming microbial mats in a very shallow, wave-dominated environment.

6.1.2. Western area

Reefs in the western area of Laurentia mainly developed in the Canadian Rockies and Northwest Territories, together with occurrences in California, Wyoming, the Great Basin, and Idaho (Table 1). In the Canadian Rockies, reefs developed in various settings, including platform margin, shallow subtidal, and intertidal. The platform margin examples include those in the Cathedral Formation (Stage 5), which demarks the famous Burgess Shale (McIlreath, 1977). Thrombolite mounds developed along the platform margin, which was composed of *Epiphyton* and *Renalcis* (Aitken, 1989). Another platform margin example occurs in the Great Basin. The Bonanza King Formation (Stage 5–Paibian) in this area contains large *Epiphyton* boundstone blocks up to 6 m large within the megabreccia-dominated succession, indicating development of *Epiphyton* boundstone along the shelf margin (Kepper, 1981; Rees, 1986; Osleger and Montañez, 1996).

Additional examples mostly developed in shallow subtidal to lower intertidal settings. They occur in Utah (Orr Formation; *Crepicephalus* Zone, Guzhangian), Idaho (Nounan Formation; *Crepicephalus* Zone, Guzhangian), and the Canadian Rockies (Sullivan and Waterfowl formations; late *Bolaspidella* Zone–early *Cedaria* Zone, Guzhangian). The Utah reefs are mound-shaped thrombolite composed of *Epiphyton* and *Renalcis* (Lohmann, 1976; Widiarti, 2011). The Idaho reefs are mentioned by Saltzman et al. (2004) as thrombolite, but no detailed research has yet been performed. In the Canadian Rockies, recrystallized

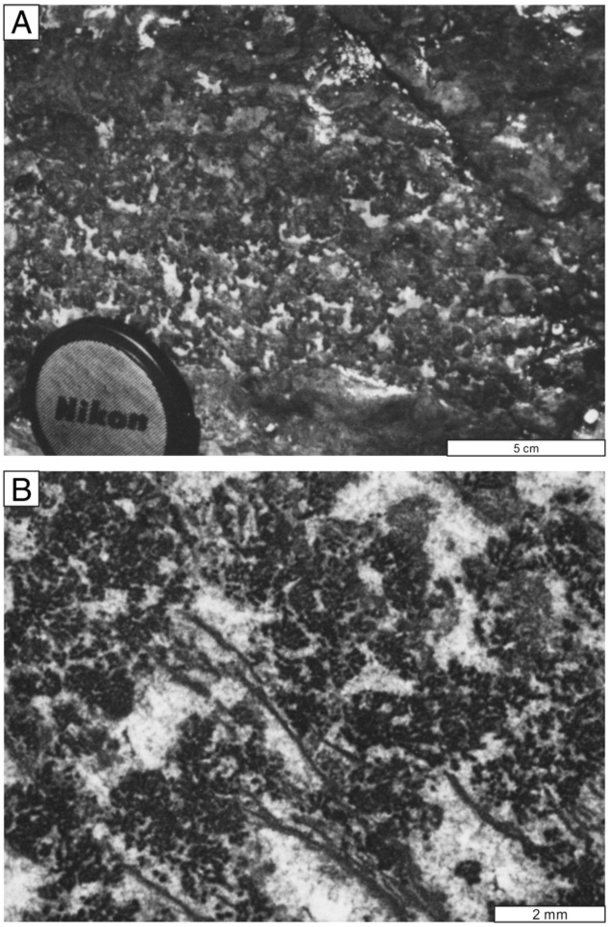

Fig. 5. Cambrian Epoch 3 reefs in Laurentia. A. Thrombolite in the Cape Ann Member of Petit Jardin Formation (Drumian–Guzhangian), Newfoundland, Canada. Mesoclots are dark gray in color. B. *Epiphyton* in the *Epiphyton* boundstone, Shady Dolomite (Cambrian Stage 5), Virginia, USA A. From Kennard et al. (1989). B. From Read and Pfeil (1983).

maceriate reefs occur in the Sullivan and Waterfowl formations, together with LLH-C type stromatolites and thrombolites (Aitken, 1967). A detailed study of some thrombolites and dendrolites in the Waterfowl Formation was done by Waters (1989). He recorded that the thrombolites were constructed by *Renalcis* and *Girvanella*, which formed in situ dendritic frameworks.

In addition, there is one exceptional example of thrombolite developed on the continental slope near or below storm wave base. In the western Northwest Territories of Canada, a large mound (120 m wide and 25 m thick) occurs in the Rockslide Formation (*Bolaspidella* Zone; Drumian), together with several smaller mounds (Pratt, 1989, 1995). The formation consists of thin- and lenticular-bedded lime mudstone, calcareous siltstone and conglomerates that were deposited on the deep slope. The mound has a crudely laminated structure that consists of synsedimentary fibrous calcite cement-filled voids, which is surrounded by *Girvanella* crusts, encrusting *Epiphyton*, and rarer *Renalcis* and micrite of microbial origin.

6.2. Furongian

During the third-order sea-level rise of Sauk III (Furongian), a vast area of Laurentia was flooded and formed an extensive shallow carbonate platform. Furongian reefs developed at various locations of Laurentia, including the Great Basin, Colorado, Tennessee, Maryland, Missouri, Pennsylvania, Oklahoma, New York, Wisconsin, Texas, the Canadian Rockies, Newfoundland, Quebec, and the Argentine Precordillera (Table 1). These reefs generally developed in intertidal to shallow subtidal as well as lagoonal environments, forming maceriate reefs and columnar stromatolites (e.g., Armella, 1994; Hersi et al., 2002; Shapiro and Awramik, 2006), but some of them developed along the shelf margin, forming thrombolites that consist of *Renalcis* and *Epiphyton* (e.g., James, 1981; Demicco, 1985) (Table 1; Fig. 6). On the other hand, minor thrombolites consist of *Renalcis*, *Epiphyton*, and *Girvanella* developed in shallow subtidal to lower intertidal settings (e.g., Markello and Read, 1981). Locally, anthaspidellid sponges (*Gallatinospongia conica* Okulitch and Bell, 1955 and *Wilbernicyathus donegani* Wilson, 1950), together with some unidentified anthaspidellid sponges, thrived within the microbial-dominant reefs (Mrozek et al., 2003; Dattilo et al., 2004; Shapiro and Rigby, 2004; Johns et al., 2007). Unfortunately, not many of the reefs have been mesoscopically or microscopically studied in detail, partly due to dolomitization and recrystallization (cf. Shapiro and Awramik, 2006).

6.2.1. Eastern area

During the Furongian, reefs developed throughout eastern Laurentia. In Quebec (Strites Pond Formation; *Cordylodus proavus* Zone, Stage 10), Wisconsin (St. Lawrence Formation; Stage 10), Maryland (Conococheague and Frederick limestones; Paibian–Jiangshanian), Missouri (various formations; Paibian–Early Ordovician?), Pennsylvania (Gatesburg Formation; *Elvinia* Zone, Jiangshanian), New York (Little Falls Formation and Hoyt Limestone; *Cordylodus proavus* Zone, Stage 10), Oklahoma (Fort Sill Limestone; *Elvinia* Zone, Jiangshanian), Texas (Wilberns Formation; *Idahoia*–*Saukia* zones, Jiangshanian–Stage 10) and the Argentine Precordillera (La Flecha Formation; *Aphelaspis*–*Saukia* zones, Paibian–Stage 10), reefs developed on shallow carbonate platforms (Table 1). The carbonate platforms were shallow subtidal to intertidal in setting, although lagoons developed locally.

Maze-like maceriate reefs generally developed in these shallow marine environments. Their sizes differ from place to place, but they are generally less than 2 m in height, with around 1–5 cm wide maceria structures (Shapiro and Awramik, 2006, table 2). The internal fabric of the maceriate reefs is generally unknown, although some studies reported *Renalcis*-like clusters with clotted fabric (Hersi et al., 2002), *Renalcis* or *Renalcis*-like forms and *Girvanella* (Demicco, 1985), and peloid, clotted micrite, and *Nuia* (Raviolo et al., 2010). The composition of these maceriate reefs is generally similar to what Lee et al. (2010) reported from maceriate reefs in Shandong, China (micrite, *Girvanella*, and *Renalcis*-like microbes), which were later revealed to be siliceous sponge-microbial reefs (Lee et al., 2014a). The Shandong example therefore emphasizes the importance of detailed microfacies analysis on these maceriate reefs in order to reveal their constituents.

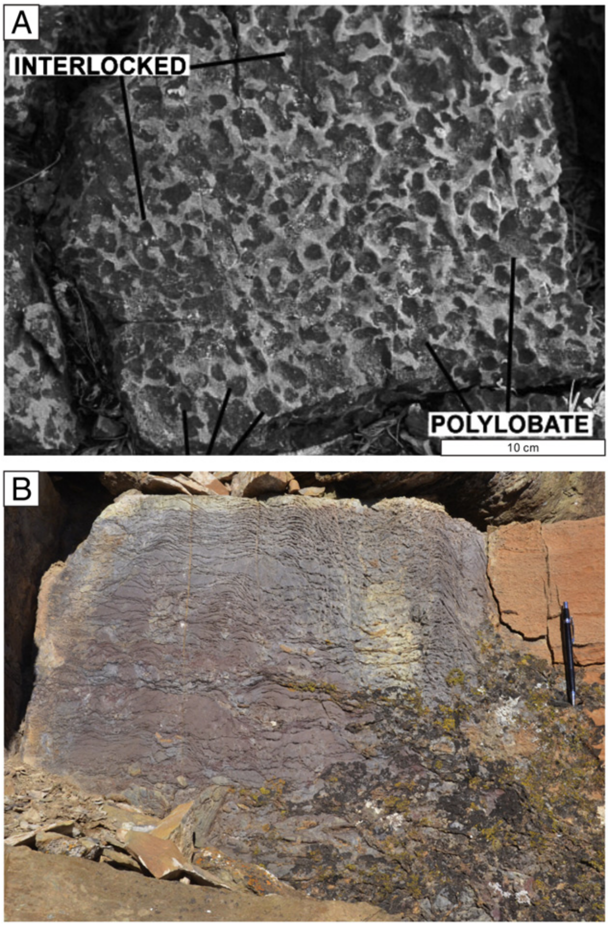

Fig. 6. Furongian reefs in Laurentia. A. Transverse view of maceriate reef in the Nopah Formation (Jiangshanian), Great Basin, USA. B. Columnar stromatolite in the Dotsero Formation (Cambrian Stage 10), Colorado, USA. Pencil for scale. A. From Shapiro and Awramik (2006).

Together with maceriate reefs, columnar stromatolites developed in shallow marine environments. These stromatolites are generally constructed of thin laminae that consist of micrite, calcite, or dolomite, but some authors have reported calcified microbes such as *Girvanella*, *Tarthinia*, *Epiphyton*, and *Renalcis* (Ahr, 1971; Chafetz, 1973; Markello and Read, 1981, 1982; Glumac and Walker, 1997; Friedman, 2000; Johns et al., 2007). It has been interpreted that the columnar stromatolites generally develop in intertidal to shallow subtidal environments (Ahr, 1971; Chafetz, 1973; Markello and Read, 1982; Glumac and Walker, 1997; Friedman, 2000).

Only two examples of shallow marine thrombolites have been reported from eastern Laurentia. Thrombolites in Tennessee are characterized by millimeter- to centimeter-scale mesoclots that consist of *Renalcis*, *Epiphyton*, and *Girvanella* (Glumac and Walker, 1997). They form domal bioherms overlying oolitic grainstone or flat-pebble conglomerate, and underlying shale and ribbon rocks. Occurring with these thrombolites are digitate stromatolite with a crudely laminated pelleted fabric, columnar stromatolites 2–3 cm in diameter, and SH stromatolites. Another example of thrombolites is in Texas (Johns et al., 2007). In this case, the anthaspidellid sponge *Wilbernicyathus* occurs within the thrombolites and constitutes up to 30% of the reef volume. The rest of the reefs were constructed primarily by *Girvanella*, with minor *Tarthinia*, *Epiphyton*, and *Renalcis*.

Compared with the Cambrian Epoch 3, the Furongian platform margin contained fewer reefs. Two examples of Furongian platform-margin reefs were reported from Laurentia, both from the eastern area. In the northern part (Newfoundland), thick beds of limestone breccia containing microbialite blocks were deposited on the slope along the platform margin, forming the Cow Head Group (Cambrian Epoch 3?–Early Ordovician) (James, 1981). Although the ages of the blocks differ, they commonly contain *Girvanella* and *Epiphyton* as main constituents, with some *Renalcis* and fine-grained sediments. It has been interpreted that the microbialites within the breccia are similar to the thrombolites of the Orr Formation (Great Basin, Nevada and Utah; Guzhangian) that consist of *Epiphyton* and *Girvanella* (Lohmann, 1976). On the other hand, it is noteworthy that the ages of the conglomerates have not been clearly determined, partly because the traditional North American 'middle Cambrian' and 'late Cambrian' cannot be directly correlated with the 'Cambrian Epoch 3' and 'Furongian' (Geyer and Shergold, 2000). The late Cambrian of North America comprises the Marjuman, Steptoean, Sunwaptan, and Skullrockian stages, among which the Marjuman and Skullrockian stages approximately correspond to the Drumian to the Guzhangian stages (Cambrian Epoch 3) and the latest Cambrian Stage 10 (Furongian) to the early Tremadocian (Early Ordovician), respectively (Peng et al., 2012). Further studies according to the redefined stratigraphic scheme are therefore required to understand what happened in the platform margin area of the Cow Head Group during that time. Another example of platform-margin reefs comes from Maryland (Frederick Limestone; Paibian–Jiangshanian). Demicco (1985) noted the occurrence of massive, gray megaclasts, which consist of *Girvanella* and *Epiphyton* within breccia that was deposited in slope to basinal settings. In this example, micritic plates of *Girvanella* are encrusted by small *Epiphyton* colonies, forming boundstone.

6.2.2. Western area

Similar to the eastern area, the vast area of western Laurentia was covered by a shallow carbonate platform during the Furongian. Reefs were reported from the Great Basin, Idaho, Colorado, and the Canadian Rockies (Table 1). In the Great Basin, reefs developed in several different areas, including the upper Bonanza King (basal Paibian) and Nopah (*Dunderbergia*–*Saukia* zones; Paibian–Stage 10) formations of eastern California-western Nevada, the Notch Peak Formation (Jiangshanian–Stage 10) of eastern Nevada and western Utah, and the Desert Valley (Stage 10) Formation of southern Nevada. Saltzman et al. (2004) reported stromatolites from the Nounan Formation (Paibian) of Idaho, but they have not been studied. Unfortunately, only reefs in the western Great Basin (Bonanza King and Nopah formations) and Colorado (Dotsero Formation) have been studied in detail. In the following, we summarize these reefs.

The uppermost Bonanza King Formation was deposited in shallow subtidal environments, where tidal effect was significant (Shapiro and Rigby, 2004). Dominant sedimentary facies of the Nopah Formation include flat-pebble conglomerate, cross-stratified oolite, lime mudstone, and microbialite, which are mostly dolomitized (Shapiro and Awramik, 2000). The Nopah Formation was deposited in subtidal environments, either restricted or open-marine (Shapiro and Awramik, 2000). Biohermal and biostromal dendrolites (30–40 cm thick; stratiform/domical, columnar, or domical in shape) containing the anthaspidellid sponge *Gallatinospongia* occur in the uppermost Bonanza King Formation (earliest Furongian) (Shapiro and Rigby, 2004). Calcified microbes within the dendrolites are recrystallized, although some of them resemble *Renalcis*. In the dolomitized succession of the Nopah Formation (Furongian), 11 types of reefs are recognized (Shapiro and Awramik, 2000). These reefs include columnar/domal/'rind-type' stratiform/stratiform stromatolites, maceriate reefs (or columnar-branching stromatolites), and columnar/domical/stratiform thrombolites/dendrolites (Fig. 6A). Microstructures of these reefs are generally unclear due to the dolomitization, except for possible evidence of clots (Shapiro and Awramik, 2006).

In Colorado, extensive stromatolites (~1.5 m thick) known as the Clinetop Bed of the Dotsero Formation (*Saukia* Trilobite Zone and *Eoconodontus notchpeakensis* Conodont Zone; Stage 10) cover 1500–2600 km^2 (Fig. 6B) (Campbell, 1976; Myrow et al., 2003; Johns et al., 2007; Myrow and Chen, 2015). The stromatolites developed on flat-pebble conglomerates. They are columnar in shape and a few tens of centimeters in width (Campbell, 1976). The columnar stromatolites are covered by laterally linked, hemispheroidal stromatolites (LLH type). Johns et al. (2007) reported that the stromatolites mainly consist of *Girvanella*, which is covered by a few centimeters of *Girvanella*–*Tarthinia*–sponge boundstone.

7. Changes in the reefs during the middle–late Cambrian

It has been questioned and discussed why the middle–late Cambrian, ca. 25 m.y., was dominated by microbialites without metazoan reefs. Rowland and Shapiro (2002) suggested several non-biogenic factors as possible reasons for the flourishing of microbialites during this time, including nutrient deficiency, high atmospheric CO$_2$ levels, global warming, and favorable seawater Mg/Ca chemistry. However, due to the absence of follow-up studies, what happened during the middle–late Cambrian is still an open question (Fig. 7).

During the Cambrian Epoch 3, thrombolites and dendrolites, which mainly consist of *Epiphyton*- and *Renalcis*-groups of calcified microbes, flourished and formed extensive reefs (Zhuravlev, 1996). There are nineteen known examples of Cambrian Epoch 3 reefs containing *Epiphyton* and *Renalcis*, among which many of these calcified microbes were important reef-building components (e.g., Read and Pfeil, 1983; Aitken, 1989; Woo et al., 2008). Thrombolites and dendrolites decreased greatly across the Cambrian Epoch 3–Furongian boundary, together with *Epiphyton* and *Renalcis* (Fig. 7A). Only eight examples of *Epiphyton* have been reported from Furongian reefs, and it is often an insignificant component within the reefs (e.g., Johns et al., 2007). Although some *Epiphyton*-dominant reefs flourished locally, especially along platform margins (e.g., Newfoundland and Kazakhstan) (James, 1981; Demicco, 1985; Cook et al., 1991; Pratt, 1995), they were rare in the platform interiors (e.g., Glumac and Walker, 1997). Thrombolites and dendrolites are also scarce in the Furongian (six examples). Instead, the Furongian reefs were dominated by maceriate reefs and columnar stromatolites. These maceriate reefs initiated during the late Cambrian Epoch 3 (Guzhangian) and gradually diversified and flourished during the Furongian (Fig. 7A). Columnar stromatolites also gradually expanded during the Furongian. It is noteworthy that the abundance of non-columnar stromatolites (e.g., mound, crust, and LLH shaped) did not change significantly and only gradually increased throughout the Cambrian Epoch 3–Furongian interval, possibly because these stromatolites reflect more of local depositional environments than global environmental changes (Bosak et al., 2013).

This change was previously recognized by Zhuravlev (1996). He noted that the abundance of dendrolites decreased greatly from the middle Cambrian (Amgan: 17, Mayan: 16) to the late Cambrian (Dresbachian: 6, Franconian: 0, Trempealuan: 7), coincident with a decline of calcified microbes and a resurgence of stromatolites and "thrombolites" (possible maceriate reefs) during the same period, although raw data were not presented. This change is also recognized in terms of microscale structures. Among 13 calcified microbe genera which flourished during the Cambrian Epoch 3, only 6 lasted into the Furongian. They diminished to 5 genera by the end of the Furongian (Fig. 7B) (Zhuravlev, 1996; Riding, 2001). These five genera include *Epiphyton*, *Gordonophyton*, *Renalcis*, *Tarthinia*, and *Girvanella*, among which the *Epiphyton* and *Renalcis* groups (*Epiphyton*, *Gordonophyton*, *Renalcis*, and *Tarthinia*) were volumetrically diminished (Table 1).

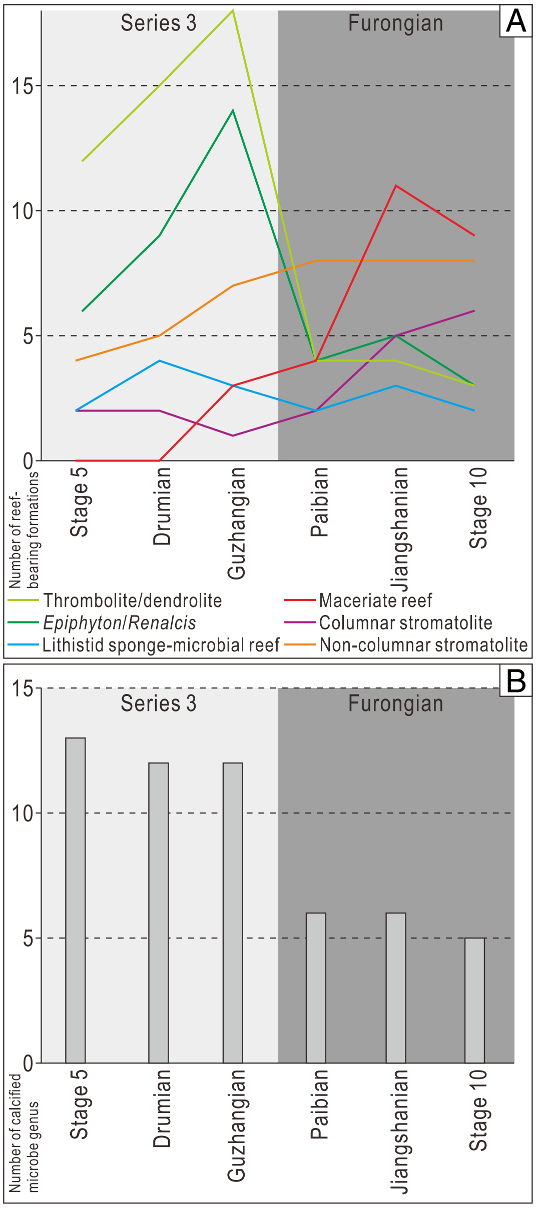

Fig. 7. A. Abundance of thrombolites/dendrolites, columnar stromatolites, non-columnar stromatolites, maceriate reefs, and *Epiphyton*/*Renalcis* during the Cambrian Epoch 3 and the Furongian. Abundance values are the number of published reef-bearing formations within each epoch. For raw data, see Table 1. B. Diversity of calcified microbes during the Cambrian Epoch 3 and the Furongian. B. *Modified from Zhuravlev, 1996 and Riding, 2001*.

These changes were previously ascribed to the appearance of grazers during the Furongian (Zhuravlev, 1996).

Considering that meso- and microstructures of microbialites are influenced by several factors, including different microbial assemblages, depositional environments, global environmental conditions such as paleoclimate and sea-water chemistry, and diagenetic effects (Pratt, 1984; Riding, 2000), it is not clear what could have caused changes in reef fabric across the Cambrian Epoch 3–Furongian boundary. We speculate that the contrasting reef fabrics most likely reflect different organic assemblages and possibly global environmental changes, in that (1) maceriate reefs (possible sponge-microbial complexes) are different in composition from thrombolites/dendrolites that lack sponges, and (2) change in reef fabric was a global phenomenon that could not have been solely affected by local factors. The factors that could have induced these changes are reviewed and discussed in the following sections.

8. Events across the middle–late Cambrian boundary

The Cambrian Epoch 3–Furongian boundary was placed where there is a great faunal turnover among polymerid trilobites (Saltzman et al., 2000; Peng et al., 2004, 2012). Recent geochemical and sequence-stratigraphic studies suggest that there were global events across the Cambrian Epoch 3–Furongian boundary, including carbon and sulfur isotope excursions and a eustatic sea-level fall (Saltzman et al., 2000, 2004; Chen et al., 2011). There are also changes in various organisms and sedimentary facies across the boundary (Zhuravlev and Wood, 2008). At the current stage, it is not clear whether these events were caused by a single major factor or several composite factors. However, the coincidence of the events and the transition in reefs suggests that at least some of these events could have affected the reefs, or vice versa. In the following sections, we summarize and discuss the events and their effects on reefs.

8.1. Carbon and sulfur isotope excursions

The base of the Furongian is characterized by a gradual increase in carbon isotope values (SPICE), which lasted ca. 2–4 Myr (Fig. 8) (Saltzman et al., 2000, 2004). The SPICE event peaks at the middle–late Paibian, with +4–6‰ in δ^{13}C, and gradually decreases until the early Jiangshanian. This event is recognized in various places, including Laurentia, Siberia, Baltica, Sino-Korean Block, South China Block, Australia, Avalonia, and Kazakhstan (Fig. 8) (Saltzman et al., 2000, 2004; Zhu et al., 2004; Kouchinsky et al., 2008; Ahlberg et al., 2009; Chen et al., 2011; Woods et al., 2011).

Together with the SPICE, a gradual sulfur isotope excursion (δ^{34}S) up to 70‰ was also recognized in samples from Laurentia, Australia, and Baltica (Fig. 8) (Gill et al., 2011). The sulfur isotope excursion was interpreted to record an increase in the burial rate of organic carbon and pyrite sulfur in sediments under anoxic and sulphidic (euxinic) conditions (Gill et al., 2011). On the other hand, it has been suggested that the level of atmospheric oxygen increased together with the SPICE, based on the stable isotope ratios of carbon ($\delta^{13}C_{carb}$) and sulfur (δ^{34}S) in carbonates, and carbon in organic matter ($\delta^{13}C_{org}$) (Saltzman et al., 2011). δ^{18}O values acquired from the apatite of inarticulate brachiopods from Laurentia suggest that sea-water temperatures changed during the SPICE: relatively low temperatures occurred during the early stage and high temperatures during the middle–late stage (Elrick et al., 2011). However, δ^{18}O values could have been altered during early diagenesis, and these inferences need further confirmation with other materials (e.g., conodonts).

8.2. Eustatic sea-level change

Across the Cambrian Epoch 3–Furongian boundary, relative sea-level fall was recognized on both Laurentia and Gondwana (Sino-Korean Block, western Mediterranean region, and Iran) (Fig. 9) (Saltzman et al., 2004; Álvaro et al., 2007; Chen et al., 2011; Bayet-Goll et al., 2014). In Laurentia, this event is known as the Sauk II–Sauk III sequence boundary, indicating a maximum regression (Glumac and Walker, 1998; Saltzman et al., 2004; Morgan, 2013). The Sauk II–III sequence boundary is characterized by the input of siliciclastic sediments onto the carbonate platform and local subaerial exposure (unconformity): the SPICE excursion and trilobite biozones including the *Dunderbergia* Zone are locally absent (e.g., in northwestern Wyoming and northern Vermont) (Palmer, 1981; Chow and James, 1987; Saltzman et al., 1998, 2004; Glumac and Spivak-Birndorf, 2002; Morgan, 2013). The sequence boundary lies within the middle–late Paibian Stage, which coincides with the peak of the SPICE event (Runkel et al., 1998, 2007; Saltzman et al., 2004). Relative sea-level fall on Laurentia would have initiated prior to the Cambrian Epoch 3–Furongian boundary, which can be evinced by the progradation of coastal sandstone during the late Guzhangian Stage (*Crepicephalus*

Zone) and the occurrence of an unconformity within the *Crepicephalus* Zone in the Upper Mississippi Valley and other areas (Runkel et al., 1998, 2007). In the Upper Mississippi Valley section, the *Crepicephalus* Zone is directly overlain by the *Elvinia* Zone, indicating the absence of the *Aphelaspis* and *Dunderbergia* zones (Paibian Stage; Furongian) in between (Runkel et al., 2007).

On Sino-Korean Block, relative sea-level fall is recognized as a subaerial unconformity, characterized by a sharp erosional surface on a widespread (ca. 100 km in distance) deformed limestone bed overlain by a glauconite-rich bioclastic grainstone (transgressive lag deposit) and shale-dominated deposit, a missing trilobite biozone (*Prochuangia* Zone; early Paibian Stage), and an abrupt increase in carbon isotope values (i.e., SPICE) in the platform interior (Shandong Province, China) (Figs. 8 and 9) (Chen et al., 2011). These data collectively suggest a major hiatus. On the other hand, continued sedimentation of siliciclastic sediments and the occurrence of the *Prochuangia* Zone are recognized in the marginal region of the platform (Taebaek region, Korea), reflecting a different response to sea-level fall across the platform (Park and Choi, 2011; Chen et al., 2012; Park et al., 2013).

In the western Mediterranean region (Morocco, Spain, and France), a sequence boundary across the Cambrian Epoch 3–Furongian boundary is widely recognized (Álvaro et al., 2007). The uppermost Cambrian Epoch 3 successions in the area are mainly characterized by back-shoal progradation and widespread occurrence of tidal-flat facies (Spain and France) with an unconformity (Morocco, Algeria, Libya, and Tunisia) indicating sea-level fall (Crossley and McDougall, 1998; Álvaro et al., 2007). Overlying the Cambrian Epoch 3 succession, the Furongian succession was deposited during the transgression, with retrograding shoal deposits and common offshore muddy sediments (Álvaro et al., 2007). In addition, recent studies from Iran recognized a major unconformity accompanied by regression in between the Cambrian Epoch 3 and the Furongian successions (Bayet-Goll et al., 2014; Geyer et al., 2014).

These sea-level fall events are biostratigraphically and chemostratigraphically well correlated (Geyer and Shergold, 2000; Chen et al., 2011; Peng et al., 2012). The occurrence of relative sea-level fall on two different continents (i.e., Laurentia and Gondwana) together with the globally correlatable SPICE excursion suggests that this sea-level fall was most likely a eustatic event. The sea-level fall was followed by a global transgression, forming dysaerobic to anoxic black shales in Avalonia, Baltica, and Argentina (Álvaro et al., 2013a), and a shale-dominant succession on Sino-Korean Block (Chen et al., 2011).

8.3. Biotic changes

Many polymerid trilobites became extinct and were replaced by new trilobite fauna across the Cambrian Epoch 3–Furongian boundary (Pratt, 1998; Saltzman et al., 2000; Peng et al., 2004, 2012; Álvaro et al., 2013b). Several workers argued that this event indicates a mass extinction that also affected other organisms such as inarticulate brachiopods (e.g., Bambach, 2006). Some organisms such as chancelloriids declined and disappeared at this time (Zhuravlev, 1996). On the other hand, it has been suggested that soft-bodied Burgess-Shale type predators became extinct at this time, based on predation features on trilobite shells (Pratt, 1998). Together with the trilobite faunal turnover, various organisms began to appear in the Furongian, including ostracoderms (Repetski, 1978), cephalopods (Chen and Teichert, 1983), bryozoans (Landing et al., 2010; but see Taylor et al., 2013, interpreting the fossil as an octocoral), and polyplacophorans (Vendrasco and Runnegar, 2004). In addition, at least five groups of metazoans (euconodonts, balstozoan echinoderms, eoorthid brachiopods, monoplacophorans, and hyperstrophic gastropods) show that their diversification initiated during the Furongian, prior to the Great Ordovician Biodiversification Event (Miller, 1984; Stinchcomb, 1986; Jeong and Lee, 2000; Rowland and Shapiro, 2002; Stinchcomb and Angeli, 2002; Nardin and Lefebvre, 2010). Together with the diversification of metazoans, the diversity of planktonic taxa increased significantly during the Furongian (Servais et al., 2008).

These new organisms changed the Earth ecosystem. For example, monoplacophorans and polyplacophorans began to occur within stromatolites and grazed on them (Runnegar et al., 1979; Stinchcomb and Angeli, 2002; Vendrasco and Runnegar, 2004). The first real

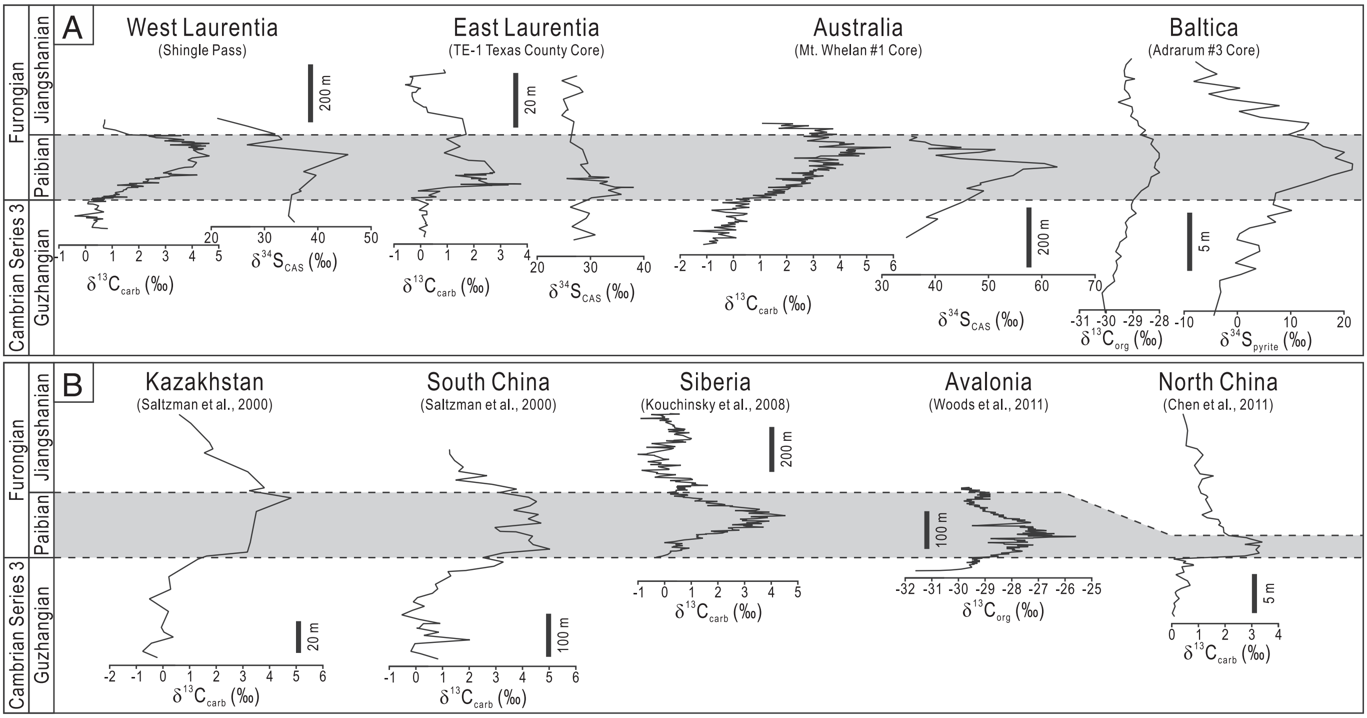

Fig. 8. Carbon and sulfur isotope excursions at the Cambrian Epoch 3–Furongian boundary (Steptoean Positive Carbon Isotope Excursion; SPICE). A. Carbon and sulfur isotope curves from Laurentia, Australia (Gondwana), and Baltica. B. Carbon isotope curves from Kazakhstan, South China, Siberia, Avalonia, and North China.
A. Modified from Gill et al. (2011) and references therein. B. Modified from Saltzman et al. (2000), Kouchinsky et al. (2008), Chen et al. (2011), and Woods et al. (2011).

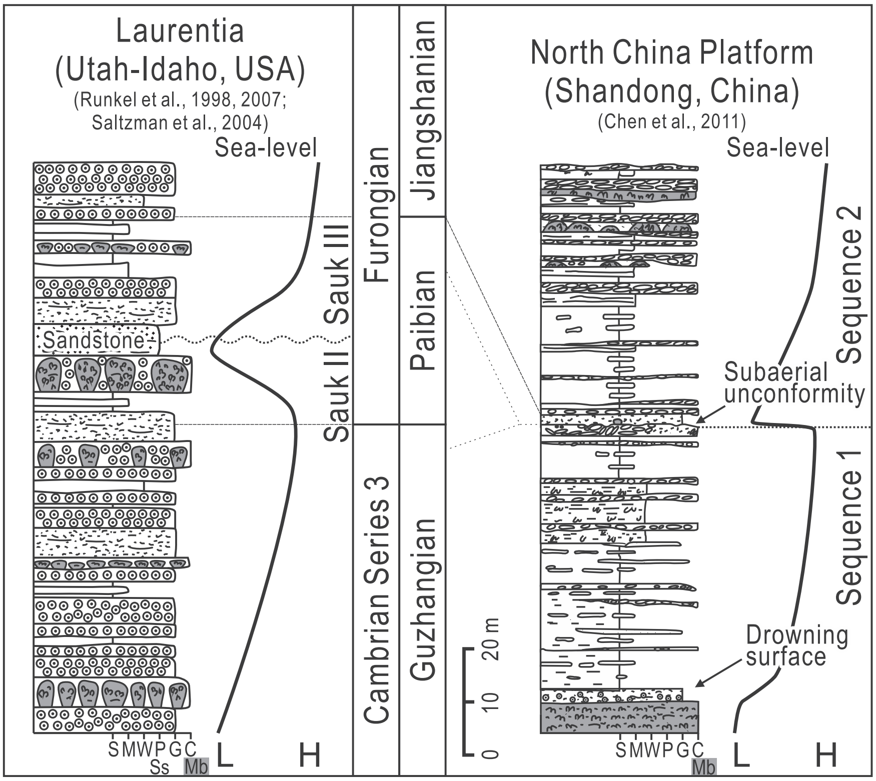

Fig. 9. Sedimentary logs and sea-level curves from Laurentia (Runkel et al., 1998, 2007; Saltzman et al., 2004) and Sino-Korean Block (Chen et al., 2011). Third-order relative sea-level fall is recognized across the Cambrian Epoch 3–Furongian boundary in both regions. S: shale, M: mudstone, W: wackestone, P: packstone, G: grainstone, C: conglomerate, Ss: sandstone, Mb: microbialite. L: low sea level, H: high sea level.

cephalopods, which are potential predators or scavengers, occupied various environments from shallow marine to outer shelf and upper continental slope (Chen and Teichert, 1983; Brett and Walker, 2002; Smith and Caron, 2010). Diverse paraconodonts and the first euconodonts began to occur in the Furongian, marking it as an important epoch for conodont evolution (Miller, 1984; Jeong and Lee, 2000). An increase in the depth and extent of bioturbation (Bottjer and Ausich, 1986; Crimes and Droser, 1992) and an increase in the abundance of infaunal suspension-feeding communities (Ausich and Bottjer, 1982) also suggest the occurrence and diversification of nonfossilized organisms (e.g., grazers) (Zhuravlev, 1996).

9. Discussion

The global occurrence of carbon and sulfur isotope excursions and eustatic sea-level fall across the Cambrian Epoch 3–Furongian boundary, followed by sea-level rise, suggest that these two events have a common cause. Initiation and duration of these two events are very similar (ca. 2–4 Myr, including the entire Paibian and the early Jiangshanian stages) (cf. Saltzman et al., 2004). It has been suggested that increased input of siliciclastic sediments to the carbonate platform due to relative sea-level fall could have increased the burial rate of organic carbon and therefore resulted in a positive carbon isotope excursion (Saltzman et al., 2004). This scenario is supported by the co-occurrence of a positive sulfur isotope excursion during the Paibian Stage, indicating increased burial of sulfur under anoxic conditions (Gill et al., 2011). It is interesting to note that in North America the proportion of glauconite-bearing siliciclastic rock units is highest during the Furongian within the entire Phanerozoic (Peters and Gaines, 2012). This can be attributed to an unusually large influx of continental chemical weathering products during the eustatic sea-level fall event (Brasier, 1980; Chafetz and Reid, 2000; Peters and Gaines, 2012). Theoretically, the large influx of weathering products could have provided nutrients to the ocean, inducing diversification of organisms during the Furongian. On the other hand, widespread anoxic conditions and the reduced areal extent of shallow environments due to sea-level fall could have caused the faunal turnover (or mass extinction) at the end of Cambrian Epoch 3 (Saltzman et al., 2000, 2004; Gill et al., 2011). The sea level subsequently rose from the middle Paibian (Palmer, 1981; Chow and James, 1987; Saltzman et al., 1998, 2004; Glumac and Spivak-Birndorf, 2002; Chen et al., 2011), resulting in vast shallow marine carbonate platforms (Peters and Gaines, 2012).

A decline of thrombolites and dendrolites, as well as *Epiphyton* and *Renalcis*, would have been caused by this event across the Cambrian Epoch 3–Furongian boundary, which can be evinced by their relatively abrupt decrease across the boundary (Fig. 7A). It could have been caused by the reduced areal extent of the shallow, reef-forming environment due to sea-level fall (cf. Palmer and James, 1979; Zhuravlev and Wood, 1996) accompanied by widespread anoxia (Gill et al., 2011). Reef-forming organisms are often severely affected and changed by global regression, e.g., the regressions that occurred at the end-Cambrian Epoch 2, end-Ordovician, late Devonian, end-Permian, end-Triassic, and end-Cretaceous (Hallam and Wignall, 1999). *Epiphyton* and *Renalcis* (specific types of microbes or environmental conditions inducing formation of these structures) could have been seriously damaged by the extinction event, which was possibly caused by the anoxia and sea-level fall. On the other hand, new grazers of the Furongian (e.g., monoplacophorans and polyplacophorans) (Runnegar et al., 1979; Stinchcomb and Angeli, 2002; Vendrasco and Runnegar, 2004) possibly preferred certain calcified microbes forming dendritic or chambered shapes, preventing their resurgence (Zhuravlev, 1996).

It is not possible to solely attribute the decline of thrombolites and dendrolites (and also *Epiphyton* and *Renalcis*) to the sea-level fall and associated reduction of the shallow marine environments, since they are common in both shallow-marine and platform-margin environments during the Cambrian Epoch 3 (Kennard, 1994; Middleton, 2001; Woo et al., 2008). On the other hand, the occurrences of Furongian *Epiphyton*-dominant reefs on the platform margin suggest that the *Epiphyton*/*Renalcis*- and thrombolite/dendrolite-forming environments (e.g., deep-water environment or high-energy conditions) could have been restricted to such an area during the Furongian (James, 1981). In addition, paleoclimatic changes (e.g., high temperatures and atmospheric oxygen level) across the Cambrian Epoch 3–Furongian boundary need to be considered (Elrick et al., 2011; Saltzman et al., 2011), which may have influenced sea level and seawater chemistry as well as biotic changes including reef transition. Further studies on depositional environments of the thrombolites and dendrolites as well as of global paleoclimatic conditions are required in order to fully understand the reason for their decline.

Reefs would have gradually recovered from the sea-level fall event as sea level rose since the early Furongian (Paibian). During this time interval, limited occurrence of shallow marine habitats in subtropical areas could have restricted the development of any kind of reefs. The appearance of maceriate reefs during the late Cambrian Epoch 3 and their minor occurrence during the early Furongian suggest that the initiation and diversification of maceriate reefs was not directly affected by the sea-level changes, but rather indirectly enhanced by the demise of thrombolites and dendrolites in shallow marine environments. It is noteworthy that the maceriate reefs may in fact be siliceous sponge-microbial reefs (Lee et al., 2014a), and the Furongian columnar stromatolites also contain some sponges (Johns et al., 2007; Chen et al., 2014). If so, the Furongian can be marked as a period of resurgence of new reef-building metazoans (siliceous sponges) after the decline of archaeocyaths at the end of the Cambrian Epoch 2. Although some lithistid sponges (mostly anthaspidellids) began to occur in the early Cambrian Epoch 3, they did not occupy a large portion within the reefs prior to the Early Ordovician (Hong et al., 2012; Kruse and Reitner, 2014; Lee et al., in press). The environmental conditions that suppressed the occurrence of *Epiphyton* and *Renalcis* apparently lasted during the entire Furongian, but disappeared during the Early Ordovician. *Epiphyton* and *Renalcis*, which are rare within the Furongian reefs, flourished within the Early Ordovician reefs (Riding and Toomey, 1972; Pratt and James, 1982; Webby, 2002; Adachi et al., 2009).

10. Conclusions

Although Cambrian Epoch 3 and Furongian reefs were simply regarded as microbialites, this integrated review reveals that reefs in these two time intervals are actually different. The Cambrian Epoch 3 reefs are characterized by thrombolites and dendrolites with some stromatolites, which mainly consist of *Epiphyton* and *Renalcis* with minor lithistid sponges. The Furongian reefs, on the other hand, are characterized by maze-like maceriate reefs (possibly siliceous sponge-microbial reefs) and columnar stromatolites containing *Girvanella* and some siliceous sponges. The reefs in these two epochs are separated by several geological events, including positive excursions of carbon and sulfur isotopes, eustatic sea-level drop, and the extinction and subsequent diversification of organisms. Among these factors, reefs would have been mainly affected by eustatic sea-level change. *Epiphyton*/*Renalcis* and thrombolites/dendrolites abruptly diminished in abundance across the Cambrian Epoch 3–Furongian boundary due to the decreased shallow marine habitat caused by sea-level fall and associated changes in organisms. While the Cambrian Epoch 3-type reefs (thrombolites and dendrolites) decreased in abundance, maceriate reefs and columnar stromatolites gradually diversified and occupied the empty ecological space during the subsequent sea-level rise and increase in shallow marine habitat. The *Epiphyton*-dominant thrombolites/dendrolites locally remained in the platform margin area. The other events such as paleoclimatic changes and/or appearance of grazers could have affected the reefs, but further studies are required in order to understand the relationships between them.

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