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DEAD CLADE WALKING: THE PERSISTENCE OF *ARCHAEOCYATHUS* IN THE AFTERMATH OF EARLY CAMBRIAN REEF EXTINCTION IN THE WESTERN UNITED STATES

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ABSTRACT: **Archaeocyaths, the first metazoan reef builders of the Phanerozoic, faced their ultimate demise during early Cambrian Age 4 but the exact timing of their local extinctions varied globally. In this study, we report archaeocyaths in strata that overlie the last robust archaeocyathan reefs of the western United States (Laurentian Cordillera). These are found in small microbial mounds in the upper unit of the Mule Spring Limestone near Split Mountain, Clayton Ridge, Nevada, as well as in storm beds in the Thimble Limestone Member of the Carrara Formation in Echo Canyon of the Funeral Mountains, Death Valley, California. Thin-section analysis revealed the presence of modular archaeocyaths, with *Archaeocyathus* being the only genus present. The small microbial mounds of the lowermost upper unit of the Mule Spring Limestone preserve frame-building *Archaeocyathus in situ*, a few meters above the well-known *Bristolia* beds of the Mule Spring Limestone. As some of the youngest known archaeocyaths of the western US, these occurrences represent the last gasp of archaeocyaths in the early Cambrian of Laurentia and one of the latest occurrences globally of archaeocyaths. We thus interpret *Archaeocyathus* in these units as an example of a dead clade walking—some of the last true archaeocyaths that locally persisted into the later Age 4 Cambrian following the disappearance of diverse archaeocyath reefs in western Laurentia. These last archaeocyath communities exhibited low diversity and disparity before the total extirpation of this reef-building hypercalcified sponge and their ecosystem.**

INTRODUCTION

Archaeocyaths are an extinct taxon of aspiculate hypercalcified sponges, and they were the first metazoan reef-builders of the Phanerozoic (Wood et al. 1992b; Pratt et al. 2000; Rowland 2001). The first appearance of archaeocyaths occurred in the middle of the Cambrian Age 2 pre-dating the first appearance of trilobites, and they reached a peak in diversity of over 600 species around the boundary of stages 3 and 4 (Cambrian Series 2) (Zhuravlev and Naimark 2005). Archaeocyathan reefs occurred on multiple paleocontinents including Siberia, Laurentia (North America), West and East Gondwana (Morocco, south-western and central Europe, Antarctica, Australia), South China, and on a number of microcontinents which are now in foldbelts of Central Asia (Debrenne 1959; Zhuravleva 1960; James and Kobluk 1978; Savarese and Signor 1989; James and Gravestock 1990; Hicks 2001; Rowland and Shapiro 2002). These reefs were widespread in low-latitude, shallow marine environments on continental shelves in both low and high energy settings (Hicks 2001; Adachi et al. 2014; Pruss et al. 2019).

Archaeocyath reef building was a geologically short-lasting ecological experiment with the extinction of archaeocyaths occurring by the end of Cambrian Series 2 (Zhuravlev and Wood 1996; Pratt et al. 2000; Rowland and Shapiro 2002). However, the exact timing of their local disappearance varied regionally. Furthermore, it has been unclear whether the local extinction of archaeocyath reefs marks the last occurrence of archaeocyaths in those particular regions (Pruss et al. 2019) or if some groups of archaeocyaths persisted beyond the last development of robust reefs until the Drumian Age (Wood et al. 1992b; Bassett-Butt 2016). Archaeocyaths became locally extinct in South China, Australia, and on the Siberian Platform in the middle of Age 4 (Toyonian) while in the Altay Sayan Fold belt they may have persisted to late Age 4 (Zhuravlev and Wood 1996; Yang et al. 2016; Kruse et al. 2017).

It is believed that the ultimate demise of most, if not all, archaeocyaths may have been triggered by a two-pulsed event in the Cambrian Age 4 (Zhuravlev and Wood 1996). Its first phase, referred to as the 'Sinsk event', is characterized by deposition of bituminous, varvite-like, black shales with a number of isotope and element redox indicators of euxinic to low oxic conditions (Zhuravlev and Wood 1996, 2018). This extinction has been observed from sites globally from the lower Stage 4 Cambrian. This first phase shows evidence for shallow-water anoxia that could have resulted in stress in tropical shallow marine environments inhabited by many early Cambrian taxa (Liu et al. 2018; Wood et al. 2019; He et al. 2019; Langsford et al. 2020). The second, later phase of extinction has been linked to both the Age 4 (early Toyonian) presumably global regression c. 511–509 Ma (Zhuravlev 1996) and to an atmospheric perturbation from the Stage 4-Wuliuan large Kalkarindji continental flood basalt eruption c. 510–500 Ma (Marshall et al. 2018, 2021), with the exact nature, trigger, and timing of this later extinction disputed.

Along the Cordilleran margin of Laurentia, in the present-day southwestern United States, archaeocyaths first occur in reefs in the lower Stage 3 Montenegro Member of the Campito Formation (McKee and Gangloff 1969) (Fig. 1). These reefs are restricted to strata bearing trilobites of the *Esmeraldina rowei* assemblage zone (Cambrian Stage 3; upper Atdabanian *Judomia* Zone of the Siberian Platform; Hollingsworth 2011). Archaeocyaths occur abundantly in the overlying Poleta and Harkless formations (upper Stage 3 to mid-Stage 4), with well-developed and extensively studied reefs preserved in both units (Knopf and Kirk 1918; Nelson 1962; McKee and Gangloff 1969; Stewart 1970; Hicks 2001; Pruss et al. 2019, 2021). In the Death Valley region, the mid-shelf equivalent of these outer shelf strata, the lowest and to-date only

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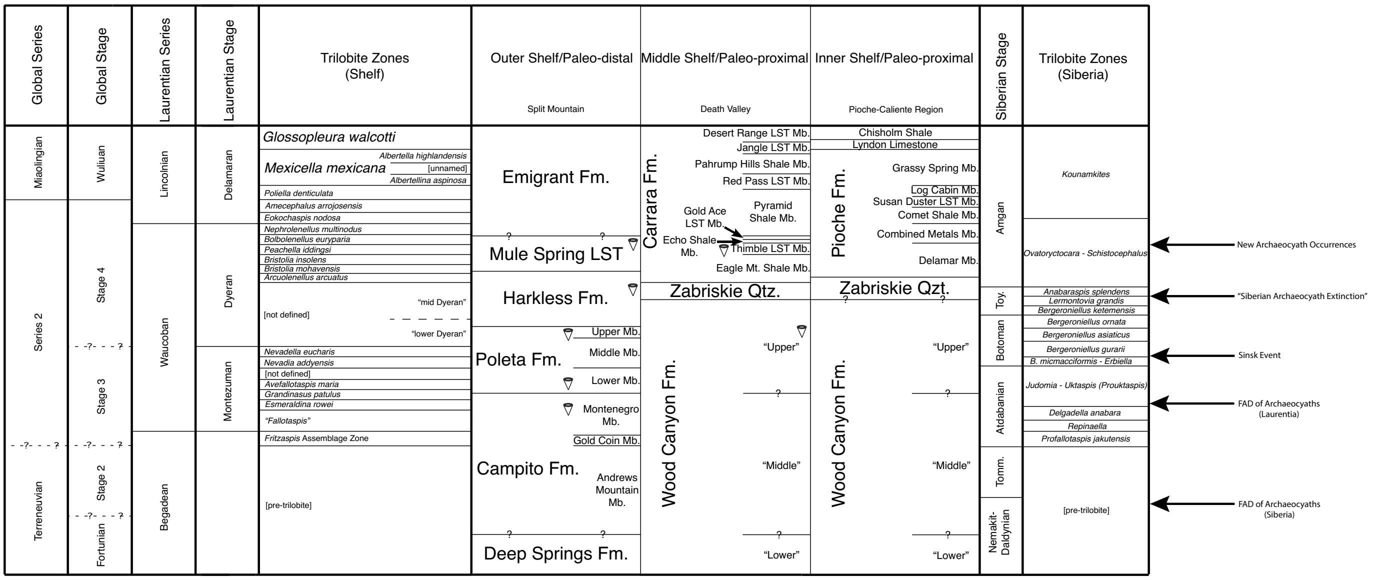

FIG. 1.—Provisional litho- and biostratigraphic correlation chart for the lower Cambrian in the southwestern United States (Cordilleran margin of Laurentia). Lithostratigraphic columns are shown for the outer shelf, the middle shelf, and (for completeness) the inner shelf, typified by the successions at Split Mountain, the Death Valley region, and the Pioche-Caliente region, respectively. Vertical scale is arbitrary and non-linear; relative thicknesses of litho- and biostratigraphic units are distorted. Rightmost two columns show working hypothesis of correlation between these Laurentian successions and Siberian stages and trilobite zones, as summarized in text. Question marks and dashed lines indicate as-yet-undefined or poorly constrained boundaries. Modified and updated from Webster (2011b) and Webster and Bohach (2014). Abbreviations: Fm. = Formation; LST = Limestone; Mb. = Member; Qtz. = Quartzite; Tomm. = Tommotian; Toy. = Toyonian. Cartoons of conical archaeocyaths in lithostratigraphic columns depict occurrences mentioned in text. Arrows to right of chart identify timing of key events in archaeocyath history.

archaeocyath occurrence can be found in limestone beds in the upper member of the Wood Canyon Formation (Cambrian Stage 3; Hunt and Mabey 1966; Stewart 1970). Despite efforts to search for archaeocyaths in younger strata across the Great Basin, and some references to isolated archaeocyaths occurring in higher intervals of Stage 4 (Nelson 1962; Hunt and Mabey 1966; Palmer and Nelson 1981), no archaeocyathan reefs had been reported from units overlying the last patch reefs in the upper Harkless Formation in the outer shelf succession (Cordie et al. 2020) or from above the Wood Canyon Formation in the mid-shelf succession. While the last robust archaeocyathan reefs of western Laurentia occur in the Cambrian Stage 4 Harkless Formation, it remains unclear whether their subsequent disappearance represented a mass extinction of all archaeocyaths, the local disappearance of reef-building, or a local extinction of Laurentian archaeocyaths. With questions like these plaguing the record of archaeocyath extinction, and with the uncertainty surrounding a global biostratigraphic framework for this time interval, it is critical to examine each of the last archaeocyath occurrences, in this case from Laurentia, their extinction interval and paleoecology to determine the exact nature of the local, and ultimately global, extinction of the first animal reef-building clade.

Here we provide detailed facies and paleoecological analyses of newly discovered archaeocyath occurrences from the Mule Spring Limestone near Split Mountain, Nevada, and the Thimble Limestone Member of the Carrara Formation in Death Valley (Fig. 2), which are the youngest known archaeocyaths on Laurentia (upper Stage 4). This last occurrence demonstrates that archaeocyaths persisted on Laurentia well beyond the collapse of their reef-forming heyday. Furthermore, after the collapse of archaeocyath reefs, the Mule Spring Limestone occurrence demonstrates that archaeocyaths continued to construct buildups despite being rare elements of the benthic community overall. The discovery of these new occurrences shows persistence of archaeocyaths in reef settings, even after the disappearance of robust patch reefs in the Harkless Formation, contrary to previous reports (Pruss et al. 2019; Cordie et al. 2020). As the sole surviving member of the archaeocyaths in Laurentia, we propose that these occurrences represent a "dead clade walking" as a persistent group beyond its principal stratigraphic range and with a reduced ecological role (Jablonski 2001, 2002; Barnes et al. 2021).

GEOLOGIC SETTING

Lithostratigraphy

Cambrian strata of the southwestern United States in our study area were deposited along a passive continental margin off what was the northwestern coast of Laurentia. These strata can be divided into an outer shelf succession in the more northern and western exposures and a correlative mid- and inner-shelf succession in the more southern and eastern exposures (Nelson 1962; Stewart 1970) (Fig. 2). The Mule Spring Limestone is part of the outer shelf succession well known from exposures in the White and Inyo ranges of eastern California and several ranges in Esmeralda County, Nevada (Nelson 1962, 1978; McKee and Gangloff 1969). Underlying the Mule Spring Limestone in the White-Inyo strata are, in ascending order, the Deep Spring, Campito, Poleta, and Harkless formations, and in some places, the Saline Valley Formation (Nelson 1962; McKee and Gangloff 1969; Stewart 1970; Ahn et al. 2012). Overlying the Mule Spring Limestone is the Emigrant Formation (Nelson 1962; Stewart 1970).

The Mule Spring Limestone is composed of blue-gray, very finely crystalline limestone and dolostone, and includes minor interbeds of gray shale (Nelson 1962; Stewart 1970; Webster 2011a, 2011b). The presence of oncolitic and fenestral structures in the upper unit has been interpreted to record subtidal to supratidal deposition (Stewart 1970; Webster 2011a, 2011b; Cordie et al. 2020). In the region of Split Mountain in Clayton Ridge (NV), where the Mule Spring Limestone is well exposed and thick, Webster (2011a) divided it into informal lower, middle and upper units. The lower unit (~ 30 m) consists of cliff-forming burrow-mottled limestone with oncolitic beds. The middle unit (~ 24 m) is a recessive interval of burrow-mottled carbonate and bioclastic limestone with oncolitic beds and interbedded shale. The upper unit (~ 170 m) is a cliff-forming unit composed predominantly of oncolitic limestone, with minor intraclastic conglomerate and fenestral limestone. The archaeocyaths in this study are found within small microbial mounds preserved near the base of the upper unit, with a few scattered occurrences of archaeocyaths reported from higher in the upper unit.

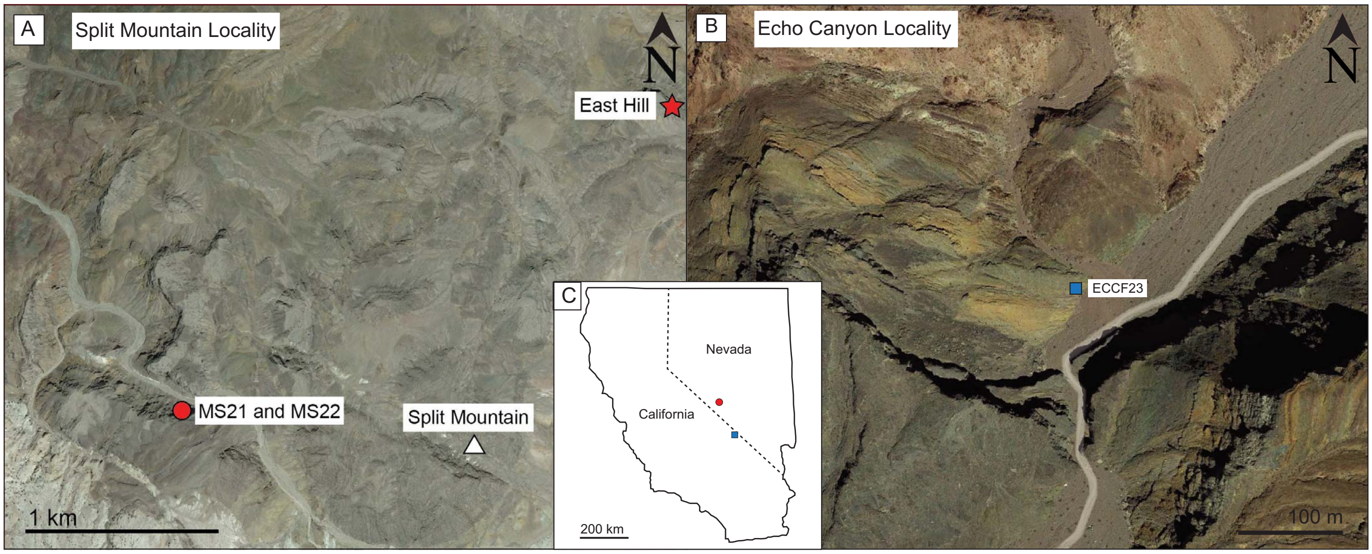

FIG. 2.—Locality maps and Google Earth images of localities. **A**) Locality map of California and Nevada. The dashed line demarcates the border between California and Nevada. The red box indicates the general location of image B; the blue box indicates the general location of image C. **B**) Locality map of Esmeralda County, Nevada containing the sampling site near Split Mountain. The red box indicates the general location of image D. **C**) Locality map of Death Valley region containing the sampling site at Echo Canyon, indicated by the red box. **D**) Google Earth image of the Split Mountain region with the 2021 and 2022 Mule Spring Limestone sample sites at West Section denoted by the red circle. The East Hillside location is indicated by the red star (Webster 2011a, 2011b; Cordie et al. 2020). **E**) Google Earth image of the Echo Canyon region of Death Valley National Park with the Thimble Limestone Member sample sites denoted by the red square labeled ECCF23.

The Carrara Formation of the middle shelf succession in the northern Death Valley region overlies the Zabriskie Quartzite, which is composed of pinkish-gray, fine- to medium-grained quartzite and siltstone (Hazzard 1937; Stewart 1970), and underlies the thickly bedded fine- to medium-grained or sandy light- to dark-gray dolostone of the Bonanza King Formation (Hazzard and Mason 1936; Hunt and Mabey 1966) (Fig. 2). The Carrara Formation consists of interbedded limestone and siliciclastic facies and has been subdivided into nine members including the Eagle Mountain Shale, Thimble Limestone, Echo Shale, Gold Ace Limestone, Pyramid Shale, Red Pass Limestone, Pharump Hills Shale, Jangle Limestone, and Desert Range Limestone members (Hunt and Mabey 1966; Palmer and Halley 1979; Adams and Grotzinger 1996). Of those, the lowest four are correlative with the Mule Spring Formation (Palmer and Halley 1979; Webster 2011a). The Carrara Formation outcrops throughout much of the Death Valley region and has been interpreted as representing shallow-water facies, including lagoon, intertidal, and subtidal settings (Palmer and Halley 1979; Adams and Grotzinger 1996). In Echo Canyon of the Funeral Mountains (CA), the Eagle Mountain Shale member is in contact with the underlying Zabriskie Quartzite; it conformably grades into the Thimble Limestone Member, which is composed of shale, siltstone, sandstone, thin silty carbonates, and thrombolites. The thin limestone beds are 0.3 to 1 m-thick throughout the ~ 25 m thick Thimble Limestone Member, with shale and siltstone interbedded, and the archaeocyaths in this study are found in a lenticular limestone ~ 5 m above the base (Fig. 3).

Biostratigraphy on Regional and Global Scales

In the southwestern United States—including at the archaeocyath-bearing localities documented herein—a high-resolution biostratigraphic zonation is being developed for the Laurentian Waucoban Series (Cambrian Series 2) using trilobites (e.g., Palmer and Halley 1979; Hollingsworth 2011; Webster 2011a, 2011b; Sundberg and Webster 2021, 2022; Sundberg et al. 2022; Fig. 1). Within this framework, the Mule Spring Limestone falls within the upper Dyeran Stage, spanning the *Bristolia mohavensis* to *Bolbolenellus euryparia* trilobite biozones (Webster 2011a, 2011b; Sundberg and Webster 2021, 2022). The archaeocyath occurrences within the Mule Spring Limestone occur within the upper *Peachella iddingsi* Zone and/or *Bolbolenellus euryparia* Zone. The Carrara Formation spans the upper Dyeran to Delamaran stages, with trilobites of the *Peachella iddingsi* and *Bolbolenellus euryparia* zones occurring within the Thimble Limestone Member (Palmer and Halley 1979; Webster 2011b); the archaeocyath occurrence lies within the *Peachella iddingsi* Zone.

A robust global chronostratigraphic scheme for the pre-Miaolingian portion of the Cambrian is yet to be developed (see Peng et al. 2020 for a recent status report). In the absence of a tightly refined scheme for correlation on a broader paleogeographic scale, it is difficult to precisely determine how the timing of events in archaeocyath history on Laurentia relate to events on other paleocontinents. A working hypothesis of correlation between Laurentia and Siberia—incorporating both regional and global biostratigraphic constraints and updating that of Peng et al. (2020) based on recently published data (e.g., Sundberg et al. 2022)—is shown in Figure 1 and is adopted herein. This hypothesis should be tested and refined with future biostratigraphic, geochronological and chemostratigraphic work.

METHODS

The small archaeocyathan reef mounds of the Mule Spring Limestone were first observed in the Split Mountain West section (by MW in summer 2005 while measuring the Mule Spring Limestone) and subsequently located and sampled by SBP and EFS during summer of 2021 and 2022 (37°42′44.16″N, 117°28′20.79″W) (Fig. 2A). A 1.1 m-thick section of the basal portion of the upper unit of the Mule Spring Limestone containing six small 40 cm-thick microbial mounds was described and sampled (MS21; Fig. 3A, 3B). Six oriented samples from mounds were collected—with two samples from mound 2—as well as samples from inter-reefal facies and from the underlying horizon. This small microbial mound horizon was revisited during the summer of 2022 for additional observations and supplemental sample collection (MS22). One small, oriented sample from mound 1 and two samples of oncoid-rich talus were collected.

Sixty-seven thin sections (~ 5 cm by ~ 7.5 cm) of the Mule Spring Limestone samples were prepared, with all of the oriented mound samples

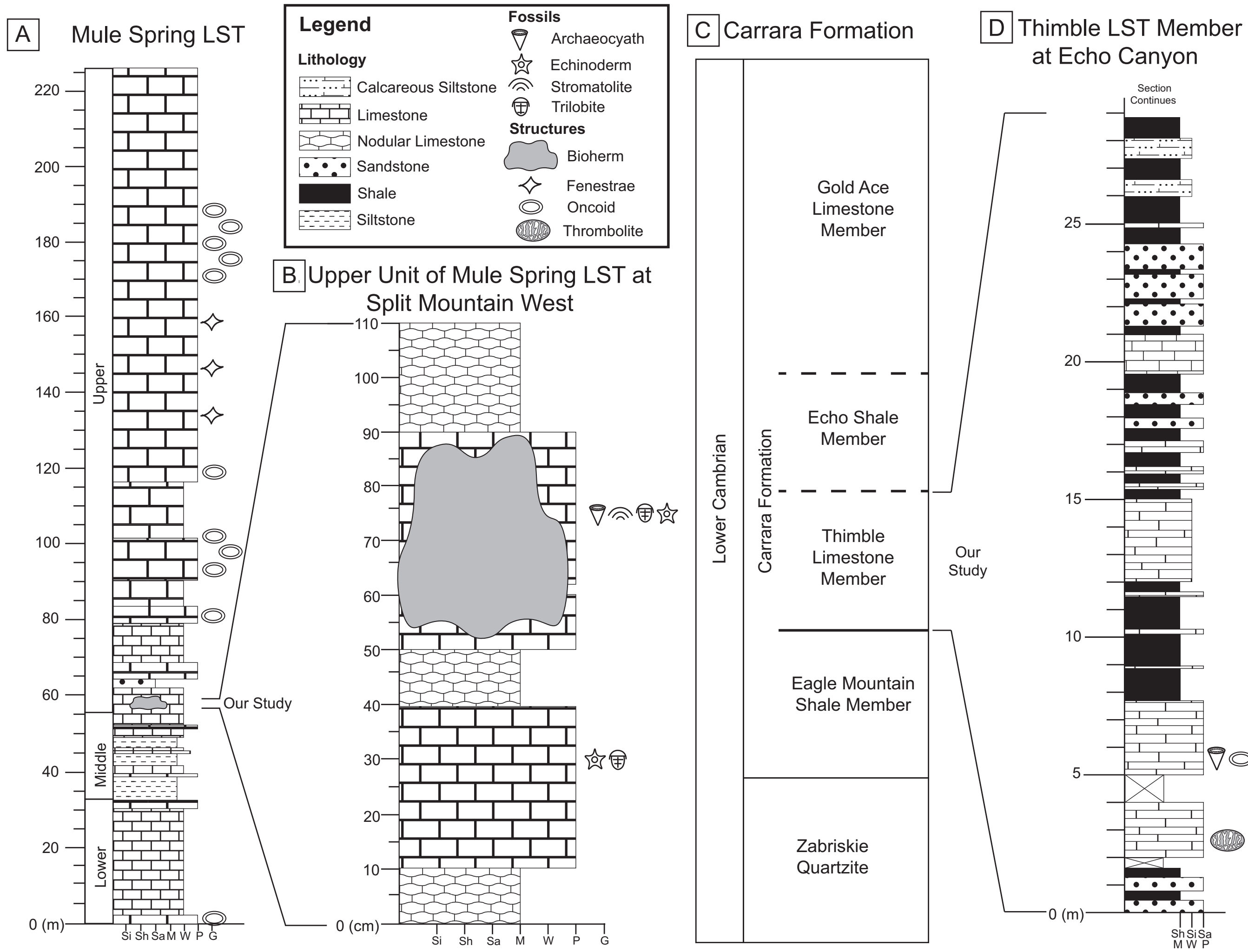

FIG. 3.—Stratigraphic columns. **A**) Lower, middle, and upper units of the Mule Spring Limestone, derived from Webster (2011a, b). **B**) Measured stratigraphic column of the lower portion of the upper unit of the Mule Spring Limestone at the Split Mountain West section, Clayton Ridge, Nevada. **C**) Stratigraphic column of the Carrara Formation with the underlying Zabriskie Quartzite and base of the Carrara Formation adapted from Adams and Grotzinger (1996). **D**) Measured stratigraphic column of the Thimble Limestone Member at Echo Canyon.

cut into smaller samples and made into thin sections to view components of the reef. A total of 11 thin sections were made from mound 1; 14 from mound 2 sample 1; nine from mound 2 sample 2; three from mound 3; 13 from mound 5; and six from mound 6. Thin sections were also made from samples below and adjacent to the mounds to view the organisms and sediments deposited below and around the mounds. All Mule Spring Limestone thin sections were viewed through a petrographic microscope, described, and photographed. Archaeocyaths and microbial textures were identified and characterized. The presence or absence of reef-dwelling fossils, such as trilobites and echinoderms, was noted. All thin sections were digitally scanned on an Epson Perfection V550 Photo Scanner. Figured thin section specimens of archaeocyaths from the Mule Spring Formation are reposited at Yale Peabody Museum (specimens YPM IP 461167-72).

About 30 meters of the Thimble Limestone Member of the Carrara Formation were measured in Echo Canyon in Death Valley National Park, California by SP (36°28′17.33″N, 116°45′11.13″W) (Fig. 2B). Two samples were taken from thrombolitic mounds about 3 m above the base of the Thimble Limestone, but no archaeocyaths were found in those. After visible recognition of archaeocyaths on an oncoidal bedding plane, eight samples were collected from meter 4.95 (Fig. 3C, 3D), six of which had visible archaeocyaths. The surfaces of those six samples that contained archaeocyaths were examined and imaged under a light microscope. Additionally, 16 thin sections (~ 5 cm by ~ 7.5 cm) of the Carrara Formation samples, including those containing archaeocyaths, were prepared and viewed under a petrographic microscope, and fossil presence/absence was noted. All thin sections were digitally scanned on an Epson V800 Photo Scanner. Figured thin section and hand sample specimens from the Carrara Formation are reposited at the Yale Peabody Museum (specimens YPM IP 461173-80).

RESULTS

Field Observations

Mule Spring Limestone.—The base of the upper unit of the Mule Spring Limestone is characterized by gray and orange limestone with ribbon-bedded limestone, followed by two 7 cm-thick horizons of fossiliferous and intraclastic packstone (Fig. 3A, 3B). These beds are overlain by a 0.40 m-thick patch-reef horizon that consists of six small reef mounds that are spread out laterally across 20 m (Fig. 4A). This reef horizon is in turn overlain by the ribbon-bedded gray and orange limestone with oncoids (Fig. 4B, 4C), a common facies within the upper unit of the Mule Spring

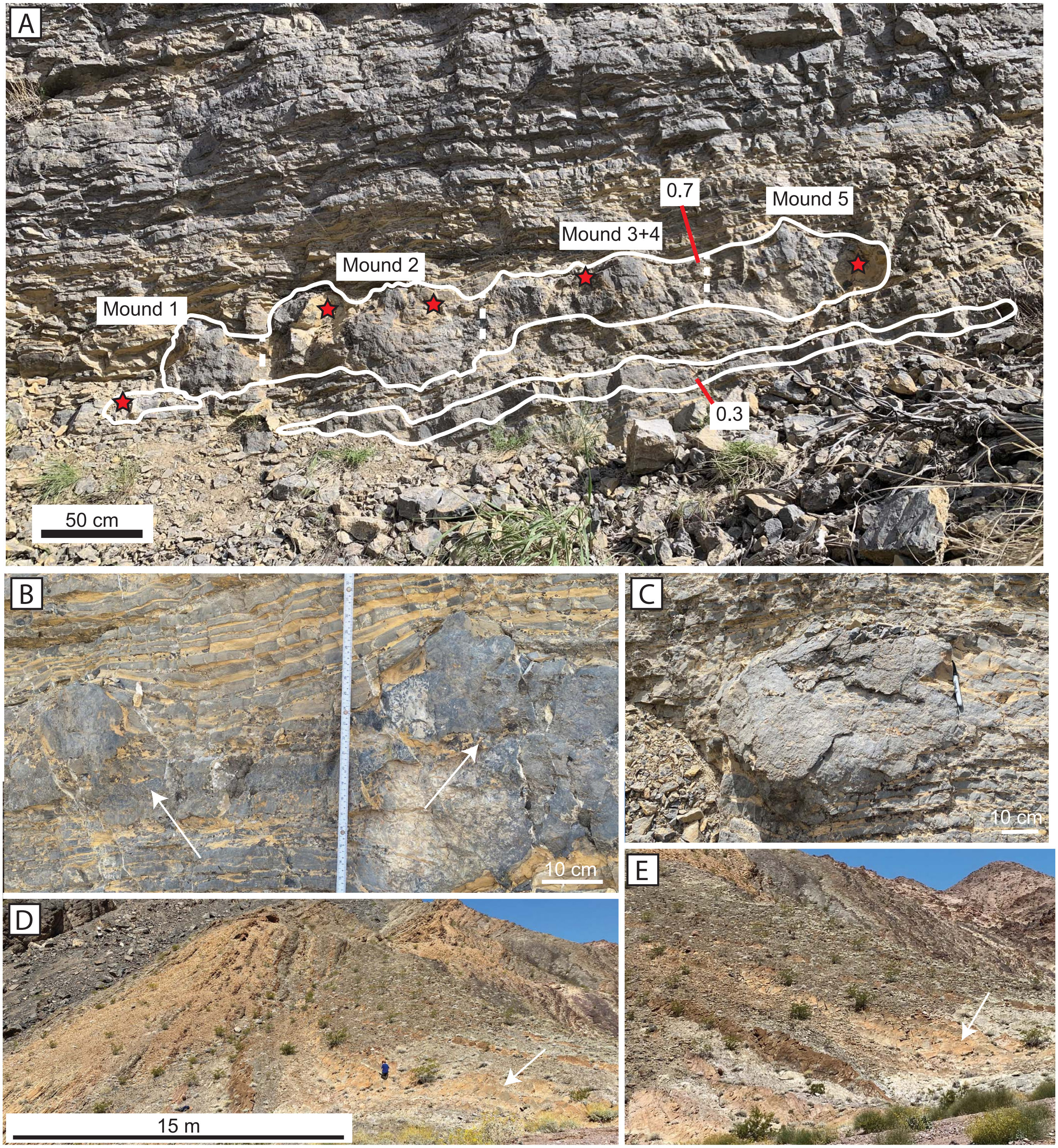

FIG. 4.—Outcrop photographs of the Mule Spring Limestone and Thimble Limestone Member of the Carrara Formation containing *Archaeocyathus*. **A**) Outcrop photograph of the small microbial mounds exposed at the base of the upper member of the Mule Spring Limestone at Split Mountain showing all mounds that were sampled, except mound 6 which occurred along strike and was out of the field of view. Stars show location of samples. **B**) Zoomed in photograph of mounds 3 + 4 and 5 from image A, arrows indicating mounds. **C**) Outcrop photograph of mound 6 (not shown in A). **D**) Outcrop photograph of the Thimble Limestone Member of the Carrara Formation. Arrow indicates bedding plane preserving archaeocyaths in an oncoidal limestone. **E**) Close-up photograph of the Thimble Limestone bedding plane preserving archaeocyaths as clasts; arrow indicates location of bedding plane preserving archaeocyaths.

Limestone at Split Mountain. A small fault passed through this reef horizon, offsetting the left and right sides of mound 2. Mounds 1 and 6 contained archaeocyaths that were visible in the field.

Carrara Formation.—At Echo Canyon, the Thimble Limestone Member was composed of shale, siltstone, sandstone, and silty carbonate beds. The silty carbonate beds contain abundant oncoids, trilobite and echinoderm hash, sponge spicules and, in a single bed, archaeocyaths. About 2 m above the base of the measured section, a lenticular oncolitic bed is exposed that laterally grades into thrombolite mounds. These thrombolite mounds were sampled, but no archaeocyaths are present in the mounds. About 5 m from the base of the first limestone ledge (Fig. 4D, 4E), archaeocyaths were found as round/oval- to irregularly shaped clasts (about 2–3 cm in diameter). In some instances, archaeocyaths had 1 to 2-mm thick micritic rims around their exteriors with oncoidal textures. This was the only unit that was found to preserve archaeocyaths at Echo Canyon.

Petrographic Observations

Mule Spring Limestone.—Petrographic examination of thin sections from the Mule Spring Limestone reveals a singular modular archaeocyath, which consists of a parental cup and outgrowths (Fig. 5). The outgrowth morphology is identical to the intervallar structure of the parental cup but a central cavity was not formed (Fig. 5D). These outgrowths connect the parental cup either with an adjacent cup or with a microbial substratum (Fig. 5C, 5D). Associated reef-dwelling organisms throughout all microbial mounds as well as areas between or below the microbial mounds exhibit trilobite fragments with rarer echinoderm plates (Figs. 6, 7). Archaeocyaths were found in all small microbial mound samples (Fig. 4A). They are closely associated with microbial fabrics, like stromatolitic and thrombolitic textures, which make up the bulk of the samples (Fig. 7A). Trilobite fragments, echinoderm debris, peloids, and stromatolites are most abundant between mounds (Figs. 6C, 7D). Additionally, there are possible burrows in the micritic-dolomicrite matrix between the reef mounds, present as vertical structures filled with dolomicrite while the hosting rock is composed of micrite (Fig. 6D). Thrombolitic and encrusting microbial textures are also present in samples from the fossiliferous and intraclastic packstone underlying the mounds as well as trilobite and echinoderm fossil debris and peloids. Lastly, intraclasts of micrite and echinoderm debris are most abundant in the fossil packstone underlying the microbial mound horizon (Fig. 6A, 6B).

Carrara Formation.—Petrographic examination of the Thimble Limestone Member revealed a few archaeocyath specimens not associated with any reef mounds (Figs. 8, 9). Only one modular archaeocyathide species was found at this locality. Archaeocyaths appear as clasts (2–3 cm wide), most of which had developed a visible microbial coating like oncoid laminae (Figs. 8, 9). The archaeocyaths (1 cm in diameter) are preserved in a ~ 1–2-m-thick lenticular bed with similarly sized oncoids, and trilobite and other fossil debris.

DISCUSSION

The archaeocyaths in the Mule Spring Limestone and Carrara Formation represent the archaeocyathide genus *Archaeocyathus*. This genus is characterized by a cup with an outer wall with pores restricted to cells formed by intervallar elements. The intervallum contains taeniae and the inner wall has one pore row per intercept and pore tubes in larger cups; taeniae are three-dimensional radial plates that are coarsely porous (Peng et al. 2020) (Figs. 5D, 8A, 8D, 9E). This genus was modular, and its parental cups produced underdeveloped daughter cups in the form of outgrowths, repeating the structure of both walls and the intervallum but without a well-developed central cavity, and this is observed in Mule Spring archaeocyath occurrences (Fig. 5A, 5C, 5D). Because the Carrara archaeocyaths were preserved as clasts, less can be determined about their life habit and morphology. This is the only archaeocyath genus found to persist in strata younger than the archaeocyathan reefs of the Harkless Formation.

The Mule Spring Limestone and Carrara Formation archaeocyaths represent the youngest occurrences in the Great Basin, occurring stratigraphically above what had been interpreted as the youngest archaeocyathan reefs in the western United States (Pruss et al. 2019) during an interval that had been deemed a "reef eclipse" (Cordie et al. 2020). In the Mule Spring Limestone, *Archaeocyathus* occurred *in situ* as framebuilders forming a three-dimensional frame for the small microbial mounds. These mounds are restricted to the base of the upper unit observed in this study. In this role, the archaeocyaths still occupy the framework building guild like their earlier reef constructions (Fagerstrom 1991) but show a reduced role ecologically, with an absence of archaeocyaths behaving as coelobionts bafflers, etc. With only one genus persisting into the Mule Spring, they also show a lower overall diversity relative to the underlying Harkless reefs. Archaeocyaths found stratigraphically higher than the Mule Spring bioherm interval appeared as debris in a limestone bed 8.2 m above the base of the upper unit and in possible lag deposits 60.23 m above the base of the upper unit (MW, personal observation).

In the Carrara Formation, archaeocyaths have been mentioned as occurring in the Gold Ace Limestone Member at Titanothere Canyon in Death Valley (Palmer and Halley 1979; Palmer 1981; Palmer and Nelson 1981, p. 21), but such occurrences have not been thoroughly documented or figured. The present report thus represents the first imaged and described archaeocyath from the Thimble Limestone Member of the Carrara Formation. The purported occurrence of archaeocyaths in the Gold Ace Limestone Member (*Bolbolenellus euryparia* Zone) would be slightly younger than the Thimble Limestone occurrence and probably of approximately the same age as the Mule Spring Limestone occurrences documented herein, but this report remains unconfirmed.

Environmental Interpretations

Paleoenvironment of the Mule Spring Limestone.—The observed section of the upper Mule Spring Limestone in this study was deposited in a shallow subtidal marine environment (Nelson 1962; Stewart 1970; Webster 2011a, 2011b). Underlying the reef horizon, the presence of fossiliferous-intraclastic packstone composed of rip-up clasts and trilobite fragment debris indicates the occurrence of high-energy storm events (Cordie et al. 2020). In the microbial mound horizons of the Mule Spring Formation, the archaeocyaths were preserved in situ as frame-builders, which used their thick skeletal outgrowths to strengthen their mutual attachment and to attach to abundant microbial fabrics within the mounds (Fig. 5). The prevalence of stromatolites between the reef mounds suggests a lower energy environment (Usychenko 1988; Wood et al. 1993), but one that periodically experienced wave/storm activity which deposited intraclasts and fossil debris around the stromatolites (Figs. 6, 7). Furthermore, the abundance of dissolution surfaces within the mounds shows hiatuses in carbonate deposition where both archaeocyaths and stromatolites colonized hardground surfaces (Fig. 7A, 7B). The presence of thrombolitic fabrics within the mounds indicates that they likely formed in a shallow subtidal paleoenvironment (Pratt et al. 2000), where the interaction between skeletal organisms and microbes shaped the microbial fabrics within the mounds (Pruss and Knoll 2017). These findings are consistent with previous research that placed the upper unit of the Mule Spring Limestone in a shallow subtidal setting within a larger carbonate shoal on the outer shelf (Webster 2011a, 2011b).

Paleoenvironment of the Carrara Formation's Thimble Limestone Member.—Beds in the Thimble Limestone Member of the Carrara Formation preserve archaeocyaths as clasts in silty fossil packstone composed of oncoids, trilobite and other fossil debris. These facies appeared similar

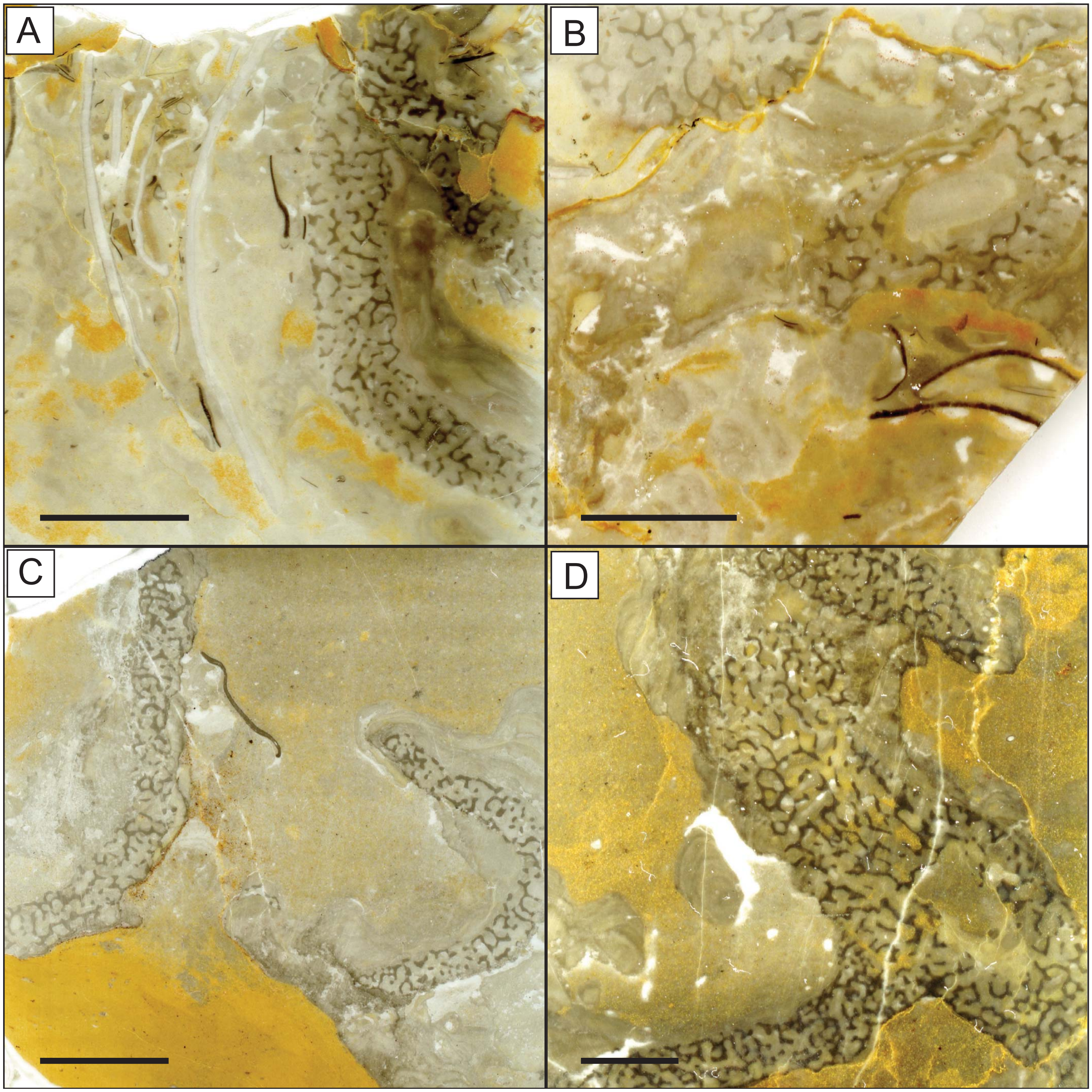

FIG. 5.—Digital scans of thin sections with *Archaeocyathus* cups and their outgrowths of Mule Spring Limestone samples. All panels show the close association between archaeocyaths and microbial fabrics and are oriented in the upward direction in which the samples were collected. **A**) Fragments of trilobite carapaces (on the left) and *Archaeocyathus* cup and outgrowth (on the right) (YPM IP 461167). **B**) Two fragmented *Archaeocyathus* cups and trilobite carapaces (dark concave plates in the right lower corner) in cross sections (YPM IP 461168). **C**) Two longitudinal sections of *Archaeocyathus* outgrowths, the right of which shows an attachment to thrombolite (YPM IP 461169). **D**) An *Archaeocyathus* cup (oblique-longitudinal section) with an outgrowth (YPM IP 461170). All scale bars = 5 mm.

to the Mule Spring Limestone samples collected below the reef mounds, which likely experienced periodic high-energy storm events. This suggests that the archaeocyaths in these storm deposits may have been allochthonous, having lived in a nearby shallow marine setting and transported to a deeper environment (Figs. 8C, 8D, 9D). The underlying thrombolites did not preserve any archaeocyaths, so the Carrara archaeocyaths at this locality were not associated with a patch-reef setting.

The Disappearance of Archaeocyathan Reefs

Laurentia.—No localities of either Cordilleran Canada or the Appalachian Laurentia preserve archaeocyaths of a coeval or younger age following a correlation by both trilobite and archaeocyath assemblages; all Laurentian occurrences outside of the Great Basin belong to the lower Stage 4 or to the Botoman Stage of the Siberian time scale (Voronova et al. 1987; Mansy et al. 1993; McMenamin et al. 2000). Similar conclusions follow from correlations

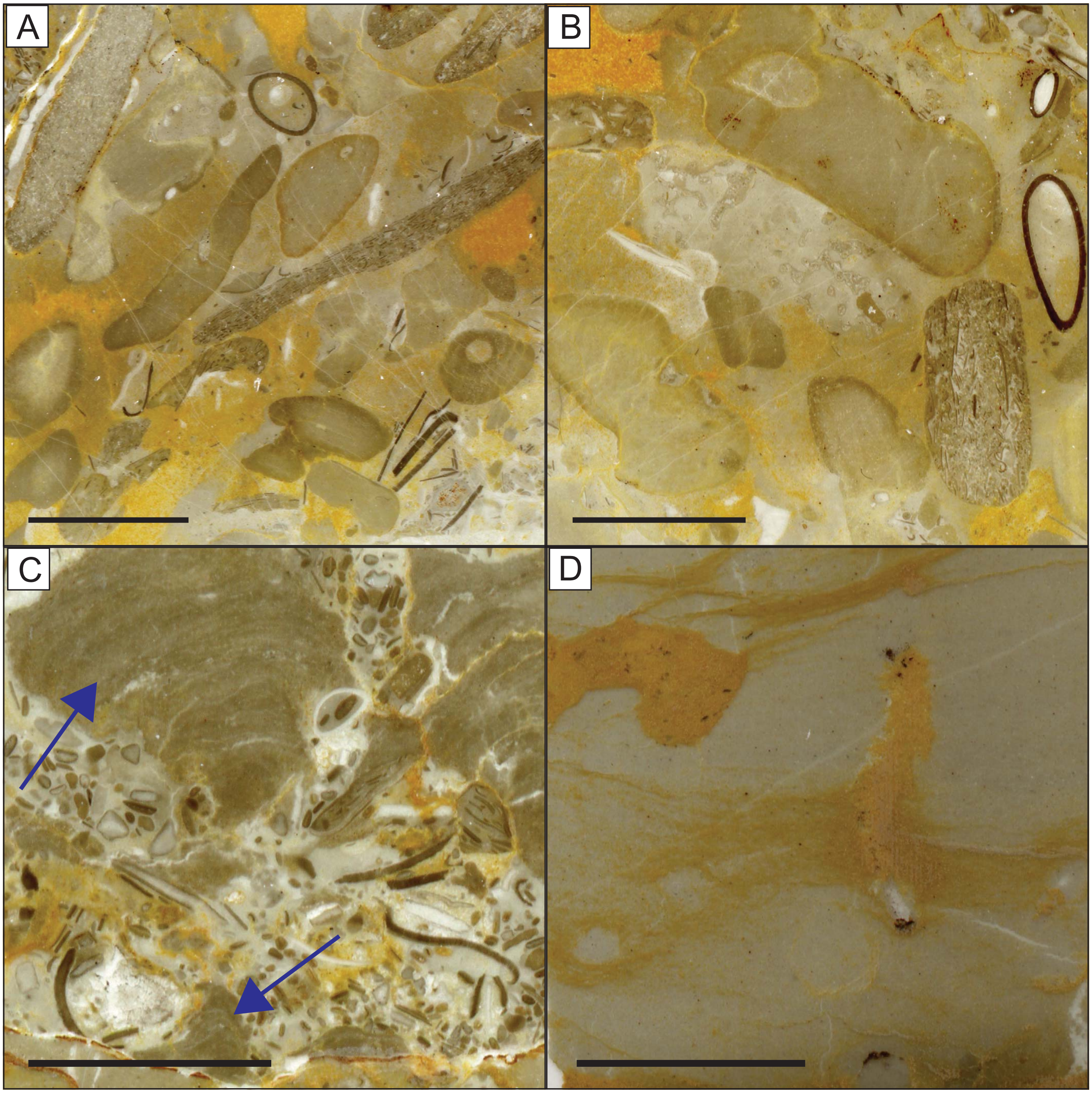

FIG. 6.—Digital scans of thin sections from Mule Spring Limestone. **A**, **B**) Samples collected from inter-reef floatstone and containing conchs of hyoliths (dark ellipses), echinoderm plates (labyrinthine pieces), and rounded fragments of grainstone and mudstone (MS21-0.3-1 and 0.3-3 respectively). **C**) A sample collected from below the reef mounds showing grainstone consisting of microstromatolites, trilobite carapace and hyolith conch fragments and peloids. Blue arrows indicate stromatolitic fabrics (MS21-0.7-2). **D**) A sample collected from below the reef mounds showing bioturbated mudstone; burrows are enriched in iron giving them a darker (orange) tint (MS21-0.7-4). All scale bars = 5 mm.

using $\delta^{13}C_{carb}$ data indicating an absence of archaeocyaths in Canadian Rocky Mountains above the $\delta^{13}C_{carb}$ positive excursion VIII according to the Siberian $\delta^{13}C_{carb}$ record (Dilliard et al. 2007). The archaeocyath assemblages of Alaska (Debrenne and Wood 1990; Gangloff 1990) and Washington (Hampton 1979) do not differ in age from those of the upper Campito, Poleta, and lower Harkless formations either (Voronova et al. 1987; Mansy et al. 1993).

Two Laurentian assemblages have been interpreted as younger, middle Stage 4 (Toyonian) ones. These are archaeocyaths from the Buelna Formation of Sonora, northwestern Mexico (Debrenne et al. 1989; Mansy et al. 1993) and from the Paralleldal Formation of North Greenland (Debrenne and Peel 1986). The Buelna Formation in the Caborca area of Sonora contains diagenetically altered oncoidal wackestone-packstone and oncoid grainstone as well as cryptalgal boundstone with solitary cups of *Archaeocyathus* sp., *Protopharetra* sp., *Cambrocyathellus* cf. *C. occidentalis*, and *Coscinocyathus* sp./*Claruscoscinus* sp. (Cooper et al. 1952; Debrenne et al. 1989). It should be noted that *Protopharetra* sp. and *Cambrocyathellus* cf. *C. occidentalis* are obliquely cut cups

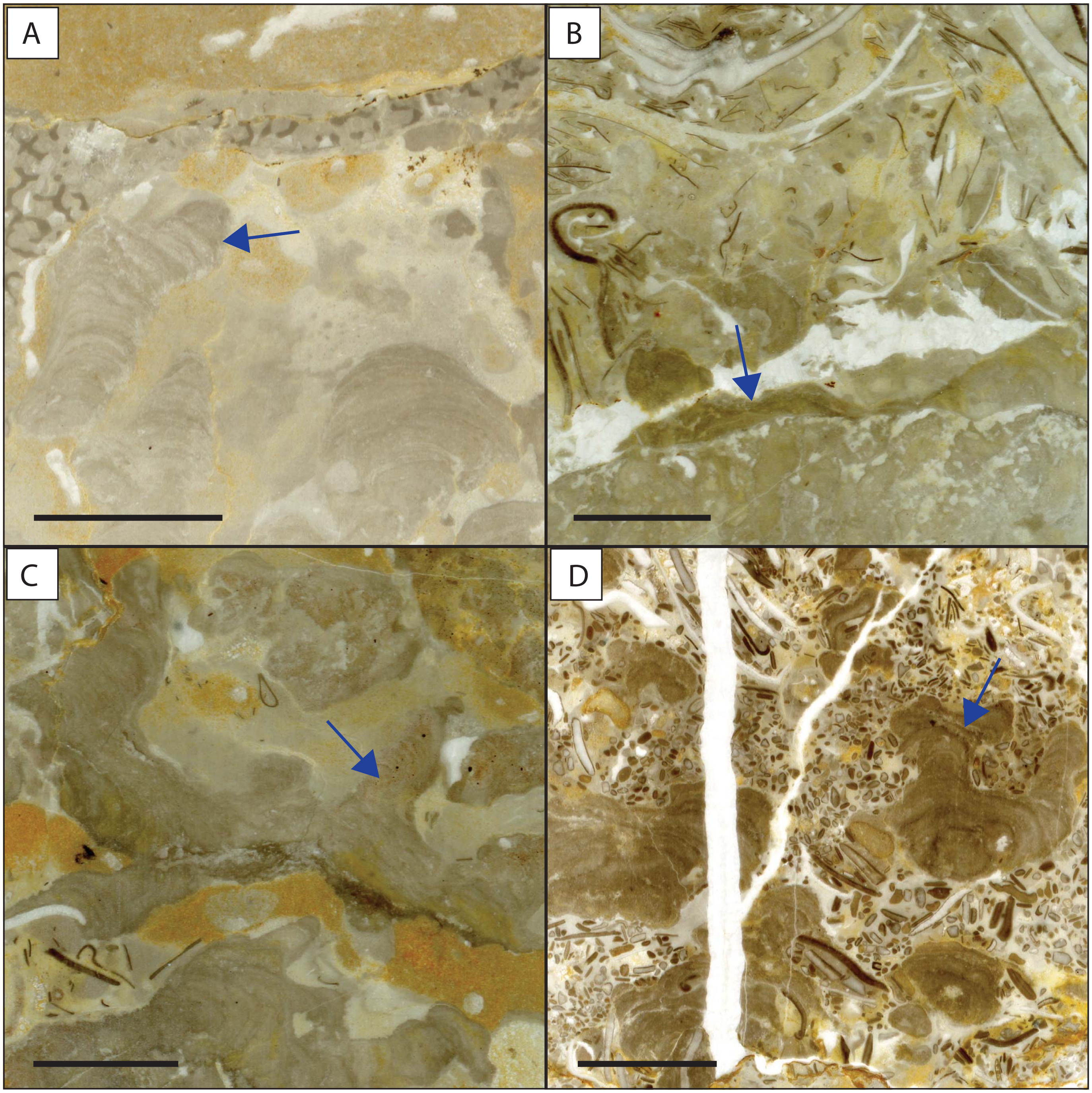

FIG. 7.—Digital scans of microbial fabrics identified in thin sections collected from the reef mound and inter-reef samples from the Mule Spring Limestone. **A**) Irregular surface of an *Archaeocyathus* cup and nearby microstromatolites (blue arrow) (YPM IP 461171). **B**) Lower thrombolitic surface encrusted by small stromatolites near the bottom of the section (blue arrow); scattered trilobite and other fossil debris deposited near the top (YPM IP 461172). **C**) Microstromatolites surrounded by carbonate mud and silt (blue arrow) with small pockets of fossil debris (MS21-2A-12). **D**) Microstromatolites surrounded by peloids, intraclasts, and fossil debris (blue arrow) within inter-reef samples (MS21-0.7-1). All scale bars = 5 mm.

of *Archaeocyathus* sp. (Mansy et al. 1993), so the diversity of this archaeocyathan assemblage is lower than previously suspected and consistent with the "dead clade walking" hypothesis (Jablonski 2001, 2002). Trilobites from the Buelna Formation indicate that the unit lies within the upper Dyeran *Bristolia mohavensis* to *Bolbolenellus euryparia* zones (Cooper et al. 1952; Webster and Bohach 2014; Cuen-Romero et al. 2018) and is therefore broadly age-equivalent to the archaeocyath-bearing strata studied herein.

Another possibly coeval archaeocyathan site occurs within the lower Paralleldal Formation of Peary Land, North Greenland and yields two species, namely, ajacicyathide *Tegerocyathus greenlandensis* and archaeocyathide *Pycnoidocyathus pearylandicus* (Debrenne and Peel 1986; Mansy et al. 1993). It has been suggested that the archaeocyath-bearing part of this formation is coeval with the trilobite-bearing Henson Gletscher Formation within Greenland (Blaker and Peel 1997; Ineson and Peel 1997; Sundberg et al. 2016). The precise trilobite zonal position of these archaeocyaths

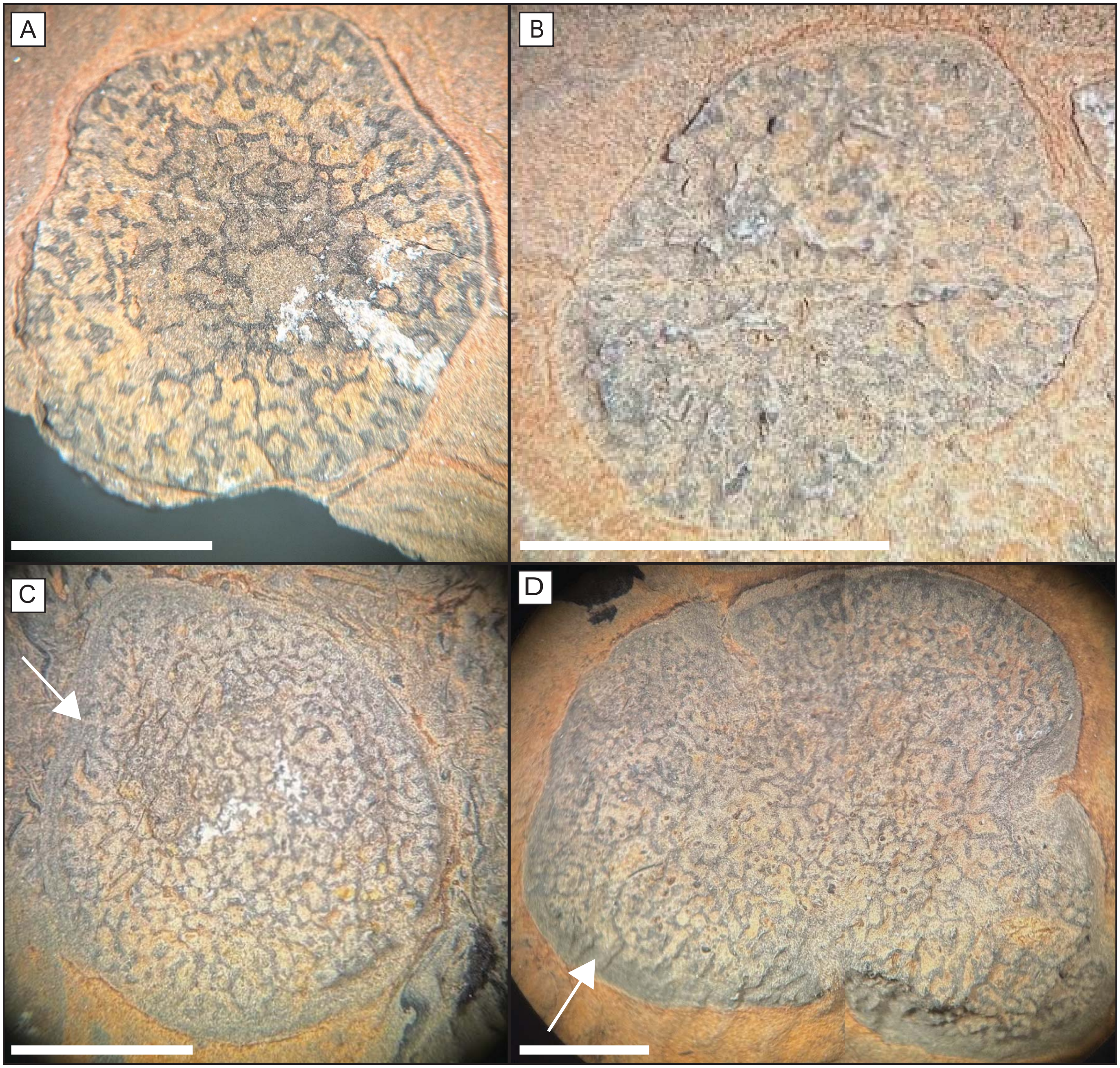

FIG. 8.—Light microscope images of the genus *Archaeocyathus* identified in Thimble Limestone Member, Carrara Formation hand samples. **A**) Slightly eroded archaeocyath (YPM IP 461178). **B**) Small archaeocyath exposed on hand sample surface (YPM IP 461179). **C**) Archaeocyath with microbial coating that was made into thin sections shown in Figure 9C, 9D. (YPM IP. 461175 and YPM IP. 461176). **D**) Largest archaeocyath from the Carrara found on hand sample surface (YPM IP 461180). White arrows show microbial coatings forming around archaeocyaths. All scale bars = 5 mm.

relative to the Henson Gletscher Formation is not resolved. Stein and Peel (2008) and Peel et al. (2016) reported the trilobite *Perissopyge phenax* occurring in the Paralleldal Formation below archaeocyaths and below the trilobites *Ogygopsis batis* and *Kootenia marcoui* and preserved together with *Fritzolenellus* cf. *F. truemani* and *Kootenia sagena* in the Henson Gletscher Formation, arguing that the archaeocyaths are potentially coeval with them. In turn, Blaker et al. (1997) reported *Perissopyge* from the basal Harkless Formation in Nevada, which would correspond to the lower portion of the Dyeran Stage (Fig. 2). However, independent of any of these suggestions, the Greenland archaeocyaths are interpreted as older than the archaeocyaths observed in the Mule Spring Limestone and Carrara Formation because the Great Basin archaeocyaths occur stratigraphically well above similar trilobites to those found associated with the "young" Greenland archaeocyaths (Fig. 1).

Thus, the Mule Spring Limestone and Carrara Formation archaeocyaths, along with possibly those of the Buelna Formation (Sonora, Mexico), are interpreted to be the youngest archaeocyaths on the entire paleocontinent of Laurentia. These occurrences of archaeocyaths are correlated with the *Peachella iddingsi* biozone and/or in the lower part of the *Bolbolenellus euryparia* biozone of the of the uppermost Cambrian

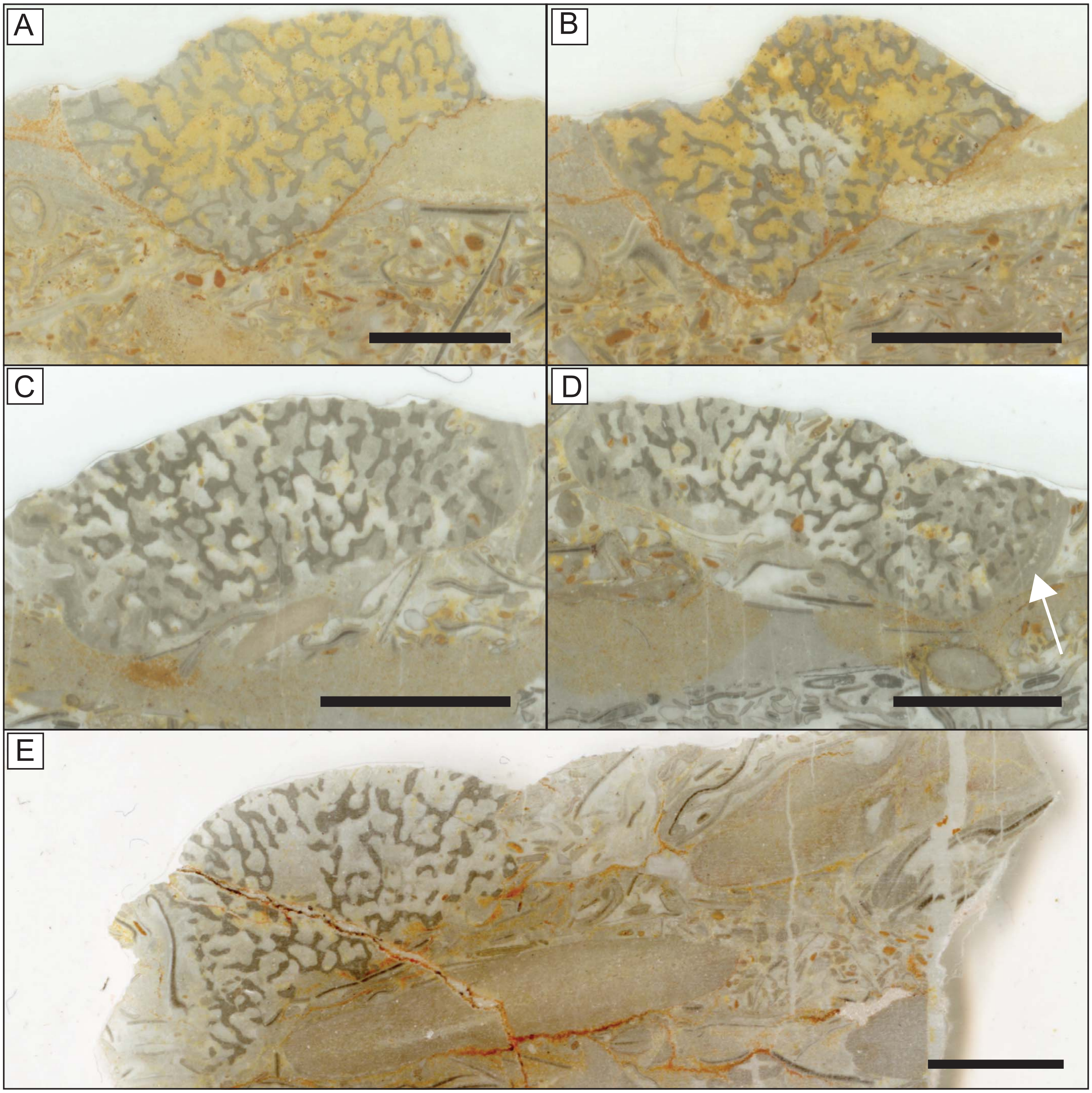

FIG. 9.—Digital scans of vertical cross sections of the genus *Archaeocyathus* identified in thin sections of the Thimble Limestone Member. **A**, **B**) The same archaeocyath specimen cut transversely in half (YPM IP. 461173 and YPM IP. 461174, respectively). **C**, **D**) Another example of a specimen of *Archaeocyathus* cut in half. White arrow in D shows microbial coating forming around archaeocyath (YPM IP. 461175 and YPM IP. 461176, respectively). **E**) An example of *Archaeocyathus* in thin section showing intraclast, trilobite, and other fossil debris associated with archaeocyath specimens in this bed (YPM IP. 461177). All scale bars = 5 mm.

Stage 4 (Sundberg et al. 2022). Thus, they are younger than any Toyonian archaeocyaths from Siberia (Fig. 1).

The Global Eclipse of Archaeocyaths

A general problem with identifying the exact disappearance of archaeocyaths globally is complicated by a common usage of the local Siberian timescale (Tommotian, Atdabanian, Botoman, and Toyonian stages in ascending order) to restrict the age of archaeocyath occurrences. These stages span the early Cambrian interval, which still lacks formally accepted subdivisions with precisely defined boundary indicators (Fig. 1). In addition, both the Botoman and Toyonian ages, which encompass nearly the entire range of archaeocyaths from their acme, near extinction, and ultimate demise, are within the Cambrian Stage 4 (Fig. 1), and these sponges disappeared almost completely before the end of this stage (Online Supplemental File). This makes using such temporal categories as 'lower, middle, or upper Stage 4' confusing. In any case, the Siberian Toyonian Stage is not the terminal lower Cambrian unit because the *Oryctocephalus indicus* first appearance datum (FAD), which defines the base of the international Miaolingian Series, is more than one trilobite zone above the Toyonian-Amgan boundary (Shabanov et al. 2008; Korovnikov and Shabanov 2016; Sundberg et al. 2022). Nonetheless, certain patterns can be identified from the global record of archaeocyaths even with the limitations of the existing timescale.

The early Toyonian archaeocyaths are thought to be present in a few localities restricted to the Altay Sayan Foldbelt because no such assemblages are distinguished in other regions (Zhuravleva et al. 1997; Sundberg et al. 2016; Yang et al. 2016). At least for the Siberian Platform, species of the middle Toyonian *Archaeocyathus okulitchi* assemblage originated from the Altay Sayan region of Mongolia, which during that time was a set of microcontinents and island arcs that collided with and accreted to the Siberian Craton (Zonenshain et al. 1985; Zhou et al. 2018; Zhuravlev et al. 2023). Very similar middle Toyonian assemblages appeared in South China (*Archaeocyathus yanjiaoensis*; Yang et al. 2016) Australia (*Archaeocyathus abacus*; Kruse 1991), and Spain (*Archaeocyathus* of Zone X; Perejón and Moreno-Eiris 2006). The re-appearance of archaeocyaths themselves after an apparent gap in their existence both locally and globally can be attributed to their survival in a refugium, from which they migrated (Zhuravlev et al. 2023), or a temporal loss of their heavily calcified skeletons (Luo et al. 2021). During the late Age 4, archaeocyaths were represented by a very limited set of species belonging almost exclusively to the archaeocyathides *Archaeocyathus* and *Pycnoidocyathus*, and the ajacicyathide *Tegerocyathus*. This low-diversity composition of archaeocyath communities around the world (Debrenne et al. 2015) points to their spreading from a single refugium.

Importantly, putative archaeocyaths have been found in even younger strata than the Cambrian Series 2/Miaolingian boundary, though not as reef builders. One occurrence is the Furongian Stage 10 archaeocyathide *Antarcticocyathus webersi,* which has been reported from the Minaret Formation of the Ellsworth Mountains in central West Antarctica (Debrenne and Kruse 1989). However, the archaeocyath affinity of the Furongian *Antarcticocyathus webersi* has been questioned recently due to a reinterpretation of its intervallar elements as calcified ladder-like trabs of an anthaspidellid demosponge (Lee 2024). In a different region of central West Antarctica, the Miaolingian Neptune Limestone of the Neptune Range preserves a different archaeocyathide *Dictyocyathus neptunensis* (Debrenne et al. 1984; Wood et al. 1992a) but these do not occur in or associated with reefs.

The new archaeocyath assemblage composed only of *Archaeocyathus* from southwestern Laurentia reported here, as well as those described from Mexico, appear to correlate to the lower Amgan stage of the Siberian Platform as a result of newly described trilobites including *Oryctocephalops frischenfeldi* and *Ovatoryctocara* cf. *O. yaxiensis* from the Saline Valley Tongue of the Harkless Formation at Split Mountain of Nevada (Sundberg et al. 2022). Similar trilobites are present on the Siberian Platform in the basal Amgan stage (Shabanov et al. 2008; Korovnikov and Tokarev 2018). Thus, the Mule Spring Limestone and Carrara Formation archaeocyaths represent a latest episode in the entire archaeocyath evolution and reef-building/dwelling capability on the eve of the final disappearance of this abundant and gregarious early poriferan clade (Online Supplemental File).

Archaeocyathus *as a Dead Clade Walking*

Archaeocyaths may have been able to persist beyond the major decline in reefs as a result of advantageous traits in unfavorable environmental conditions. Modularity, indeterminant development of clonal forms from a single parental individual, became dominant during the diversification of archaeocyaths due to its ecological advantages, such as developing greater organization of cells and branching morphologies in addition to being able to grow larger and better regenerate after tissue loss (Wood et al. 1992b). Modularity is a term adapted for truly integrated colonies of metabolically connected individuals as well for those that are disconnected by skeletal boundaries (Coates and Jackson 1987). Low modular (branching) and medium integrated (catenulate and pseudo-cerioid) archaeocyaths formed pseudocolonies almost exclusively while, in highly integrated (encrusting and massive) forms, a thin soft-tissue veneer connected individual entities (Wood et al. 1992b). Of the major archaeocyath orders comprising over 95% species, the archaeocyathides were more complex in skeletal form and modularity than monocyathides, ajacicyathides, and capsulocyathides, and were able to acquire greater modularity as they steadily evolved over time. Due to the favorability of this trait, it was believed that these modular archaeocyathides were more resilient to environmental perturbations relative to the various taxa of solitary and in few cases low modular monocyathides, ajacicyathides and capsulocyathides (Wood et al. 1992b). These traits are likely how *Archaeocyathus*—a modular archaeocyathide—survived into the Mule Spring Limestone and Thimble Limestone Member of the Carrara Formation, extending beyond the reefs of the underlying Harkless Formation.

It has been noted that, in the aftermath of mass extinctions, following a sharp decline, some surviving taxa persisted briefly and without recovery before the entire taxon became extinct, but these groups existed at lower abundance and diversity and with a reduced ecological role, a phenomenon defined by Jablonski (2001, 2002) as a "dead clade walking". The surviving taxa exhibited such low population numbers that they were no longer able to contribute sufficiently to their ecosystems, thus they became ecologically functionally extinct before they became physically extinct. Barnes et al. (2021) believed that clades who reached these points were unlikely to recover and to reestablish their population numbers. This "dead clade walking" pattern was observed after mass extinctions in a number of previously successful metazoan clades, manifested as a brief and minimal rebound in disparity (Jablonski 2002; Kaim and Nützel 2011; MacDougall et al. 2019; Landman et al. 2021; Barnes et al. 2021).

Archaeocyaths present in the Mule Spring Limestone and Carrara Formation represent archaeocyathides, potential examples of a "dead clade walking", given their morphological simplification (disparity of morphotypes), extremely low diversity, abundance and disparity, and limited ecological presence in the small biostromes of the Mule Spring Limestone following the initial disappearance of archaeocyathan reefs. These represent some of the youngest global occurrences of archaeocyaths following the disappearance of many other taxa during the early Cambrian (Series 2 Stage 4).

It is noteworthy that the only definite archaeocyath species that survived beyond the early Cambrian (Stage 4) globally was modular *Dictyocyathus neptunenensis* in the Neptune Range of West Antarctica (Wood et al. 1992a). This species morphologically resembles the *Archaeocyathus* described herein: both possess a similar outer wall and intervallar structure. The only difference is in the development of the inner wall, which, in a number of *Archaeocyathus* species has a rather simple morphology without apparent pore tubes. Thus, this Antarctic species can represent a direct dead end of *Archaeocyathus*-like forms, which were widespread during Age 4. This species formed ephemeral thickets among sessile echinoderms and did not build any reefs (Wood et al. 1992a).

There are a number of explanations for the total archaeocyath extinction. In the absence of direct competitors for reef-builder and reef-dwelling niches, which appeared later in the Cambrian (Lee et al. 2019), abiotic factors seem to be more significant for archaeocyath extirpation. These factors can include a global regression, further anoxic events and a greenhouse effect unfavorable for high-magnesium calcite reef-builders (Zhuravlev and Wood 1996; Faggetter et al. 2017; Marshall et al. 2021). However, similar to the extinction of the Pleistocene megafauna, local climatic and other environmental deterioration could force the decline of regional faunas rather than a singular global event (Broughton and Weitzel 2018; Cantalapiedra et al. 2021; Allen et al. 2023; Payne et al. 2023) and minimize the ability for these groups to migrate and re-establish a significant population size. In turn, a small effective population size and highly isolated populations drastically increased the probability for extinction (Rogers and Slatkin 2017; Pečnerová et al. 2017).

CONCLUSIONS

The Mule Spring Limestone reflects a shallow subtidal paleoenvironment in which microbial mounds with archaeocyaths formed following the disappearance of reefs. The occurrence of stromatolitic and thrombolitic fabrics interbedded with trilobite and echinoderm fossil debris and peloids between the reef mounds indicate possible perturbations to a low energy intertidal environment, such as occasional higher energy storms. The Thimble Limestone Member of the Carrara Formation reflects a subtidal paleoenvironment in which archaeocyaths, trilobite debris, and rip-up clasts were deposited in storm beds during high energy events. These archaeocyaths were deposited allochthonously as clasts, and therefore, we cannot interpret their original life habit. The abundance of microbial fabrics throughout the Mule Spring Limestone could provide insight into the changes to reef ecology from the early to middle Cambrian as archaeocyaths, a once-prominent framework builder, diminished.

The Mule Spring Limestone and Carrara Formation preserve archaeocyaths in small patch-reef ecosystems and in storm beds, respectively. As some of the youngest archaeocyaths in Laurentia, the discovery of archaeocyaths in the Mule Spring Limestone and Carrara Formation provide insight into the timing of the archaeocyath extinction in Laurentia in addition to the possible paleoenvironmental conditions that threatened the longevity of archaeocyaths towards the end of the early Cambrian.

The Mule Spring Limestone and the Carrara Formation (upper Dyeran; Cambrian Series 2, Stage 4) preserve archaeocyaths that post-date the major extinction event in the Harkless Formation (mid-Dyeran) that decimated the reef-forming group. These youngest Laurentian archaeocyaths were limited in diversity and abundance. In both formations, the only genus of archaeocyaths present is the modular genus *Archaeocyathus*, with indeterminate growth patterns. The low diversity, disparity and abundance of archaeocyaths in the upper portion of Cambrian Stage 4 suggest that *Archaeocyathus* survived as a dead clade walking, its ecological role greatly diminished relative to that during the reef-forming heyday of the group.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: https://www.sepm.org/supplemental-materials.

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