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PYRITIZED CRYOGENIAN CYANOBACTERIAL FOSSILS FROM ARCTIC ALASKA

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ABSTRACT: The Cryogenian was a time of climatic extremes, with two extended and severe global glaciations bracketing hothouse conditions. The effect of these extreme climate conditions on ocean chemistry and the marine biosphere remain poorly understood. Most of the previous studies of the fossil record from this interval focus on benthic organisms, with few examples of organisms with an inferred planktonic lifestyle and no firm evidence for photosynthetic organisms. Here, we present helically coiled, straight, and curved fossils composed of fine crystalline or framboidal pyrite in limestone samples from the Ikiakpuk formation of Arctic Alaska. These structures are morphologically identical to fossils of *Obruchevella*, a cyanobacterial form genus reported in pre-Sturtian and post-Marinoan strata, but not in deposits from the Cryogenian non-glacial interlude. We interpret fossils of the Ikiakpuk formation as planktonic cyanobacteria based on their morphology, which is identical to that of some modern planktonic cyanobacteria. Further evidence for a planktonic lifestyle comes from the preservation of these pyritized fossils in deep-water facies that lack evidence of microbial lamination. They provide the first direct evidence for bacterial primary productivity in the pelagic realm during the Cryogenian non-glacial interlude.

INTRODUCTION

The Earth experienced two Neoproterozoic Snowball Earth events: the older Sturtian ($\sim$ 717–660 Ma) and the younger Marinoan ($>$ 640–635 Ma) glaciations (Rooney et al. 2015). During the Sturtian glaciation, glaciers are thought to have been $\sim$ 1000 m thick on the continents (Liu and Peltier 2010) and oceans (Tziperman et al. 2012), with ice extending to the equator. The low temperature and ice covering the oceans decreased the availability of liquid water and sunlight, and likely reduced primary productivity (Costas et al. 2008). As a result of the stress placed on microbial ecosystems during the Sturtian glaciation, it has been suggested that there was a significant decrease in diversity during the 20 million years of the Cryogenian non-glacial interlude (Riedman et al. 2014; Cohen and Macdonald 2015). The interval during and after the deglaciation saw greenhouse conditions with increased temperatures and other rapid changes in pCO$_2$, continental weathering, alkalinity, and salinity (Hoffman et al. 1998; Kasemann et al. 2005; Bao et al. 2008), though many of these environmental conditions were likely short lived. The effects of these changes on the emerging biosphere are poorly constrained, largely due to the scarcity of fossil assemblages described from this time.

Sedimentary deposits that sample a range of environments and lithologies enable the assessment of biodiversity during the Cryogenian non-glacial interlude. Most recently, this has included investigation of cap carbonates deposited after the Sturtian glaciation. For example, fossil assemblages in the dark, micritic facies of cap carbonates in Zambia, Namibia, and Mongolia preserve communities of diverse eukaryotes (Bosak et al. 2011a; Dalton et al. 2013; Moore et al. 2017). These communities include a variety of agglutinated testate eukaryotes (Bosak et

al. 2011a, 2012; Dalton et al. 2013; Moore et al. 2017), some organic-walled fossils of presumed planktonic eukaryotes from cap carbonates (Bosak et al. 2011b), benthic eukaryotes from later Cryogenian carbonates (Cohen et al. 2015), and organic remnants of filamentous and coccoidal microorganisms (Bosak et al. 2011a). In contrast, analyses of the siliciclastic facies including glacial deposits and shales deposited after the Sturtian glaciation reveal rare spheroidal vesicles, interpreted as eukaryotes, and few examples of filamentous microfossils, interpreted broadly as the remnants of bacteria (Riedman et al. 2014). However, the simple morphologies of these fossils prevent further characterization of their taxonomic identity, and hinder inferences relating to the life modes of such organisms before death and burial (Riedman et al. 2014). The abundance and morphological diversity of fossils found in carbonates from the Cryogenian non-glacial interlude, therefore, highlight the importance of continued investigation of carbonate facies to build a more complete fossil record from this interval.

Here, we describe an assemblage of pyritized microfossils preserved in Cryogenian limestone of the Ikiakpuk formation in Arctic Alaska (Strauss et al. in press). Such microfossils have never before been described from this interval and come from strata that are distally deposited age equivalents of Cryogenian platform carbonates of unit 1 of the Katakturuk Dolomite (Macdonald et al. 2009). The limestone samples contain pyritized fossils with distinct coiled morphologies that are identical to the previously described fossil *Obruchevella,* interpreted as a type of photosynthetic cyanobacterium analogous to some modern planktonic cyanobacteria. This finding provides the first direct evidence of oxygenic, photosynthetic bacteria that were primary producers in the marine water column during the Cryogenian non-glacial interlude.

GEOLOGIC SETTING

Fossils were recovered from thin-bedded black limestone of the informal Ikiakpuk formation (Strauss et al. in press), sampled in the Fourth Range of Arctic Alaska (Fig. 1). This unit has previously been referred to as the "Black Limestone" or "Fourth Range Limestone" (Macdonald et al. 2009 and references therein). Carbon and strontium isotope chemostratigraphy suggest that the Ikiakpuk formation is Cryogenian in age and a deep-water equivalent of unit K1 of the Katakturuk Dolomite in the Sadlerochit, Shublik, and Kikiktat Mountains (Macdonald et al. 2009; Strauss et al. in press). Unit K1 consists predominantly of shallow marine dolostone and contains a Sturtian-age cap carbonate that overlies the Hula Hula diamictite. A maximum age on the Hula Hula diamictite is provided by a U/Pb zircon date of 719.47 ± 0.29 Ma on the underlying Kikiktat volcanics (Cox et al. 2015). Globally, strata deposited in the Cryogenian non-glacial interlude are constrained in age between ca. 660 Ma and > 635 Ma (Rooney et al. 2015).

In the Fourth Range, the Ikiakpuk formation is ∼ 1000 m thick and consists predominantly of thin-bedded, platy limestone with minor shale and sandstone (Macdonald et al. 2009). The base of the Ikiakpuk formation is not exposed and is unconformably overlain by the Devonian–Carboniferous Endicott and Lisburne groups. The samples analyzed here come from 10.3 to 49 m of the Ikiakpuk formation in the Fourth Range. The limestone lacks microbial lamination and some samples display normal grading from calcisiltite to micrite, consistent with lower-slope turbidite deposition on the flanks of a carbonate bank (Macdonald et al. 2009; Strauss et al. in press). Dark micritic limestone facies were sampled for this study because previous work on carbonates from the Cryogenian non-glacial interlude have shown that they are more likely to preserve fossils than lighter, more cement-rich facies or other carbonate facies (e.g., Bosak et al. 2011a; supplemental material in Bosak et al. 2012; Dalton et al. 2013). Future work will focus on examining different facies.

METHODS

Twelve samples from dark, unlaminated limestone facies of the Ikiakpuk formation that covered ∼ 40 m of section were analyzed in this study. Approximately 4–10 g of each sample was placed in a solution of 10% HCl to remove any surficial contaminants, and was then dissolved in a solution of 10% acetic acid buffered with 0.65 M hydrated ammonium acetate to produce a residue containing microfossils following Dalton et al. (2013). The residues were filtered through 0.2 μm, 41μm, and 100 μm Millipore nylon net filters (EMD Millipore, HNWP04700, NY4104700, and NY1H04700, Billerica, MA, USA) using vacuum filtration. A Nikon SMZ645 stereoscopic microscope was used to examine residues in the > 100 μm and the 41–100 μm size fractions, because those sizes were previously shown to contain microfossils (e.g., Dalton et al. 2013). Structures that had repeating morphologies and were distinct from the angular minerals in the surrounding residues were isolated for further analysis. Such structures occurred in eight of the 12 samples.

Samples with distinct morphological characteristics were imaged using a scanning electron microscope (FEI Quanta 450, Smith College, Northampton, MA). Before imaging, samples were placed on 12.7 mm diameter SEM stubs (Ted Pella Inc., Product #16111, Redding, CA, USA) with 12 mm ultra-thin carbon adhesive tabs (Electron Microscopy Sciences, Product #77825-12-SP, Hatfield, PA) and coated with gold and palladium using a Hummer V Sputter Coater (Smith College, Northampton, MA). We used EDS Team software with the 20 kV acceleration voltage to analyze the elemental composition of structures using point analyses and elemental mapping.

To determine whether organic carbon was present in putative microfossils, we acquired their Raman spectra using a Horiba LabRam Evolution Spectrometer (Harvard University, Center for Nanoscale Systems, Cambridge, MA). Samples were placed on glass slides and spectra were collected at 50× magnification using a 633 nm wavelength laser. Data were analyzed with LabSpec software. We also examined thin sections of the eight samples determined to be fossiliferous by residue analysis to further characterize the mineralogy of the limestone matrix and the fossils, but microfossils observed in thin section were generally rare.

RESULTS

Morphology

Residues from the Ikiakpuk formation contained microfossils with coiled morphologies that were not previously reported at other fossiliferous localities from this time. A total of 44 microfossils were identified in eight out of 12 analyzed samples. The structures included both coil fragments and complete coils that exhibited varying degrees of degradation (Fig. 2). Coiled structures consisted of a single solid strand, ∼ 20 μm to 30 μm-thick, wound helically into a coil. Coil diameters ranged from ∼ 50 μm to 170 μm. Some specimens had a uniform grainy, fine crystalline texture (18 out of 44 specimens; e.g., Fig. 2A), while others had ∼ 5 μm to 10 μm-wide spherical structures embedded within the strands (26 out of 44 specimens; e.g., Fig. 3A). The textures and thicknesses of the strands were consistent among specimens and across samples from different parts of the examined ∼ 40 m of limestone. In most specimens, the strand was wound tightly into a helically coiled, hollow cylinder ∼ 50 μm to 170 μm in diameter (Fig. 2A–2D). Some forms were more loosely coiled (Fig. 2E, 2F), and many fragments of coiled structures were present as curved (Fig. 3A, 3B) or straight strands (Fig. 3C, 3D) between ∼ 70 μm and 200 μm-long and ∼ 20 μm to 40 μm-wide. The loosely coiled structures were still broadly helical and appeared to have been either compressed or uncoiled.

Chemical Data and Petrography

To understand the processes that preserved microfossils in the Ikiakpuk formation, we determined the elemental composition of microfossils using Energy Dispersive X-ray Spectroscopy (EDS) point analysis spectra and chemical maps. These showed strong iron and sulfur peaks (Fig. 4) consistent with the mineral pyrite (FeS_2) in specimens from all samples. Pyrite was also present as cubes and framboids in the insoluble residues. We used additional chemical analysis with Raman spectroscopy to determine whether or not the process of pyritization preserved organic matter in the microfossils. Spectra revealed that microfossils contained carbonaceous material, shown by distinct peaks at ∼ 1348 cm^{-1} and ∼ 1609 cm^{-1} (Fig. 5), consistent with a D-band and G-band Raman shift indicative of organic carbon (e.g., Ferrari and Robertson 2000; McNeil et al. 2015).

We examined petrographic thin sections of limestone samples that yielded fossils in the preceding residue analysis to demonstrate that microfossils were found in situ. Microfossils were difficult to identify in thin sections of limestone samples from the Ikiakpuk formation, perhaps because both the microfossils and the microcrystalline limestone matrix were dark, or because fossils were generally rare. However, we identified a few distinct examples in thin section, with cross sections of the coiled helices visible as two parallel lines of dark circles separated by ∼ 50 μm of micrite (Fig. 6). These dark circles were mineralogically distinct, as demonstrated by their dark, opaque appearance against the surrounding micritic matrix, and showed that the microfossils were preserved in situ.
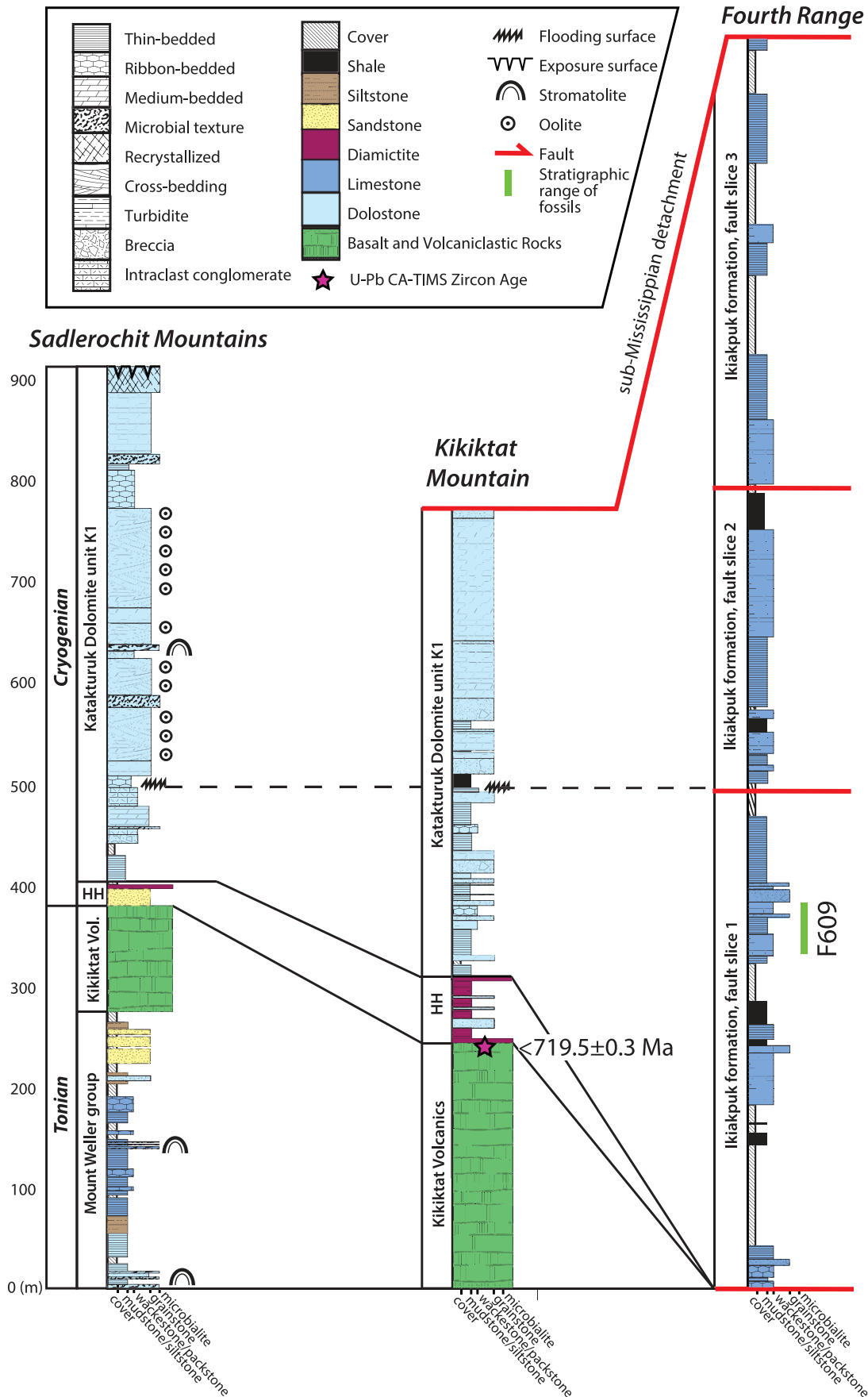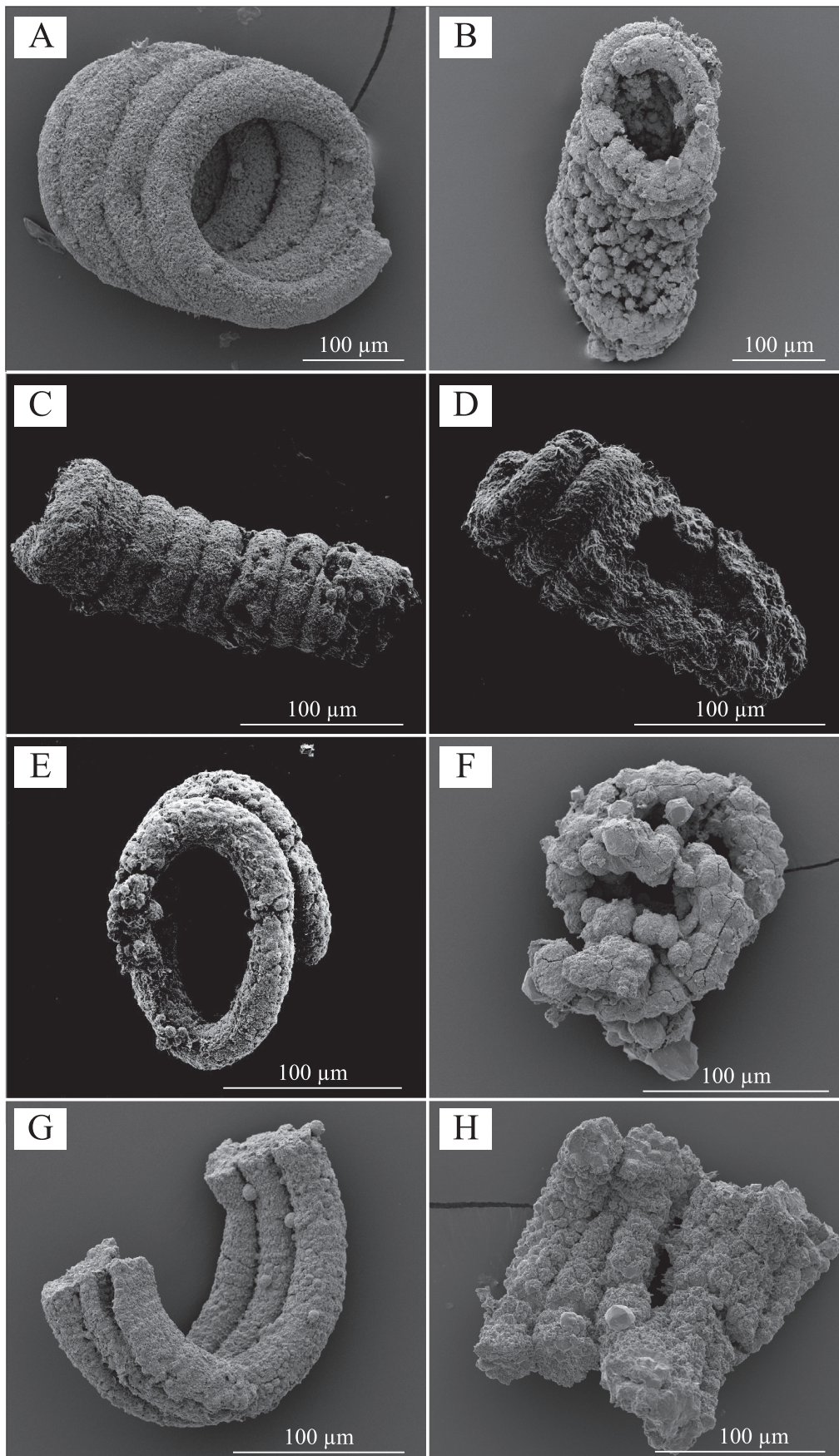
FIG. 1.—Stratigraphic column of the Sadlerochit and Kikiktat Mountains and the Fourth Range of Artic Alaska (Strauss et al. in press; Macdonald et al. 2009 and references therein). Samples (labeled in green as F609) come from the base of the Ikiakpuk formation in the Fourth Range.

DISCUSSION

Interpretation of Pyritized Structures

Coiled structures of the Ikiakpuk formation of Arctic Alaska closely resemble the previously described fossil *Obruchevella* (Knoll and Ohta 1988; Knoll 1992; Mankiewicz 1992; Butterfield and Rainbird 1998). The oldest *Obruchevella* were found in shales of the Neoproterozoic Wynniatt Formation of arctic Canada ($\sim$ 800 Ma; Butterfield and Rainbird 1998), in which the three dimensional, organic-walled, coiled fossils had an overall helix diameter of $\sim$ 40 μm and were made up of filaments $\sim$ 10 μm-wide. These fossils are one component of a more diverse fossil assemblage that includes other filamentous morphologies as well as acritarchs (Butterfield and Rainbird 1998). *Obruchevella* have also been identified as a component of assemblages containing other organic-walled filaments in younger siliciclastic deposits that postdate the Marinoan glaciation. Fossils preserved in chert in metasedimentary rocks of the Neoproterozoic Baklia Formation from the Prins Karls Forland, western Svalbard (Ediacaran in age), are morphologically similar to those of the Wynniatt Formation, comprised of single filaments helically coiled into cylinders (Knoll and Ohta 1988; Knoll 1992). The Ediacaran fossils are described in two size classes: a smaller form with strand diameters $\sim$ 4 μm to 5 μm and cylindrical coil diameters between 25 and 30 μm, and a larger form with strand diameters $\sim$ 28 μm to 33 μm and cylindrical coil diameters up to 230 μm (Knoll and Ohta 1988; Knoll 1992). Mankiewicz (1992) also described *Obruchevella* from the Burgess Shale (middle Cambrian), and these have variable helix (36.4 μm to 71.5 μm) and filament diameters (9.1 μm to 18.2 μm). The largest fossils of the Cambrian assemblages have coil and filament diameters similar to the largest *Obruchevella* from the Prins Karls Forland (Knoll and Ohta 1988; Knoll 1992), and both are nearly identical in size and shape to those of the Ikiakpuk formation.

Other occurrences include 2–3 μm-wide, helically coiled *Obruchevella* from the pre-Sturtian Chichkan Formation of Kazakhstan preserved in chert ($\sim$ 800 to 750 Ma; Sergeev and Schopf 2010) and $\sim$ 40 μm-wide loosely coiled *Obruchevella* in chert nodules from the post-Marinoan Doushantuo Formation of China ($\sim$ 600–550 Ma; Zhang et al. 1998; Xiao 2004). Both of these occurrences have identical shapes to coiled microfossils preserved in the Ikiakpuk formation. The previously described occurrences of *Obruchevella* span $\sim$ 300 My period between their first appearance Neoproterozoic ($\sim$ 800 Ma) and those preserved in the middle Cambrian Burgess Shale ($>$ 500 Ma). However, there has been a clear gap in the fossil record of *Obruchevella* between the beginning of the Sturtian glaciation and end of the Marinoan glaciation. The fossils described here are morphologically identical to previously described *Obruchevella*, and are the first occurrence of these fossils to bridge that gap. Their presence in limestone deposited during the Cryogenian non-glacial interlude shows that these cyanobacteria not only survived in geographically restricted environments through the glaciations, but were also an important component as primary producing organisms in some pelagic marine ecosystems during or after the deglaciation.

The coiled structures of the Ikiakpuk formation are analogous to the range of morphologies described in previous assemblages of *Obruchevella*, with tightly coiled helices identical to those of the Baklia, Wynniatt, and Chichkan formations (Knoll and Ohta 1988; Knoll 1992; Butterfield and Rainbird 1998), and loosely coiled forms similar to those of the Doushantuo Formation (Zhang et al. 1998; Xiao 2004). Furthermore, coils of the Ikiakpuk formation have size ranges (strand diameters $\sim$ 20 μm to 30 μm and total structure diameter $\sim$ 50 μm to 170 μm) comparable to the larger classes of *Obruchevella* described in the Baklia Formation (Knoll and Ohta 1988), the Wynniatt Formation (Butterfield and Rainbird 1998),

and the Burgess Shale (Mankiewicz 1992). The straight and curved strands of the Ikiakpuk formation are less diagnostic than the coiled structures, and may be either fragments of *Obruchevella* or remnants of other filamentous bacteria with uncertain taxonomic affinities.

The microfossils described here as well as some previously described *Obruchevella* fossils are much larger than most modern cyanobacteria, but their helically coiled morphology closely resembles that of modern cyanobacteria including *Spirulina*, *Cyanospira*, *Arthrospira*, and some species of *Anabaena* (Florenzano et al. 1985; Margheri et al. 2003; Komárek and Zapomělová 2007). All of these modern groups have helically coiled trichomes that can be either loosely coiled (e.g., *Cyanospira* and *Anabaena*; Florenzano et al. 1985; Komárek and Zapomělová 2007) or tightly coiled (e.g., *Spirulina*; Margheri et al. 2003). In fact, some species such as *Cyanospira capsulata* possess a mucilaginous capsule that creates a single smooth coating over the trichome with diameters up to $\sim$ 20 μm (Sili et al. 2011), consistent with the size of coiled structures of the Ikiakpuk formation (Fig. 2).

Some modern filamentous algae, such as *Spirogyra*, *Zygnema*, *Mougeotia,* and *Klebsormidium*, have cell diameters of $>$ 10 μm (Poulíčková et al. 2007; Mikhailyuk et al. 2014), but these lack the coiled morphology characteristic of the microfossils described here. In the case of *Spirogyra,* it is the chloroplast organelle that demonstrates a spiraled morphology, not the filamentous organism itself, and the chloroplast has a width of $<$ 10 μm (Wongsawad and Peerapornpisal 2015), much smaller than the fossils of the Ikiakpuk formation. Filamentous sulfur oxidizing bacteria like *Beggiatoa* have similar cell widths up to 200 μm, but lack any spiraled morphology (Salman et al. 2013). Some strains of sulfate-reducing bacteria have been described as spiraled, including some species of *Desulfovibrio* and *Desulfonatronospira* (Caumette et al. 1991; Tee et al. 1996; Castro et al. 2000; Sorokin and Chernyh 2017), but these forms are rod shaped, occasionally forming wavy chains (e.g., Zaarur et al. 2017). Such morphological characters are entirely distinct from the long, wide, tightly coiled filaments of the Ikiakpuk formation.

In summary, two arguments can be made in support of a cyanobacterial origin for the pyritized coiled fossils described here: (1) fossils of the Ikiakpuk formation are morphologically identical to the larger-size classes of previously described *Obruchevella*, which have been interpreted as cyanobacteria (Knoll and Ohta 1988; Knoll 1992; Mankiewicz 1992; Butterfield and Rainbird 1998), and (2) these and previously described *Obruchevella* are similar to modern coiled planktonic cyanobacteria (Florenzano et al. 1985; Tomaselli 1997; Tomaselli et al. 1997; Margheri et al. 2003; Komárek and Zapomělová 2007) whose morphologies are not found among other modern bacterial or eukaryotic groups.

Preservation and Depositional Environment

All microfossils described here are composed of pyrite (FeS_2; Fig. 5), and pyrite is also present in the insoluble residues as grains. Pyritization is an important form of fossil preservation in both Proterozoic and Phanerozoic fossil assemblages (e.g., Oehler and Logan 1977; Steiner and Reitner 2001; Anderson et al. 2011; Wacey et al. 2013; Borjigin et al. 2014). The pyrite framboids and the smooth, fine-crystalline pyrite that preserves fossils in the Ikiakpuk formation (Figs. 2, 3) closely resemble pyritized filamentous fossils reported in the Proterozoic McArthur H.Y.C. deposit (Oehler and Logan 1977), the Neoproterozoic Ust-Pinega Formation of Russia (Steiner and Reitner 2001), and the Ediacaran Doushantuo Formation of China (Anderson et al. 2011; Borjigin et al. 2014). Still, few examples of pyritized filamentous fossils interpreted as bacteria have been reported in Proterozoic sediments, and those that are

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FIG. 2.—SEM images of dominant coil morphologies. **A**–**D**) Tightly coiled helices with fine crystalline granular texture. **E, F**) Loosely coiled helices with fine crystalline granular texture. **G, H**) Broken coils showing solid cross sections of the strands comprising the coils.
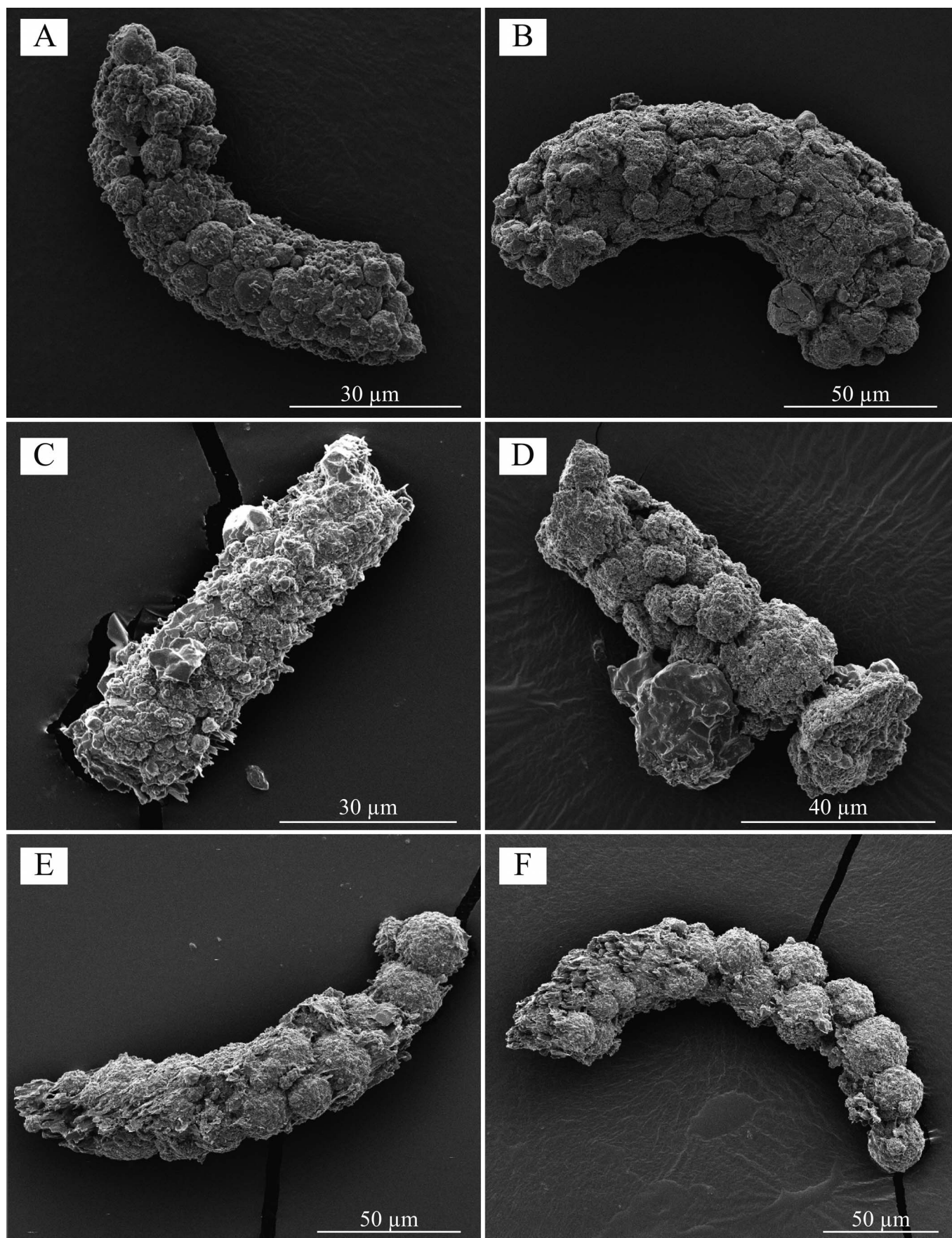
Fig. 3.—SEM images of other morphologies. **A**, **B**) Curved strands with uniform thickness throughout the specimen, comprised of framboids. **C**, **D**) Straight strands with framboids and some areas of fine crystalline granular texture. **E**, **F**) Curved strands that taper toward a narrow point, comprised of framboids.
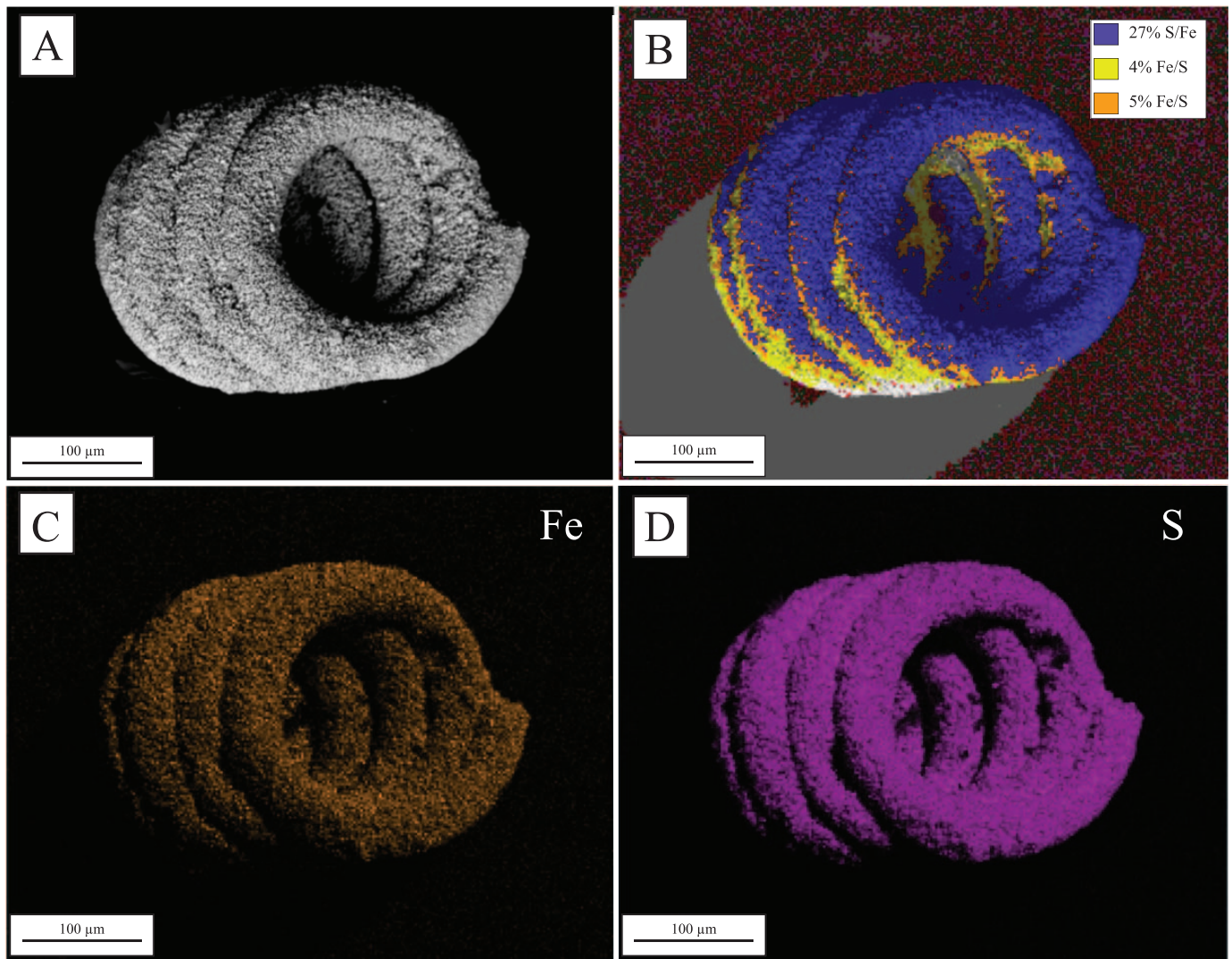
FIG. 4.—EDS chemical map of a representative coil. **A, B**) Map show the compositional distribution of all elements present. **C, D**) Maps demonstrate a clear dominance of Fe and S, respectively, covering the structure.
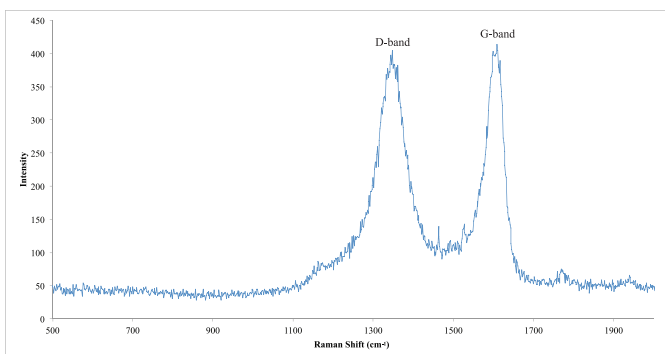

FIG. 5.—Raman spectrum of a representative coil demonstrating dominant peaks at ~ 1348 cm^{-1} and ~ 1609 cm^{-1}, consistent with D-band and G-band Raman shift indicative of organic carbon (e.g., Ferrari and Robertson 2000; McNeil et al. 2015).

known are preserved in siliciclastic deposits from either before the Sturtian glaciation or after the Marinoan glaciation. The fossils from the Ikiakpuk formation are the first examples of preservation by pyritization in carbonates of the Cryogenian non-glacial interlude, and are one of the few examples of pyritized bacteria in the fossil record.

This study is among one of the few three-dimensional analyses of *Obruchevella*, which is largely possible due to their unique preservation by pyrite within carbonate rocks. Previously described assemblages of *Obruchevella* are preserved as organic remnants compressed in shales and cherts, and are therefore predominantly studied petrographically, although Butterfield and Rainbird (1998) were also able to isolate three-dimensional organic-walled fossils using HF dissolution in addition to their petrographic analyses. The preservation of *Obruchevella* in dark, unlaminated limestone is unique for this interval and rare for these fossils, and highlights an important distinction between the environment in which these organisms lived and the environment in which they were preserved. *Obruchevella* are the remnants pelagic photosynthetic bacteria that lived in surface waters, but were preserved by pyritization in deep-water carbonates that lack microbial lamination. Raman spectra reveal the presence of the D-
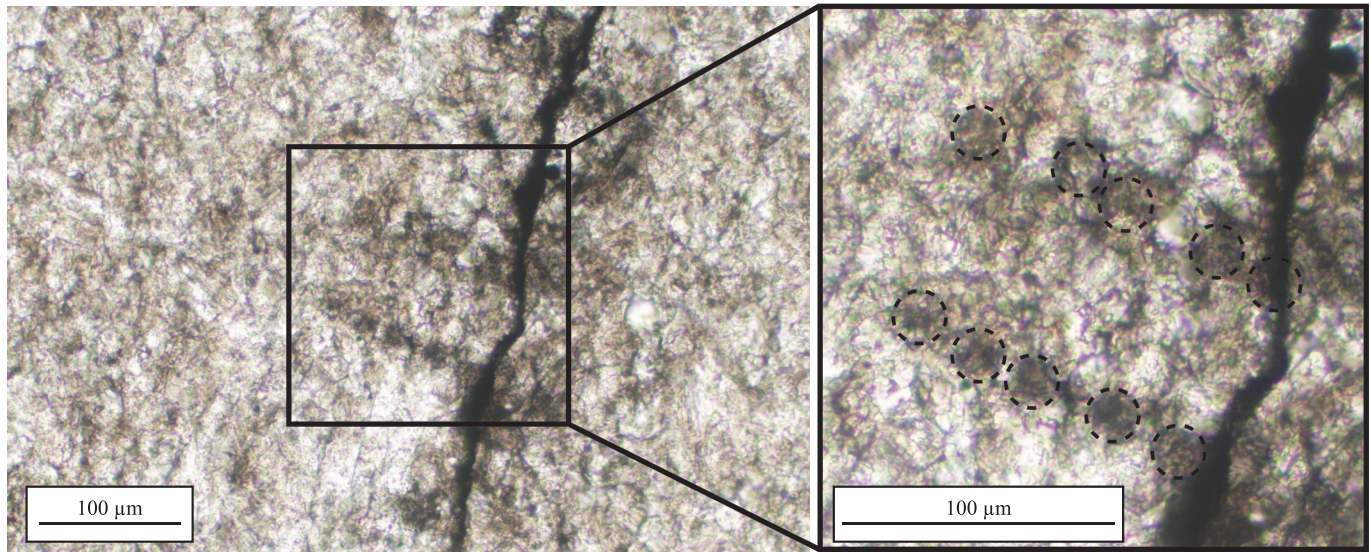
Fig. 6.—Petrographic thin section of a representative limestone of the Ikiakpuk formation showing dark circles (outlined in dotted lines). These circles are rarely observed in thin section due to the surrounding dark micrite, and show cross-sections through the solid pyritized strands.

and G-bands of fossil kerogen (Fig. 5), which further support an originally carbonaceous composition of the structures and suggest that pyrite precipitated immediately around and within the formerly organic filaments and preserved their shape. The preservation of these organic filaments by pyrite and the occurrence of pyrite in the insoluble residues not associated with the fossils suggests that the zone of sulfate reduction and sulfide release was very close to the sediment-water interface, possibly extending up into the water column. The organisms would have sunk to the seafloor after death, where they were preserved through localized and rapid post-mortem pyritization prior to degradation in the carbonate sediments.

Microbial Ecology

Microfossils preserved in the Ikiakpuk formation contribute to our growing understanding of the marine realm during the Cryogenian non-glacial interlude, and suggest a clear presence of primary productivity in the pelagic marine realm during this greenhouse interval. The coiled structures and fragments are identical to previously described *Obruchevella*, interpreted as photosynthetic cyanobacteria (Knoll and Ohta 1988; Knoll 1992; Mankiewicz 1992; Butterfield and Rainbird 1998). The life mode of *Obruchevella* preserved in the Ikiakpuk formation is different from that of agglutinated or carbonaceous benthic eukaryotes preserved in the Rasthof Formation of Namibia, the Kakontwe Formation of Zambia, and the Taishir Formation of Mongolia (Bosak et al. 2011a, 2012; Dalton et al. 2013; Cohen et al. 2015; Moore et al. 2017), which are interpreted as eukaryotic organisms similar to testate amoebae, foraminifera, or other unicellular eukaryotes or multicellular algae. Riedman et al. (2014) identified filamentous *Siphonophycus* sp. and *Rugosoopsis tenuis* in shale deposits from the Cryogenian non-glacial interlude, though the ecological niche of these organisms was not specified, and other occurrences of *Siphonophycus* have been reported in benthic rather than planktonic assemblages (Buick and Knoll 1999). The fossils described here—identical to some older and younger *Obruchevella*, which were previously interpreted as cyanobacteria (Knoll and Ohta 1988; Knoll 1992; Mankiewicz 1992; Butterfield and Rainbird 1998)—provide the first direct evidence that planktonic, photosynthetic, oxygen-producing organisms were present in surface waters during this interval.

Little is known about the recovery of the biosphere following the Sturtian glaciation. The few fossil assemblages preserved in marine deposits from the Cryogenian non-glacial interlude are key to understanding the response of organisms and ecosystems to the hypothesized environmental conditions during this time. This is especially true for fossils from the Ikiakpuk formation. *Obruchevella* first appear in the fossil record during the Neoproterozoic, and were described in formations that both predate and postdate the Snowball Earth events. Therefore, it follows that these organisms must have survived through these events. However, to the best of our knowledge, this study provides the first tangible evidence for the presence of such organisms in post-Sturtian marine ecosystems. The morphology of *Obruchevella* is interpreted as diagnostically cyanobacterial, as has been previously suggested (Knoll and Ohta 1988; Knoll 1992; Mankiewicz 1992; Butterfield and Rainbird 1998). The presence of cyanobacteria in the Ikiakpuk formation suggests that these organisms were the main primary producers in surface waters, and that the overall morphological and species diversity was limited. However, further studies of carbonate deposits from the Cryogenian non-glacial interlude are necessary to test the hypothesis of limited diversity against the alternative hypothesis of taphonomic bias.

CONCLUSIONS

The Ikiakpuk formation of Arctic Alaska preserves fossils of photosynthetic, planktonic organisms that lived during the Cryogenian non-glacial interlude. We interpret fossils recovered in this study with distinctly coiled morphologies as *Obruchevella* because their coiled morphology is identical to that of previously described older and younger fossil occurrences of *Obruchevella* and to some modern planktonic cyanobacteria such as *Spirulina*, *Cyanospira*, or *Anabaena*. Microfossils are preserved as pyritized internal molds, indicating that pyrite formed inside of the cells soon after the organisms died. In contrast to previously studied carbonates from this interval—including the Kakontwe, Taishir, and Rasthof formations, which preserve agglutinated and other benthic eukaryotic organisms—the Ikiakpuk formation was deposited in a deeper water setting and preserved mostly planktonic cyanobacteria. The fossil cyanobacteria preserved in the Ikiakpuk formation provide the first direct evidence of photosynthetic, oxygen-producing, planktonic organisms in the marine realm following the Sturtian glaciation, and expand our understanding of the pelagic ecosystem and the preservational conditions of deep-water settings during the Cryogenian non-glacial interlude. The

presence of coiled and straight filaments, and the absence of other morphologies in this assemblage may indicate a reduced diversity in open marine ecosystems during this interval, though further time-equivalent marine deposits are necessary to fully address this hypothesis.

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