Palaeogeography, Palaeoclimatology, Palaeoecology 520 (2019) 251–262

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Lithistid sponge-microbial reefs, Nevada, USA: Filling the late Cambrian 'reef gap'

Jeong-Hyun Lee[a,*], Benjamin F. Dattilo[b], Stephanie Mrozek[c], James F. Miller[d], Robert Riding[e]

[a] Department of Geological Sciences, Chungnam National University, Daejeon 34134, Republic of Korea
[b] Department of Biology, Purdue University Fort Wayne, IN 46805, USA
[c] Economic Geology Research Centre (EGRU), Department of Geoscience, James Cook University, Townsville, Queensland, Australia
[d] Department of Geography, Geology, and Planning, Missouri State University, Springfield, MO 65897, USA
[e] Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA

ARTICLE INFO

Keywords:
Arrow Canyon Range
Great Basin
Skeletal-microbial reefs
GOBE

ABSTRACT

Cambrian–Ordovician sponge-microbial mounds in the Great Basin of the western USA reveal reef structure and composition immediately prior to the Great Ordovician Biodiversification Event (GOBE). Here we describe lithistid sponge-microbial reefs from the upper Cambrian (Furongian, Stage 10) strata of the Arrow Canyon Range, Nevada. The reefs are mound-like structures up to 1 to 2 m high and a few meters wide that consist of an unidentified thin-walled, bowl-shaped anthaspidellid sponge, columnar microstromatolite fabric, and the calcified microbe *Angusticellularia*. The reefs formed in low-energy, subtidal environments in which lime mud filled spongocoels and inter-reef spaces around undisturbed, in place, thin-walled sponges. The reefs colonized stable substrates provided by oolitic and bioclastic grainstone shoals. The mutually attached lithistid sponges form the main framework of the reefs. These thin-walled and bowl-shaped lithistids most likely were adapted to low-energy environments. Spaces beneath the overhanging sponge walls were filled by microbial carbonates. These include pendent micro-dendritic *Angusticellularia* attached to dermal sponge surfaces and upward-growing masses of microstromatolites. After death the lithistid spongocoels were mainly filled by micritic sediment that hosted soft-bodied burrowing organisms and keratose-like sponges. These lithistid sponge-microbial reefs, together with an earlier example of late Cambrian (Paibian) dendrolite-lithistid reefs in the same area, characterize skeletal-microbial reefs immediately prior to the GOBE.

1. Introduction

The early Paleozoic was a time of significant transition between microbial-dominant and metazoan-dominant reefs (Fagerstrom, 1987; Wood, 1999; Rowland and Shapiro, 2002; James and Wood, 2010; Lee et al., 2015; Riding et al., 2019). Archaeocyaths were the earliest skeletal reef builders of the Phanerozoic to flourish globally, forming archaeocyath-microbial reefs (James and Debrenne, 1980; Rowland and Gangloff, 1988; Rowland, 2001; Rowland and Shapiro, 2002; Gandin and Debrenne, 2010). It has been postulated that microbes dominated reef ecosystems after archaeocyath extinction in the late early Cambrian (Fagerstrom, 1987; Zhuravlev, 1996; Rowland and Shapiro, 2002) until the rise of the lithistid sponge *Archaeoscyphia*, the probable sponge *Calathium*, stromatoporoid-like pulchrilaminids and other sponge and sponge-like organisms that formed reefs with microbes in the Early Ordovician (Webby, 2002; Adachi et al., 2011). This phase of reef building diminished in the late Middle Ordovician as stromatoporoids, tabulate and rugose corals, and bryozoans began to dominate reef ecosystems. The middle to late Cambrian has therefore been regarded as the longest metazoan "reef gap" of the Phanerozoic (Sheehan, 1985; Zhuravlev, 1996; Rowland and Shapiro, 2002; Kiessling, 2009). Studies during the past 20 years, however, recognized lithistid sponge-microbial reefs in middle to upper Cambrian strata worldwide, closing this gap (Lee et al., 2016a; Lee and Riding, 2018).

Compared with both archaeocyath-microbial reefs of the early Cambrian and *Archaeoscyphia-Calathium*-microbial reefs of the Early Ordovician, records of middle to late Cambrian reefs are scarce. Only about ten examples have been reported, and less than half of these have been studied in sedimentological and paleoecological detail (Kruse and Zhuravlev, 2008; Kruse and Reitner, 2014; Adachi et al., 2015; Hong et al., 2016; Lee et al., 2016a). Every new example can therefore assist understanding of the evolutionary pattern of middle to late Cambrian reefs. In this study, we describe lithistid sponge-microbial reefs from the upper Cambrian (Stage 10) succession of Nevada, USA, reported by

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[*] Corresponding author.
E-mail address: jeonghyunlee@cnu.ac.kr (J.-H. Lee).

https://doi.org/10.1016/j.palaeo.2019.02.003
Received 4 September 2018; Received in revised form 3 February 2019; Accepted 3 February 2019

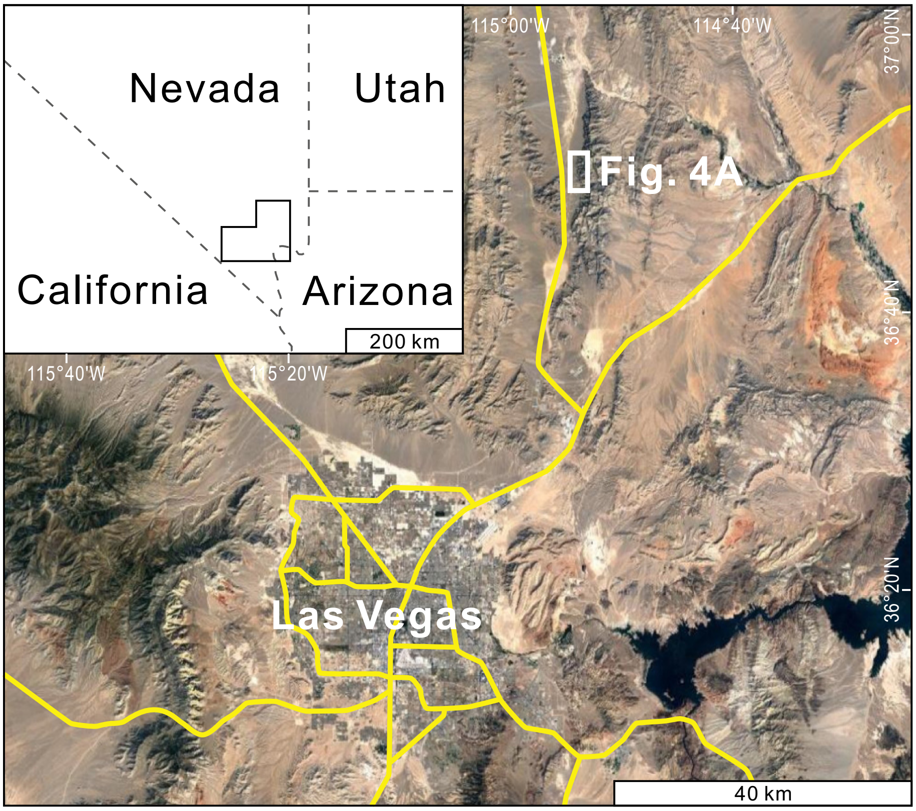

Fig. 1. Locality map, southern Nevada. The Arrow Canyon Range (36°39′48″N, 114°53′39″W) is located about 60 km NNE of Las Vegas. The white box indicates the locality studied, which is illustrated in Fig. 4A.

Mrozek et al. (2003). These are the youngest Cambrian examples of reefs of this type yet known, and therefore they provide valuable information about the timing and character of the transition from Cambrian lithistid-microbial reefs to Early Ordovician lithistid-microbial-calathiid reefs.

2. Geological setting and methods

Lithistid sponge-microbial reefs occur discontinuously on the western slopes of the Arrow Canyon Range in Clark County, Nevada, USA (Fig. 1). The reef-bearing horizons occur in the middle of a dolomitized succession as patches of well-preserved carbonates up to 15 m thick and 50 m wide (Figs. 2, 3). Although the shape and extent of the original reefs is uncertain due to uneven dolomitization, reef-like textures within the dolostone suggest that they formed a series of mounds > 50 m wide, or possibly even a single continuous biostrome, extending laterally for > 8 km. Revised lithostratigraphic and biostratigraphic classifications of the upper Cambrian and Lower Ordovician in eastern Nevada, including the Arrow Canyon Range, suggest that the reef-bearing strata described here belong to the Red Tops Member of the Notch Peak Formation and, based on the occurrence of *Eoconodontus notchpeakensis* from the reef unit, to the *E. notchpeakensis* Subzone of the *Eoconodontus* Zone (Figs. 2, 3) (Dattilo et al., 2004, 2011).

The sponge-microbial reefs in the Arrow Canyon Range correlate with two microbial reefs in the Red Tops Member of the Notch Peak Formation of Utah and in coeval strata in Colorado (Miller et al., 2003). The Arrow Canyon Range reefs described here occur slightly above the base of the *Eoconodontus notchpeakensis* Subzone of the *Eoconodontus* Zone (Mrozek et al., 2003; Dattilo et al., 2004). This horizon correlates with the lower reef in western Utah (Fig. 2) and indicates its age as Stage 10 of the uppermost Cambrian (Peng et al., 2012; Miller et al., 2015). The Nevada and Utah reefs also correlate biostratigraphically with the Clinetop Stromatolite Bed at the top of the Dotsero Formation

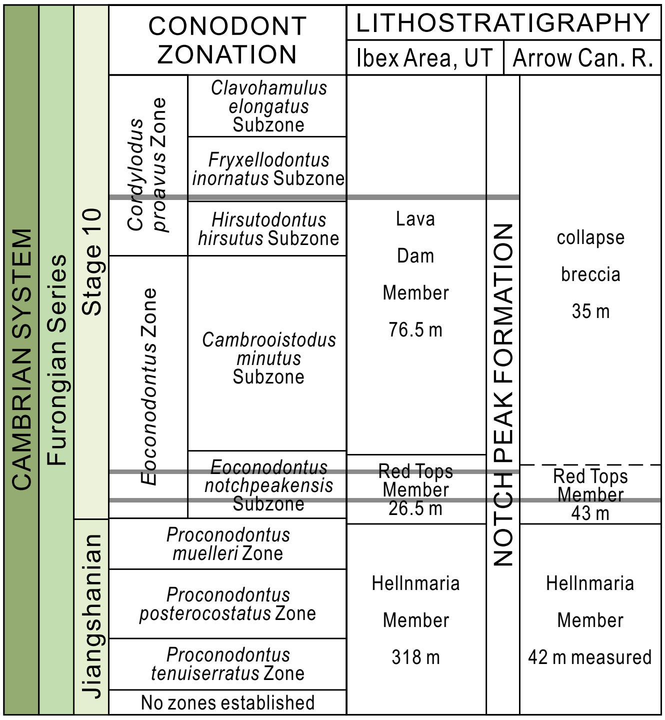

Fig. 2. Stratigraphic relationships for the Notch Peak Formation in western Utah, USA and the Arrow Canyon Range. Thin gray shaded intervals indicate stratigraphic levels of stromatolitic reefs. The Lawson Cove Stromatolite Bed in the middle of the Lava Dam Member is widespread in western Utah. Modified after Miller et al. (2003, fig. 3).

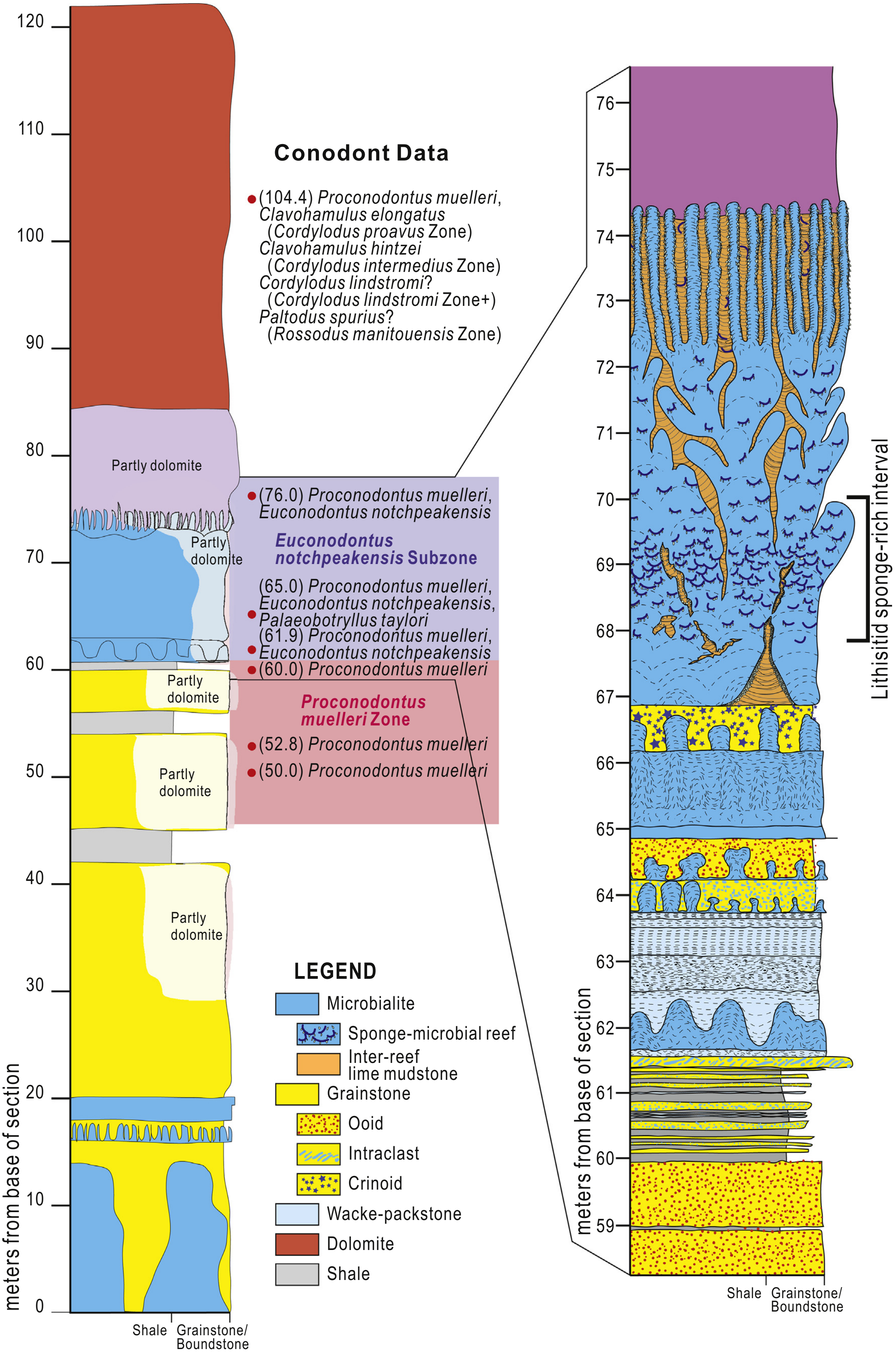

Fig. 3. Sedimentological log of Cambrian–Ordovician strata in the area studied in the Arrow Canyon Range. The lithistid sponge-rich interval occurs in the interval between 68 and 70 m, and belongs to the lower part of the *Eoconodontus notchpeakensis* Subzone.

in western Colorado (Myrow et al., 2003).

In the Ibex area of western Millard County, Utah, Miller et al. (2003) described in detail nine sections that include some or all of the Red Tops Member. Some of those sections have neither reef, some have either the lower or the upper reef shown on Fig. 2, but no section has reefs at both levels. A comparable microbial reef, the Lawson Cove Stromatolite Bed (Miller et al., 2003), occurs in the middle of the Lava Dam Member in western Utah (Fig. 2). The Lawson Cove Stromatolite Bed is widespread in western Utah and has been identified in the Delamar Mountains, ~75 km north of the Arrow Canyon Range. A stromatolite bed occurs at this stratigraphic level in central Texas in the San Saba Member of the Wilberns Formation (Ahr, 1971; Miller, 1992). Among the reefs that Miller et al. (2003) described, as well as those in Texas, sponges have been reported only from the thin stromatolitic reef in the Arrow Canyon Range that is the subject of this article, and locally in the Clinetop Bed (possibly *Wilbernicyathus*; Johns et al., 2007). Further study of the other reefs along strike from the measured traverses might reveal such fossils.

This study is based on samples collected by Mrozek et al. (2003) and by J.-H. Lee in 2015. Samples were serially slabbed and thin sectioned to provide several sets of slabs and thin sections to display three-dimensional structures of the reef fabric and the sponges, respectively.

3. Results

3.1. Reef description

The Arrow Canyon Range lithistid sponge-microbial reefs are mound-like structures about 1 to 2 m high and few meters wide, with undulose domal upper surfaces (Fig. 4B). Each mound consists of several smaller mounds that merge together, separated by irregular lateral boundaries. The mounds overlie grainstone with recrystallized ooids and fragments of trilobites, gastropods, and echinoderms and are sharply overlain by grainstone. Partly dolomitized and bioturbated lime mudstone-wackestone occupies mound interspaces. The reefs consist of three main components: an unidentified bowl-shaped lithistid sponge, microstromatolite, and the calcified microbe *Angusticellularia* (Fig. 5). Accessory fabrics and components, such as burrows, keratose-like sponges and fossil fragments are also recognized.

3.2. Lithistid sponges

The lithistid sponges observed are mostly about 5 cm wide and 3 cm high, with the largest examples up to 14 cm wide and 10 cm high (Fig. 5). They mainly have upward-widening bowl shapes, with oscula opening upward, suggesting in situ preservation. Fragmented or downward facing examples have not been observed. The lithistid sponge walls are a few millimeters thick, extremely thin relative to their size (Fig. 6). Wall thickness usually thins upward. Ladder-like spicule networks suggest that these sponges belong to the Family Anthaspidellidae, but their internal structures (e.g., trab arrangements and canals) and their external morphologies differ from other Cambrian anthaspidellid genera such as *Rankenella*, *Gallatinospongia*, and *Wilbernicyathus* (cf. Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Kruse and Reitner, 2014; Lee et al., 2016c), and detailed taxonomic analysis is required to elucidate their evolutionary significance (Fig. 7C, D).

The most common reef component is lithistid sponge which, if intraspongocoel sediment is included, occupies about half of the surface of the reef outcrops (Figs. 5, 6, 7). Sponges are usually closely packed within a few centimeters of one another. In some cases, mutually attached examples of lithistid sponges are observed (Figs. 6, 7B, E). A single example of a sponge apparently attached to the wall of another sponge is observed in transverse serial section (Fig. 7B), but it might represent branching of a single sponge. In longitudinal section, sponge walls meet perpendicularly and are clearly demarcated from each other (Fig. 7A, E). Spongocoels were partly encrusted by thin microstromatolite layers, filled by lime mudstone and then bioturbated (Figs. 6, 7A). Fossil fragments, including hexatines (6-pointed spicules) and numerous small branched pores that closely resemble remains of keratose-like sponge (cf. Luo and Reitner, 2014) occur within these lime mudstone fills (Fig. 7F).

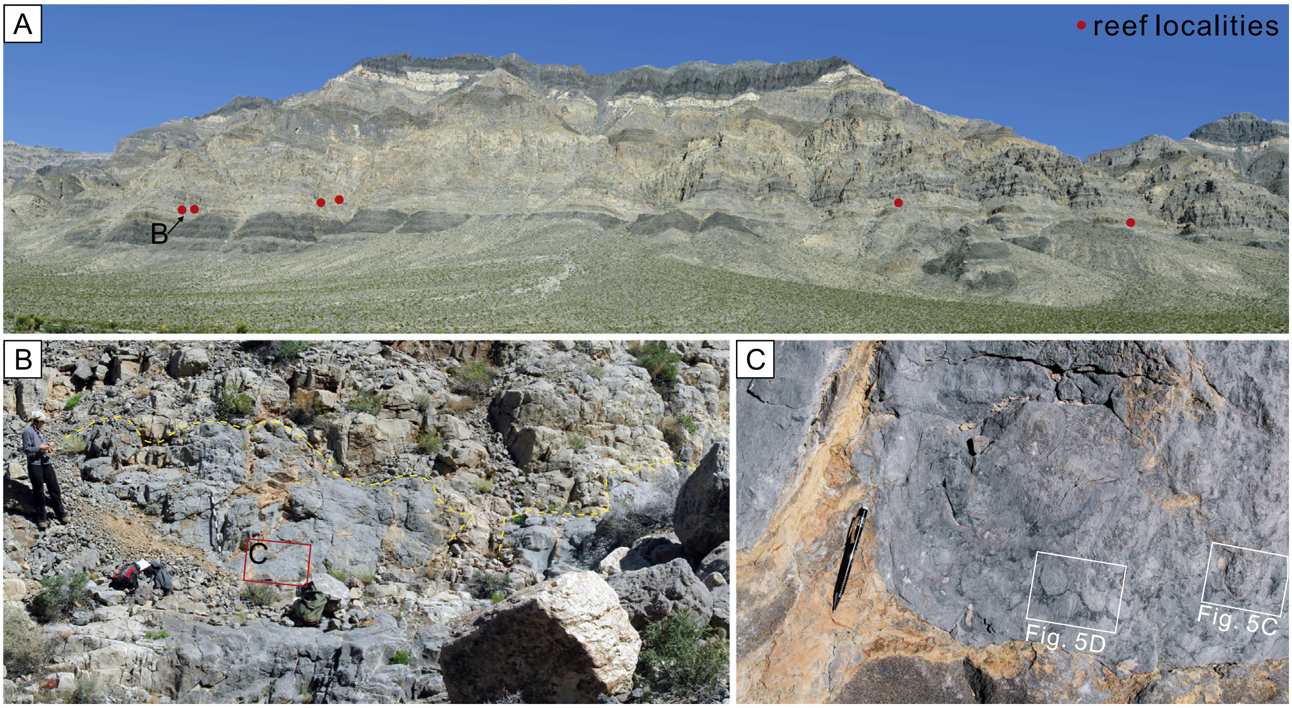

Fig. 4. Outcrop photograph of the Arrow Canyon Range localities. (A) General view of the outcrop from the west. Red dots indicate location of reef localities. (B) Reef mounds marked with yellow dotted line (36°39′48″N, 114°53′39″W). (C) Close up of basal reef mound. Pencil for scale is 14.5 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

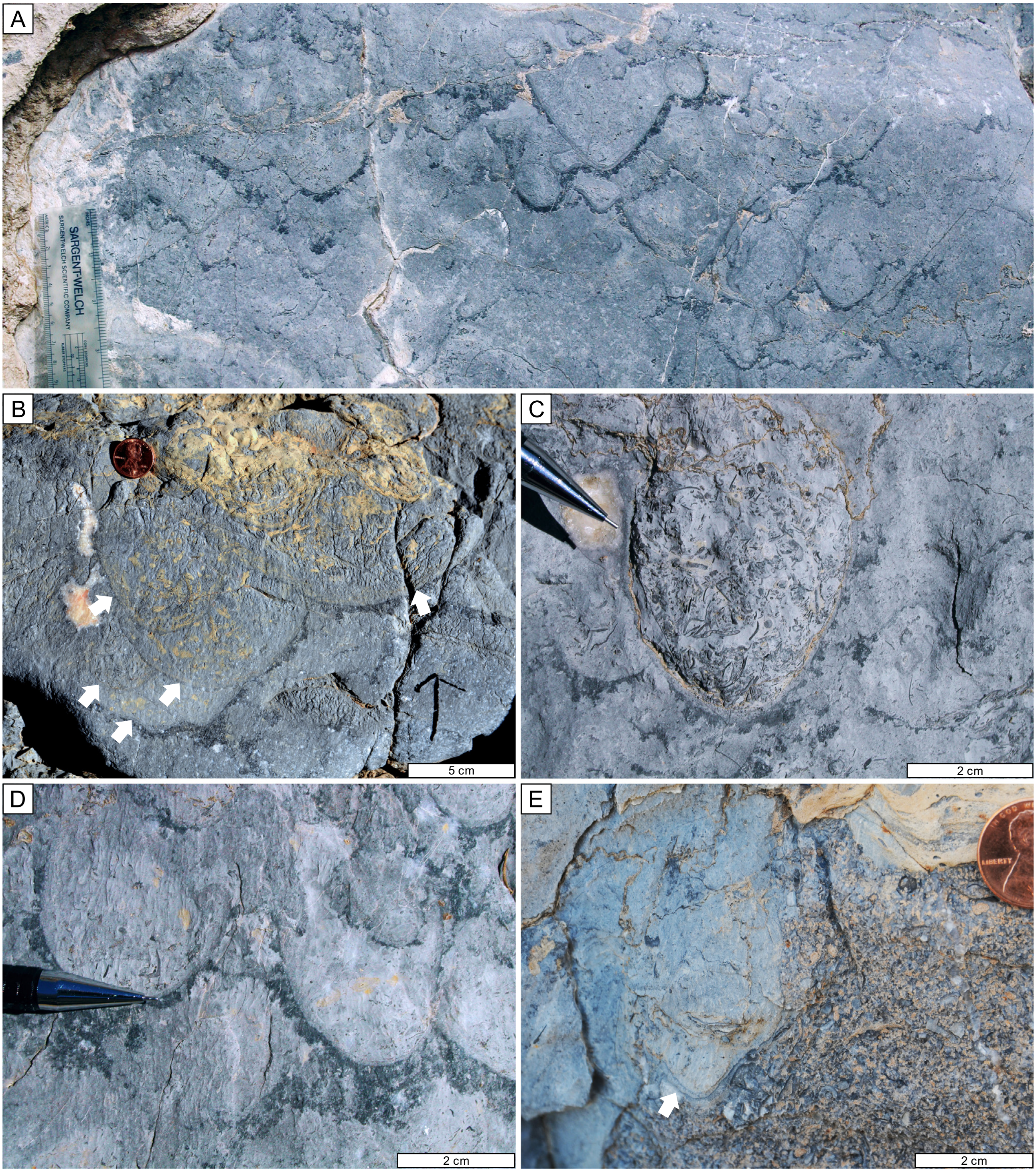

Fig. 5. Outcrop view of the lithistid sponge-microbial reef. (A) Several upward-widening bowl-shaped sponges are packed together, with pendent dark-colored *Angusticellularia* attached at their dermal surfaces. (B) Closely packed sponges (arrows). (C) An example of spongocoel filled with bioclastic wackestone. (D) Pendent *Angusticellularia* attached below sponges. (E) An example of lithistid sponge growing on oolitic-bioclastic grainstone.

3.3. Microstromatolites

Microstromatolites outside the lithistid sponges have a dark-gray chaotic texture in outcrop. They are a close second in terms of importance as reef components, occupying an approximately similar area to that of lithistids. Under the microscope, microstromatolites are characterized by convex-upward, thin, alternating laminae of lighter- and darker-colored micrite (Fig. 8). They usually form small columnar to bulbous morphologies, 1–3 mm wide and ~5 mm high. They mostly grew subvertically. Thin layers of microstromatolites occupy the bases of spongocoels, following the gastral surface of the sponges (Fig. 8D). The internal fabrics of microstromatolites are often poorly preserved and appear to be microscopically clotted (cf. Lee et al., 2016b) (Fig. 8C). No calcimicrobes have been observed within microstromatolites. Some keratose-like sponges occur between microstromatolites.

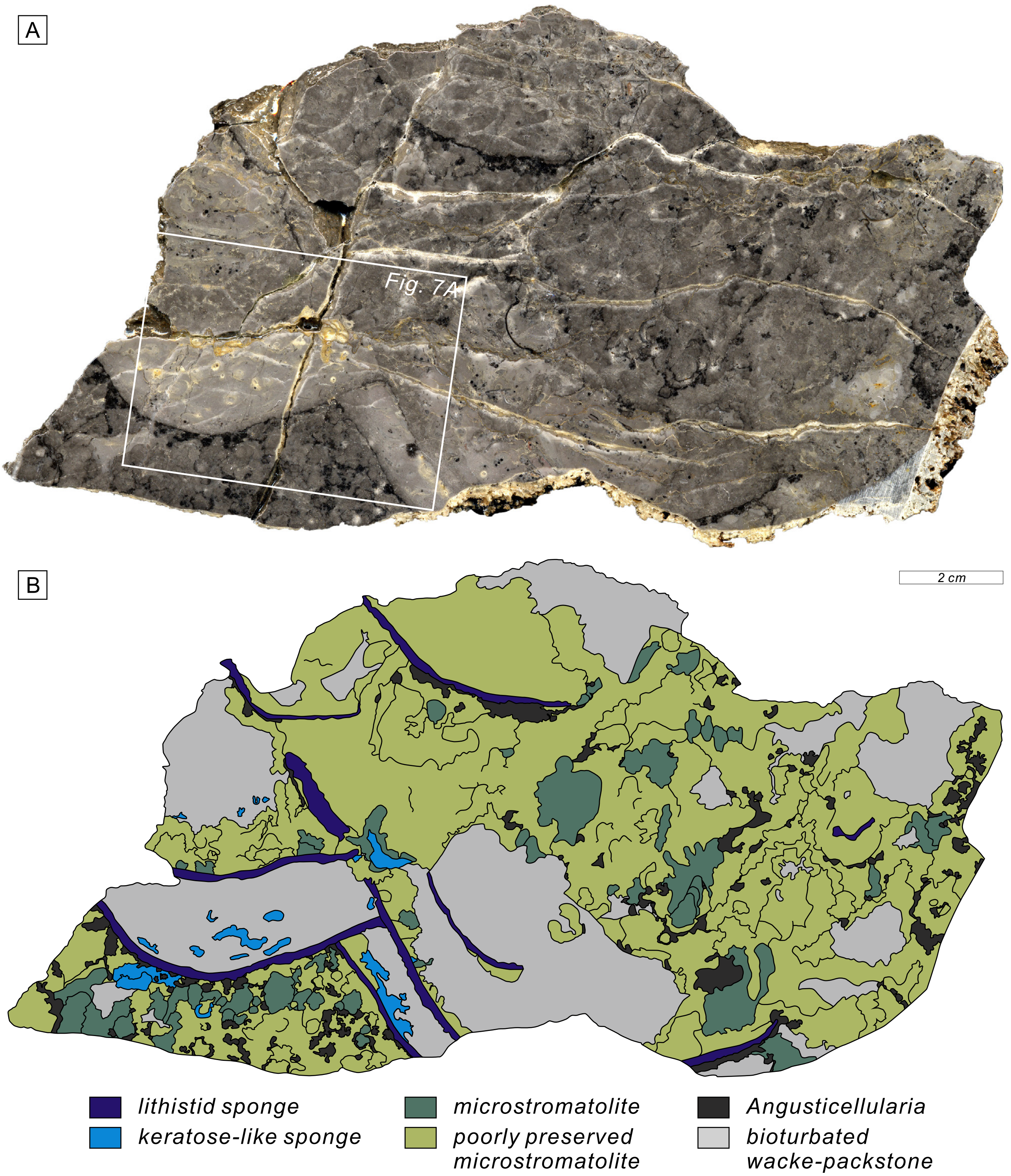

Fig. 6. (A) Slab and (B) interpretive sketch of the lithistid sponge-microbial reef.

3.4. *Angusticellularia*

The calcified microbe *Angusticellularia* characteristically forms dark, irregular masses of micrite with an irregularly dendritic fabric (Riding and Voronova, 1982; Riding, 1991). *Angusticellularia* within Arrow Canyon Range reefs mostly consists of a dark reddish opaque hematite-like mineral (Fig. 9). Individual *Angusticellularia* shrubs are typically less than a few millimiters in size and mainly occur pendent on dermal sponge surfaces (Figs. 5, 6, 9A). They are a relatively minor component, occupying approximately 5 to 10% of the reef surface. Microscopically, some *Angusticellularia* occur between microstromatolite and follow the outlines of columnar microstromatolites (Fig. 9B). In such cases, their growth direction is uncertain.

3.5. Reef architecture and construction

Overall, these Arrow Canyon Range lithistid sponge-microbial reefs developed under low-energy conditions where lime mud was a common

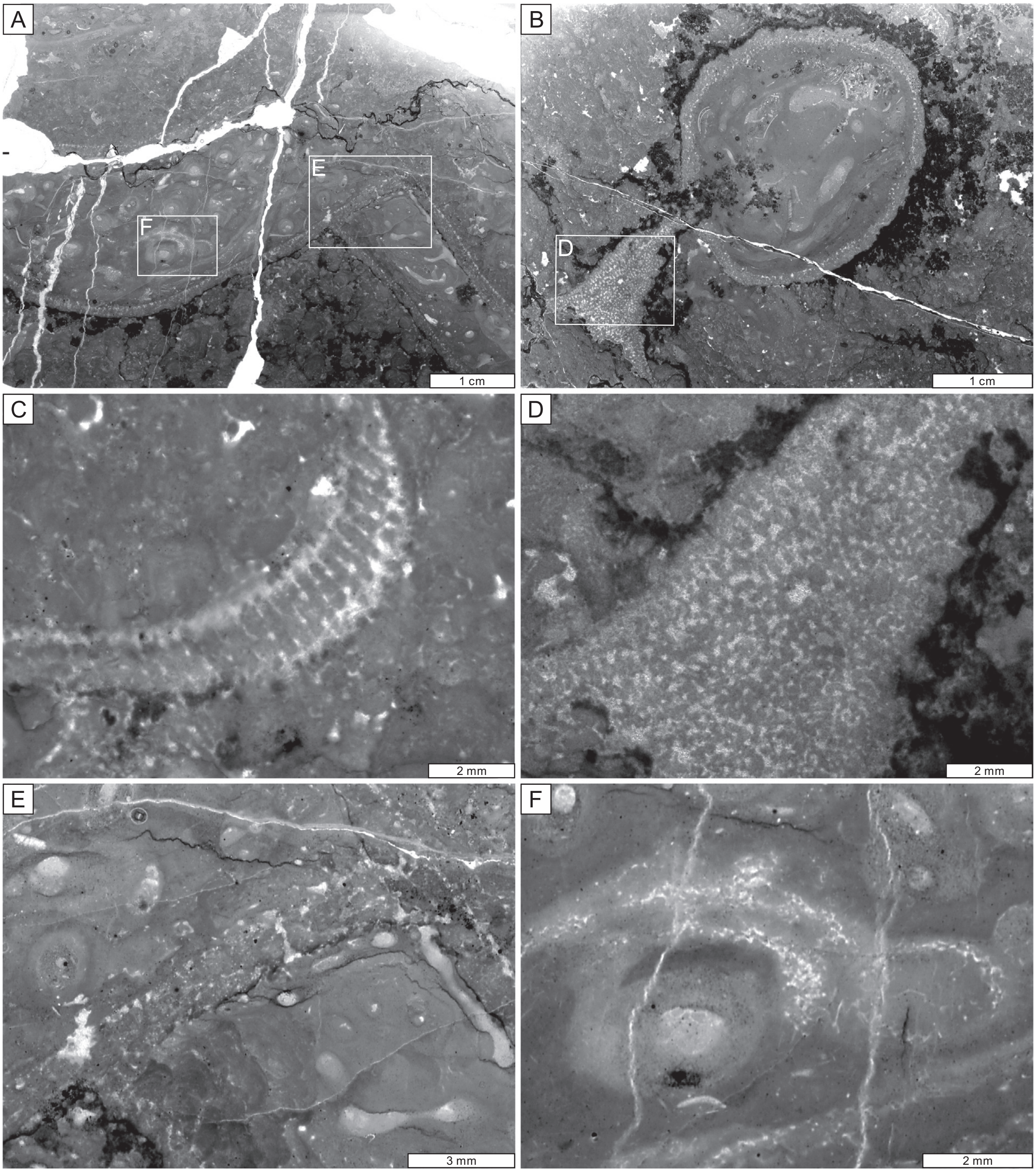

Fig. 7. Photomicrograph of sponges. (A) Several closely-packed lithistid sponges. For general view, see Fig. 6B. (B) A thin section cut parallel to the bedding, showing a thin donut-shaped transverse cut of a bowl-shaped sponge in the center and another sponge attached on the wall of the bow-shaped sponge. (C) Close-up of sponge, showing ladder-like anthaspidellid-type spicule network. (D) Close-up of (B). (E) Margins of lithistid sponges demarcated by other lithistid sponges. (F) Keratose-like sponge within spongocoel of a lithistid sponge, occurring with a burrow.

allochthonous component of the deposits and sponges could be preserved in situ without fragmentation. Reef growth initiated on oolitic and bioclastic grainstone shoals that appear to have provided stable substrates for the initial growth of the reef-building organisms (Fig. 5E). The overall pattern of facies change, from grainstone below, through bioturbated wackestone, and to grainstone above the reef mounds suggests two possibilities. First, that Arrow Canyon Range reef growth was localized by the presence of coarse bioclastic/ooid substrates. Second, that there may also have been a reduction in water energy during reef growth. The thin walled sponges and abundant lime mud filling the spongocoels and occupying intermound space support the view that these sponge-microbial reefs took advantage of both coarse substrates and a reduction in water-energy. The thin walls of these lithistid sponges could reflect a low-energy environment (Palumbi, 1986). They mainly grew upward, with an upward-widening growth pattern. Such a pattern is not observed in Cambrian–Ordovician lithistid-microbial reefs in high-energy, shallow subtidal environments in which thicker-walled conical lithistids mainly grew in sub-horizontal to downward directions (Table 1) (Kruse and Zhuravlev, 2008; Lee et al., 2016a). The Arrow Canyon Range lithistid sponges therefore could have inhabited a relatively low-energy environment compared with most other described Cambrian examples.

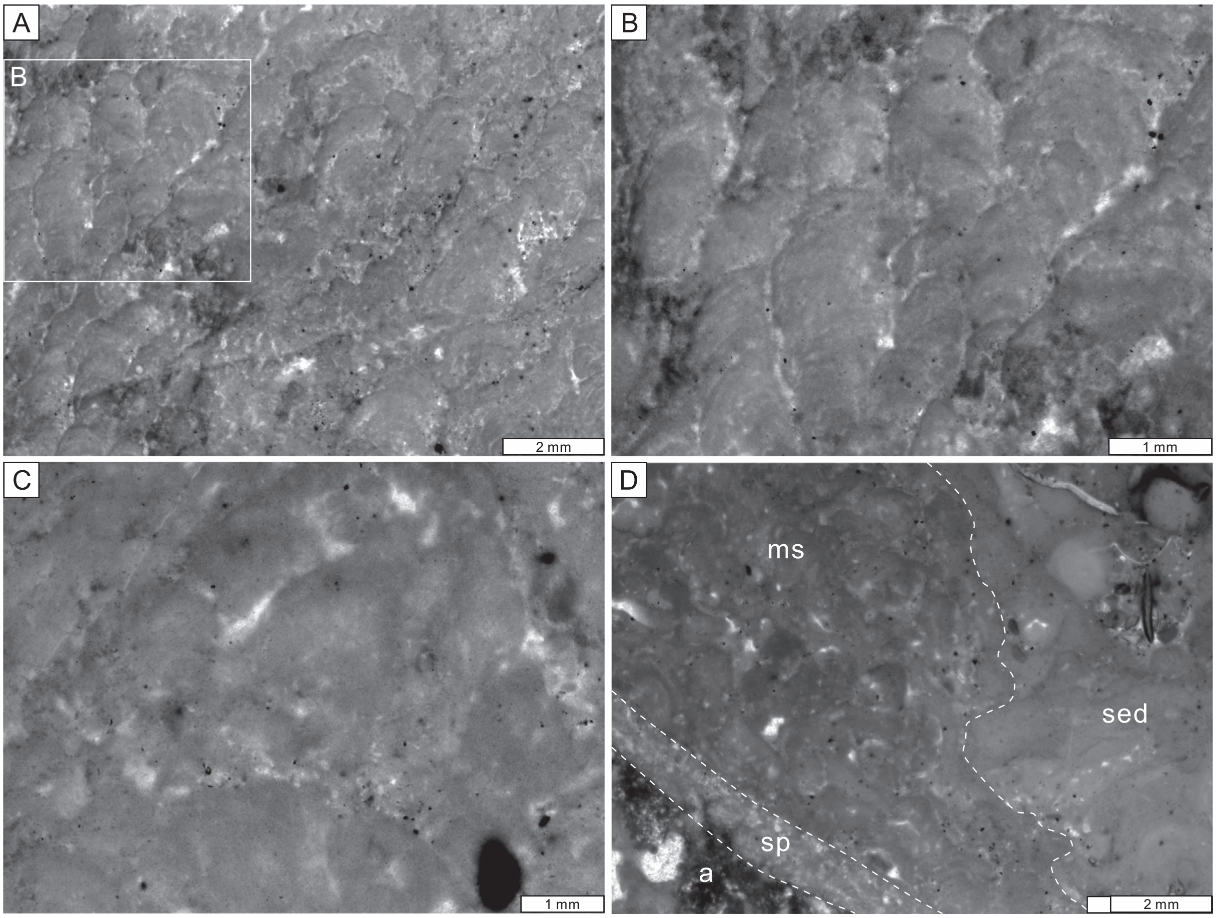

Fig. 8. Photomicrograph of microstromatolite. (A) General view of microstromatolite, showing columnar to bulbous shape. (B) Details of microstromatolite in (A). (C) Poorly preserved examples of microstromatolites showing microscopically clotted fabric. (D) Examples of thin-layered microstromatolite growing on gastral surface of a lithistid sponge.

The dominant presence of allochthonous sediment and the rarity of microstromatolites within the spongocoels suggest that the living sponges and their effective water filtering activity inhibited internal encrustation by microstromatolites (Fig. 10A). Microstromatolites only encrusted gastral surfaces of the sponges during the short interval between the death of the sponge and deposition of the infilling wackestone (Fig. 10B). On the other hand, external spaces beneath the sponges were open while the sponges were still alive, as shown by the presence of downward-growing encrusting *Angusticellularia* (Fig. 10B). Lithistid sponges were therefore the major framework-builders of these Arrow Canyon Range reefs. The spaces beneath the sponges were favorable for microbial growth, in this case *Angusticellularia* and upward-growing columnar microstromatolites. In view of their overall volume and thickness, *Angusticellularia* crusts seem unlikely to have significantly stabilized the framework. In contrast, the volumetrically more abundant microstromatolites that filled the empty spaces are likely to have provided substantial strength and rigidity to the reef structure (Fig. 10C). After death, the lithistid spongocoels were mainly

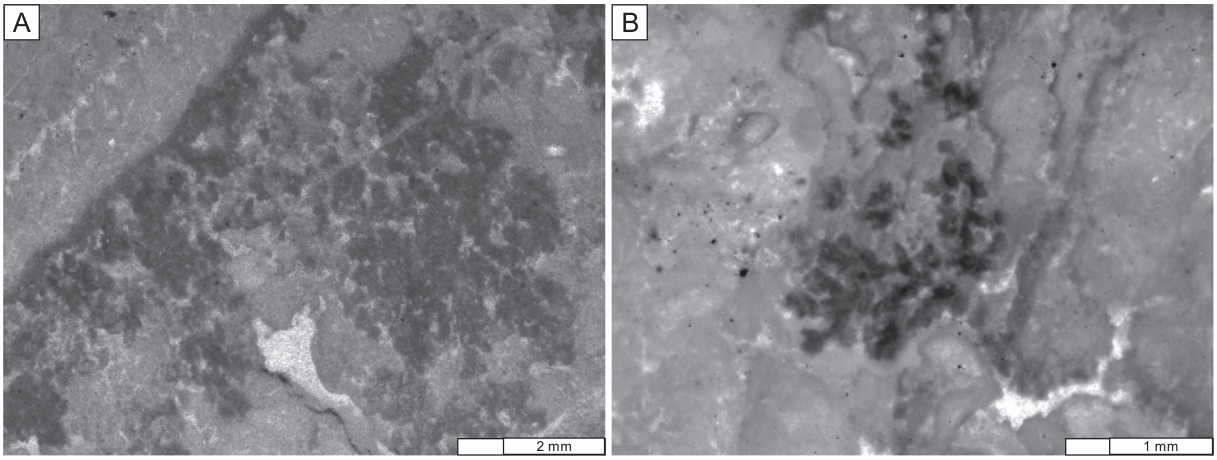

Fig. 9. Photomicrograph of *Angusticellularia* (A) attached below a lithistid sponge and (B) between microstromatolites.

Table 1
Global occurrence of Cambrian lithistid sponge-microbial reefs.

Age	Lithologic unit	Locality	Depositional environment	Major reef-building components	Sponge shape	Reef-building role	References
Upper Wuliuan–Drumian	Zhangxia Formation	Shandong, North China	Shallow subtidal	Anthaspidellid sponge (*Rankenella zhangxianensis*), *Epiphyton*, microstromatolite	Cone	Lithistid sponges and *Epiphyton* formed frameworks; microstromatolite encrusted frameworks	Lee et al. (2016a)
Wuliuan?	Dedebulak Formation	Kyrgyzstan	No data	Lithistid sponge? (*Orlinocyathus*), *Epiphyton*	No data	No data	Teslenko et al. (1983)
Drumian	Daegi Formation	Taebaek, Korea	Shallow subtidal	Anthaspidellid sponge, *Epiphyton*, non-lithistid demosponge	Cone?	*Epiphyton* constructed reefs; lithistid sponges dwelled between *Epiphyton*	Hong et al. (2012, 2016)
Upper Drumian	Ranken Limestone	Georgina Basin, Australia	Bioclast-rich ramp debris	*Angulocellularia*, *Taninia*, anthaspidellid sponge (*Rankenella mors*)	Explanate	Microbes mostly constructed reefs; role of sponges passive	Kruse and Reitner (2014)
Lowermost Paibian	Deh-Molla Formation	Iran	Subtidal	Anthaspidellid sponge (*Rankenella hamdii*), *Girvanella*	Cone	Sponges formed reef frameworks; *Girvanella* encrusted frameworks	Hamdi et al. (1995), Kruse and Zhuravlev (2008)
Lowermost Paibian	Bonanza King Formation	Great Basin, USA	Shallow subtidal	Anthaspidellid sponge (*Gallatinospongia conica*), dendrolite	Cone	Dendritic clots constructed framework; role of sponges unknown (possibly framebuilder)	Shapiro and Rigby (2004)
Jiangshanian	Wilberns Formation	Texas, USA	Shallow marine	Anthaspidellid sponge (*Wilbernicyathus donegani*), *Girvanella*, *Tarthinia*	Cone	No data (sponges probably formed reef frameworks)	Johns et al. (2007)
Stage 10	Dotsero Formation	Colorado, USA	Shallow marine	*Girvanella*, *Tarthinia*, anthaspidellid sponge (*Wilbernicyathus donegani*)	Cone?	No data	Johns et al. (2007)
Stage 10	Notch Peak Formation	Nevada, USA	Relatively deep subtidal	Anthaspidellid sponge, microstromatolite, *Angusticellularia*	Thin bowl	Lithistid sponges formed frameworks; microstromatolites filled interspace between frameworks; *Angusticellularia* cryptically grew below sponges	This study

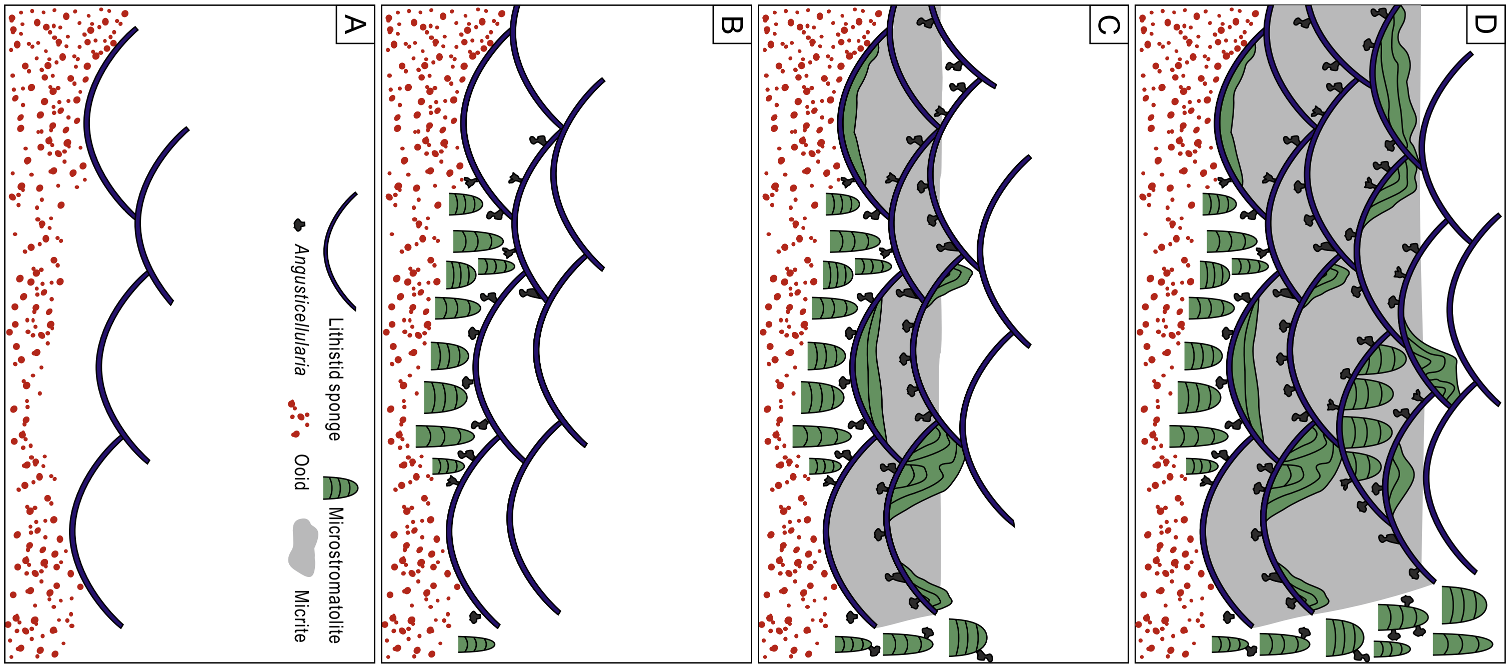

Fig. 10. Proposed model of Arrow Canyon Range lithistid sponge-microbial reef development. (A) Thin, bowl-shaped lithistid sponges grew mutually attached on grainy sediment, locally leaving empty spaces below. (B) Microstromatolites filled most of the space below the lithistid sponges. *Angusticellularia* attached on the dermal surfaces of the sponges and on the microstromatolites. (C) After death, the spongocoels were partly coated by microstromatolites and then largely infilled by skeletal wackestone which was commonly burrowed. Some keratose-like sponges also grew within the spongocoel sediment. (D) New sponges grew above the dead sponges as the reef accreted.

filled by micritic sediment that hosted soft-bodied burrowing organisms (Fig. 10C, D). Allomicrite also filled inter-mound spaces, together with transported spicules and other disarticulated bioclasts. However, keratose-like sponges observed within spongocoels likely grew in situ, because their delicate fabrics would have easily been destroyed if they were transported.

4. Discussion

4.1. Implications for Cambrian reef evolution

Since the initial report of Cambrian reef-building lithistids from the lowermost Furongian of Iran by Hamdi et al. (1995), similar sponges have been recognized from a number of localities worldwide during the past twenty years (Table 1). The Arrow Canyon Range lithistid sponge-microbial reefs described here are the youngest of their kind, along with minor occurrence of possible *Wilbernicyathus* from the Clinetop Stromatolite Bed in Colorado (Johns et al., 2007). Many of these lithistid sponges are small and cone-shaped with thick walls. They are mutually attached and constructed sponge-dominated reef frameworks (Table 1). An exception is the explanate sponges covering stromatolites in the upper Drumian of Australia (Kruse and Reitner, 2014). *Rankenella zhangxianensis* from the upper Wuliuan–Drumian of China (Lee et al., 2016a) and *R. hamdii* from lowermost Furongian of Iran (Kruse and Zhuravlev, 2008) formed in shallow subtidal environments surrounded by bioclastic packstone to grainstone and were able to form strong reef frameworks by mutual attachment. Small cup-shaped *Gallatinospongia conica* (Okulitch and Bell, 1955) from lowermost Furongian of the Great Basin, USA is enclosed within dendrolite and grew on a shallow subtidal ramp with numerous tidal channels filled with oolite (Shapiro and Rigby, 2004). The Jiangshanian–Stage 10 *Wilbernicyathus donegani* from Texas, USA has a conical to cylindrical shape with thick walls and is surrounded by eocrinoid grainstone to siltstone (Johns et al., 2007).

The Arrow Canyon Range reefs are basically dominated by sponge frameworks that are unlikely to have been strong enough to resist high-energy conditions similar to those in which most other Cambrian lithistid sponge frameworks appear to have developed. They also differ from Early Ordovician lithistid sponge-microbial reefs dominated by the conical lithistid *Archaeoscyphia*, which rather resemble other Cambrian lithistid-microbial reefs (Church, 1991, 2017; Adachi et al., 2009, 2011; Hong et al., 2014, 2015; Li et al., 2015, 2017), as well as from those early Cambrian archaeocyath-microbial reefs in which conical archaeocyaths formed wave-resistant frameworks in high-energy shallow subtidal environments (Gandin and Debrenne, 2010). Arrow Canyon Range reefs therefore represent a distinctive type of lithistid sponge-microbial reef that developed in the latter part of the Cambrian. Therefore, it is possible that by the late Cambrian lithistids had developed various shapes in different environments. They initially developed heavily silicified, thick-walled cones able to withstand high-energy shallow subtidal conditions, but subsequently they developed thin-walled, bowl-shaped structures such as those in the Arrow Canyon Range described here. Early Ordovician reef-building anthaspidellids subsequently developed transverse ridge-and-trough ornamentation in addition to thick-walled cones, which would have been helpful to withstand high-energy waves (Church, 2017). However, more examples with detailed sedimentological background are required to explore these interpretations.

4.2. Late Cambrian to Early Ordovician reef evolution in the Great Basin

The Great Basin provides a laboratory to examine Cambrian–Ordovician changes in reef-building during and immediately before the initial stage of the Great Ordovician Biodiversification Event (GOBE) (Fig. 11). Shapiro and Rigby (2004) described a lithistid sponge (*Gallatinospongia*)-dendrolite mound in the upper Cambrian (basal Paibian Stage; Furongian Series) of Nevada and California. More recently, Coulson and Brand (2016) reported abundant keratose-like sponges within 'stromatolites' from the Jiangshanian–Stage 10 succession (upper Hellnmaria Member) of western Utah. These macroscopically resemble dolomitized 'maceriate thrombolites' from coeval successions throughout the Great Basin (Shapiro and Awramik, 2006) and are almost identical to some sponge-microbial reefs from North China (Lee et al., 2014). The Arrow Canyon Range reefs described here, which are slightly younger than the Hellnmaria Member, are lithistid-microbial in composition. The Lower Ordovician succession of this region also contains several reef-bearing horizons in the Fillmore Formation (Tremadocian–middle Floian) and Wah Wah Limestone (upper Floian). Several of these have been named after early workers, successively Miller's, Hintze's, Church's, *Calathium*, and Wyatt's reefs (see Miller et al., 2012) (Fig. 11). Miller's reef (lower Fillmore Formation; Stairsian Stage, mid-Tremadocian) is characterized by columnar stromatolites with a few lithistid sponges, which mostly occur within intercolumnar sediments, with some attached on the stromatolites (Miller et al., 2012, fig. 128). Hintze's reef (lower Fillmore Formation; Stairsian Stage, mid-Tremadocian) is mainly thrombolite with many lithistid sponges (Miller et al., 2012, fig. 131). In the mid-Fillmore Formation, Church's reef (mid-Tulean Stage, near the Tremadocian–Floian boundary), consists of massive micrite with sparse *Calathium* and rare anthaspidellid sponges (Church, 1991). '*Calathium*' reef in the upper Fillmore Formation (Blackhillsian Stage, mid–late Floian) is, as its name indicates, dominated by *Calathium* (Church, 1974, 1991). The late Floian (upper Blackhillsian Stage) Wah Wah Limestone contains Wyatt's reef, consisting primarily of microbial micrite with some bioclastic debris of sponges, echinoderms, and other fossils (Wyatt, 1979).

These examples of changes in reef development in the Great Basin are consistent with the view that microbial carbonates were gradually supplemented by animals, such as lithistid sponges, attached echinoderms, and calathiids, during the early stage or prelude to the GOBE (Webby, 2002), and that these changes are likely to have been mediated by marine oxygenation as Cambrian 'greenhouse' conditions ameliorated (see references in Lee and Riding, 2018). At the same time, however, these Arrow Canyon examples appear to be typical of the Late Cambrian and do not show any obvious features suggesting inception of the GOBE. In the Great Basin, therefore, it appears that the main change in reef composition occurred in the mid-Tremadocian, though the change was gradual. In South China, mid–late Cambrian reefs appear to be microbial-dominant reefs (Adachi et al., 2014) and – so far as we are aware – have not been reported to contain lithistids. In contrast, in South China, the marked change in reef composition appears to have occurred abruptly in the mid-Tremadocian and Floian when lithistid-microbial-calathiid reefs appeared, together with a variety of novel skeletal reef builders, including bryozoans, pelmatozoans, *Pulchrilamina* and stromatoporoids (Adachi et al., 2011; Li et al., 2017). However, in western Argentina, new components, such as the coralomorph *Amsassia*, are reported in the lowermost Tremadocian (Carrera et al., 2017). It therefore appears that, globally, the main change in reef development during this period occurred within the Tremadocian as new skeletal reef builders augmented lithistids, but that there were significant regional variations in evolutionary patterns (Webby, 2002). These timings do not preclude the likelihood that, overall, the GOBE could have commenced in the late Cambrian (Servais et al., 2016), but so far as reef evolution was concerned noticeable developments may not have occurred until within the Tremadocian. These were the prelude to more abrupt and profound changes in reef construction that occurred in the late Darriwilian (Kröger et al., 2017; Lee and Riding, 2018).

5. Conclusions

1. Lithistid sponge-microbial reefs from the Arrow Canyon Range, Nevada, represent a distinctive type of late Cambrian metazoan-microbial reef, consisting of thin-walled, bowl-shaped sponges

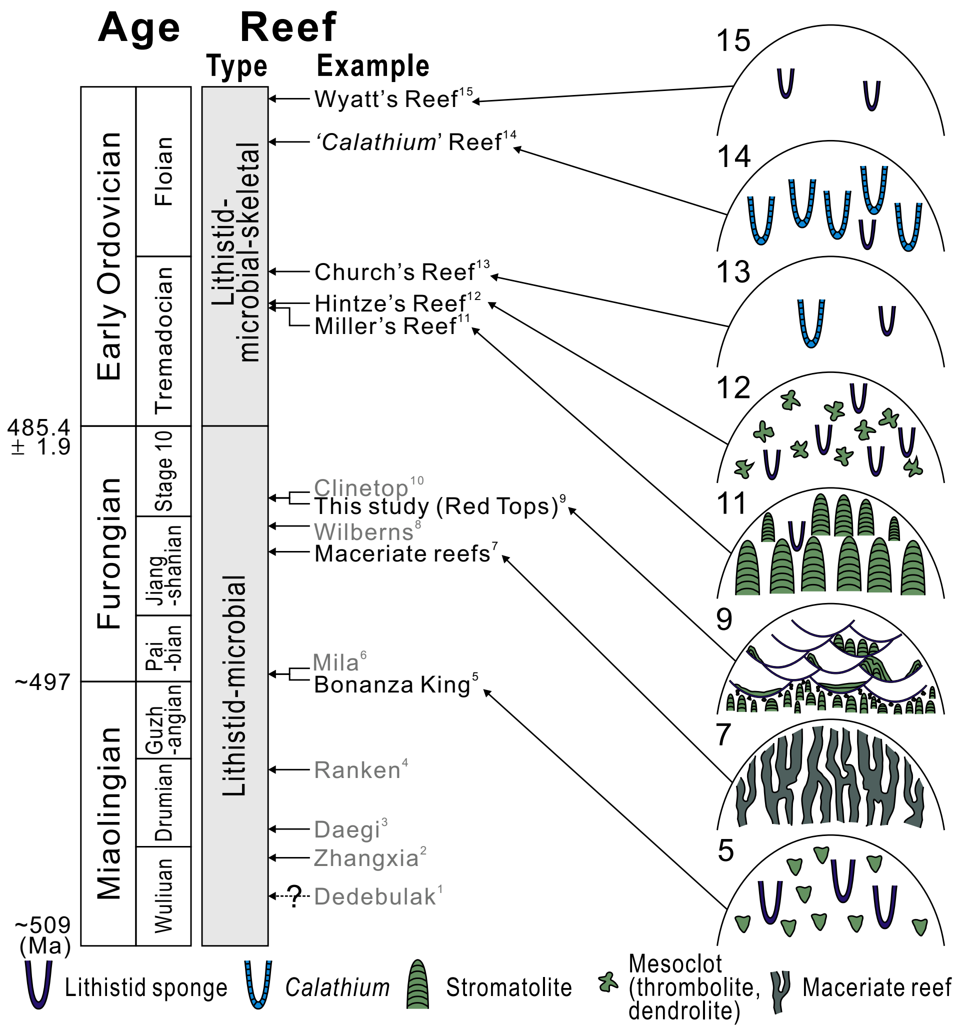

Fig. 11. Successive change of metazoan-bearing reef type in the southern Great Basin from the Furongian to the Early Ordovician (black) and comparable Cambrian reefs in the other parts of the world (gray). 1. Lithistid sponge? (*Orlinocyathus*)-*Epiphyton* reef, Dedebulak Formation, Kyrgyzstan (Teslenko et al., 1983). 2. Lithistid sponge *Rankenella zhangxianensis*-*Epiphyton*-*Cambroctoconus* reef, Zhangxia Formation, Shandong Province, China (Lee et al., 2016a). 3. Siliceous sponge (possible anthaspidellid)-*Epiphyton* reef, Daegi Formation, Taebaeksan Basin, Korea (Hong et al., 2012, 2016). 4. *Angulocellularia*-*Taninia*-lithistid sponge (*Rankenella mors*) reef, Ranken Limestone (Georgina Basin), Australia (Kruse and Reitner, 2014). 5. Lithistid sponge *Gallatinospongia* within dendrolite mound, Bonanza King Formation (Shapiro and Rigby, 2004). 6. Lithistid sponge *Rankenella hamdii*-*Girvanella* reef, Deh-Molla Formation, Iran (Hamdi et al., 1995; Kruse and Zhuravlev, 2008). 7. 'Maceriate' reefs with keratose-like sponges and microbes (Coulson and Brand, 2016). 8. Lithistid sponge *Wilbernicyathus*-*Girvanella*-*Tarthinia* reef, Wilberns Formation, Texas (Johns et al., 2007). 9. Reefs constructed by large, thin, bowl-shaped lithistid sponges with microstromatolites and subordinate *Angusticellularia* in the Red Tops Member, Notch Peak Formation, Nevada (this study). 10. *Girvanella*-*Tarthinia*-lithistid sponge (possibly *Wilbernicyathus*) reef, Dotsero Formation, Colorado (Johns et al., 2007). 11. Miller's reef mainly consisting of stromatolites with minor lithistid sponges (Miller et al., 2012). 12. Hintze's reef with abundant lithistid sponges within thrombolites (Miller et al., 2012). 13. Church's reef with some *Calathium* and lithistid sponges (Church, 1974, 1991). 14. '*Calathium*' reef with abundant *Calathium* (Church, 1974). 15. Wyatt's reef with minor skeletal debris of sponges (Wyatt, 1979).

forming frameworks, with columnar microstromatolites growing beneath them and pendant, *Angusticellularia* attached to their sides. They formed under low-energy conditions surrounded by lime mud, whereas most Cambrian–Ordovician lithistid-microbial reefs commonly appear to have developed in higher-energy shallow subtidal environments.

2. The sequence of metazoan-bearing reefs in the Great Basin does not show any very significant change in reef composition across the Cambrian–Ordovician boundary, apart from the gradual introduction of *Calathium*. This appears to be consistent with several other areas, including South China, where the main change from microbial-dominant reefs to lithistid-microbial-calathiid reefs together with several novel skeletal reef builders occurred within the Early Ordovician, marking the inception of the GOBE so far as it affected reef evolution.

Acknowledgments

We are grateful to two anonymous reviewers, and to Guest Editor Christian Rasmussen and Editor Thomas Algeo, for very helpful comments and suggestions that enabled us to improve the final version of this article. JHL was supported by grants from the National Research Foundation of Korea (2016R1C1B1012104 and 2018R1A4A1059956) and the Chungnam National University. Miller's research was funded by grants from Missouri State University. This study is a contribution to IGCP Project 653 'The Onset of the Great Ordovician Biodiversity Event'.

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