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PYRITIZED CRYOGENIAN CYANOBACTERIAL FOSSILS FROM ARCTIC ALASKA

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1 **PYRITIZED CRYOGENIAN CYANOBACTERIAL FOSSILS FROM ARCTIC**

2 **ALASKA**

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16

17 **ABSTRACT**

18

19 **The Cryogenian was a time of climatic extremes, with two extended and**

20 **severe global glaciations bracketing hothouse conditions. The effect of these extreme**

21 **climate conditions on ocean chemistry and the marine biosphere remain poorly**

22 **understood. Most of the previous studies of the fossil record from this interval focus**

23 **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 that has been 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 (~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 ~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

47   during the 20 million years of the Cryogenian non-glacial interlude (Riedman et al.,

48   2014; Cohen and Macdonald, 2015). The interval during and after the deglaciation saw

49   greenhouse conditions with increased temperatures and other rapid changes in pCO_2,

50   continental weathering, alkalinity, and salinity (Hoffman et al., 1998; Kasemann et al.,

51   2005; Bao et al., 2008), though many of these environmental conditions were likely short

52   lived. The effects of these changes on the emerging biosphere are poorly constrained,

53   largely due to the scarcity of fossil assemblages described from this time.

54   Sedimentary deposits that sample a range of environments and lithologies enable

55   the assessment of biodiversity during the Cryogenian non-glacial interlude. Most

56   recently, this has included investigation of cap carbonates deposited after the Sturtian

57   glaciation. For example, fossil assemblages in the dark, micritic facies of cap carbonates

58   in Zambia, Namibia, and Mongolia preserve communities of diverse eukaryotes (Bosak

59   et al., 2011a; Dalton et al., 2013; Moore et al., 2017). These communities include a

60   variety of agglutinated testate eukaryotes (Bosak et al., 2011a, 2012; Dalton et al., 2013;

61   Moore et al., 2017), some organic-walled fossils of presumed planktonic eukaryotes from

62   cap carbonates (Bosak et al., 2011b), benthic eukaryotes from later Cryogenian

63   carbonates (Cohen et al., 2015), and organic remnants of filamentous and coccoidal

64   microorganisms (Bosak et al., 2011a). In contrast, analyses of the siliciclastic facies

65   including glacial deposits and shales deposited after the Sturtian glaciation reveal rare

66   spheroidal vesicles, interpreted as eukaryotes, and few examples of filamentous

67   microfossils, interpreted broadly as the remnants of bacteria (Riedman et al., 2014).

68   However, the simple morphologies of these fossils prevent further characterization of

69   their taxonomic identity, and hinder inferences relating to the life modes of such

70 organisms before death and burial (Riedman et al., 2014). The abundance and

71 morphological diversity of fossils found in carbonates from the Cryogenian non-glacial

72 interlude, therefore, highlight the importance of continued investigation of carbonate

73 facies to build a more complete fossil record from this interval.

74   Here, we describe an assemblage of pyritized microfossils that were preserved in

75 Cryogenian limestone of the Ikiakpuk formation in Arctic Alaska (Strauss et al., in press).

76 Such microfossils have never before been described from this interval and come from

77 strata that are distally deposited age equivalents of Cryogenian platform carbonates of

78 unit 1 of the Katakturuk Dolomite (Macdonald et al., 2009). The limestone samples

79 contain pyritized fossils with distinct coiled morphologies that are identical to the

80 previously described fossil *Obruchevella,* interpreted as a fossil of a type of

81 photosynthetic cyanobacterium analogous to some modern planktonic cyanobacteria.

82 This finding provides the first direct evidence of oxygenic, photosynthetic bacteria that

83 were primary producers in the marine water column during the Cryogenian non-glacial

84 interlude.

85

86   GEOLOGIC SETTING

87

88   Fossils were recovered from thin-bedded black limestone of the informal

89 Ikiakpuk formation (Strauss et al., accepted), sampled in the Fourth Range of Arctic

90 Alaska (Figure 1). This unit has previously been referred to as the "Black Limestone" or

91 "Fourth Range Limestone" (Macdonald et al., 2009 and references therein). Carbon and

92 strontium isotope chemostratigraphy suggest that the Ikiakpuk formation is Cryogenian in

4

93   age and a deep-water equivalent of unit K1 of the Katakturuk Dolomite in the

94   Sadelerochit, Shublik, and Kikiktat Mountains (Macdonald et al., 2009; Strauss et al., in

95   press). Unit K1 consists predominantly of shallow marine dolostone and contains a

96   Sturtian-age cap carbonate that overlies the Hula Hula diamictite. A maximum age on the

97   Hula Hula diamictite is provided by a U/Pb zircon date of 719.47 ± 0.29 Ma on the

98   underlying Kikiktat volcanics (Cox et al., 2015). Globally, strata deposited in the

99   Cryogenian non-glacial interlude are constrained in age between ca. 660 Ma and >635

100   Ma (Rooney et al., 2015).

101   In the Fourth Range, the Ikiakpuk formation is ~1000 m thick and consists

102   predominantly of thin-bedded, platy limestone with minor shale and sandstone

103   (Macdonald et al., 2009). The base of the Ikiakpuk formation is not exposed and is

104   unconformably overlain by the Devonian-Carboniferous Endicott and Lisburne groups.

105   The samples analyzed here come from 10.3 to 49 m of the Ikiakpuk formation in the

106   Fourth Range. The limestone lacks microbial lamination and some samples display

107   normal grading from calcisiltite to micrite, consistent with lower-slope turbidite

108   deposition on the flanks of a carbonate bank (Macdonald et al., 2009; Strauss et al., in

109   press). Dark micritic limestone facies were sampled for this study because previous work

110   on carbonates from the Cryogenian non-glacial interlude have shown that they are more

111   likely to preserve fossils than lighter, more cement-rich facies or other carbonate facies

112   (e.g. Bosak et al., 2011a; supplemental material in Bosak et al., 2012; Dalton et al.,

113   2013). Future work will focus on examining different facies.

114

115   METHODS

116

117   Twelve samples from dark, unlaminated limestone facies of the Ikiakpuk

118   formation that covered ~40 m of section were analyzed in this study. Approximately 4-10

119   g of each sample was placed in a solution of 10% HCl to remove any surficial

120   contaminants, and was then dissolved in a solution of 10% acetic acid buffered with 0.65

121   M hydrated ammonium acetate to produce a residue containing microfossils following

122   Dalton et al. (2013). The residues were filtered through 0.2 μm, 41μm, and 100 μm

123   Millipore nylon net filters (EMD Millipore, HNWP04700, NY4104700, and

124   NY1H04700, Billerica, MA, USA) using vacuum filtration. A Nikon SMZ645

125   stereoscopic microscope was used to examine residues in the >100 μm and the 41-100

126   μm size fractions, because those sizes were previously shown to contain microfossils

127   (e.g., Dalton et al., 2013). Structures that had repeating morphologies and were distinct

128   from the angular minerals in the surrounding residues were isolated for further analysis.

129   Such structures occurred in eight of the twelve samples.

130   Samples with distinct morphological characteristics were imaged using a scanning

131   electron microscope (FEI Quanta 450, Smith College, Northampton, MA). Before

132   imaging, samples were placed on 12.7 mm diameter SEM stubs (Ted Pella Inc., Product

133   #16111, Redding, CA, USA) with 12 mm ultra thin carbon adhesive tabs (Electron

134   Microscopy Sciences, Product #77825-12-SP, Hatfield, PA) and coated with gold and

135   palladium using a Hummer V Sputter Coater (Smith College, Northampton, MA). We

136   used EDS Team software with the 20 kV acceleration voltage to analyze the elemental

137   composition of structures using point analyses and elemental mapping.

138   To determine whether organic carbon was present in putative microfossils, we

139   acquired their Raman spectra using a Horiba LabRam Evolution Spectrometer (Harvard

140   University, Center for Nanoscale Systems, Cambridge, MA) at 50X magnification.

141   Samples were placed on glass slides and spectra were collected at 50X magnification

142   using a 633 nm wavelength laser. Data were analyzed with LabSpec software. We also

143   examined thin sections of the eight samples determined to be fossiliferous by residue

144   analysis to further characterize the mineralogy of the limestone matrix and the fossils, but

145   microfossils observed in thin section were generally rare.

146

147   RESULTS

148

149   Morphology

150

151   Residues from the Ikiakpuk formation contained microfossils with coiled

152   morphologies that were not previously reported at other fossiliferous localities from this

153   time. A total of 44 microfossils were identified in 8 out of 12 analyzed samples. The

154   structures included both coil fragments and complete coils that exhibited varying degrees

155   of degradation (Figure 2). Coiled structures consisted of a single solid strand, ~20 μm to

156   30 μm-thick, wound helically into a coil. Coil diameters ranged from ~50 μm to 170 μm.

157   Some specimens had a uniform grainy, fine crystalline texture (18 out of 44 specimens;

158   e.g., Figure 2.A), while others had ~5 μm to 10 μm-wide spherical structures embedded

159   within the strands (26 out of 44 specimens; e.g. sample 3.A). The textures and

160   thicknesses of the strands were consistent among specimens and across samples from

161   different parts of the examined ~40 m of limestone. In most specimens, the strand was

162   wound tightly into a helically coiled, hollow cylinder ~50 μm to 170 μm in diameter

163   (Figure 2.A, B, C, D). Some forms were more loosely coiled (Figure 2.E, F), and many

164   fragments of coiled structures were present as curved (Figure 3.A, B) or straight strands

165   (Figure 3.C, D) between ~70 μm and 200 μm-long and ~20 μm to 40 μm-wide. The

166   loosely coiled structures were still broadly helical and appeared to have been either

167   compressed or uncoiled.

168

169   Chemical Data and Petrography

170

171   To understand the processes that preserved microfossils in the Ikiakpuk

172   formation, we determined the elemental composition of microfossils using Energy

173   Dispersive X-ray Spectra (EDS) spectra and chemical maps. These showed strong iron

174   and sulfur peaks (Figure 4) consistent with the mineral pyrite (FeS_2) in specimens from

175   all samples. Pyrite was also present as cubes and framboids in the insoluble residues. We

176   used additional chemical analysis with Raman spectroscopy to determine whether or not

177   the process of pyritization preserved organic matter in the microfossils. Spectra revealed

178   that microfossils contained carbonaceous material, shown by distinct peaks at ~1348 cm^{-1}

179   and ~1609 cm^{-1} (Figure 5), consistent with a D-band and G-band Raman shift indicative

180   of organic carbon (e.g., Ferrari and Robertson, 2000; McNeil et al., 2015).

181   We examined petrographic thin sections of limestone samples that yielded fossils

182   in the preceding residue analysis to demonstrate that microfossils were found *in situ*.

183   Microfossils were difficult to identify in thin sections of limestone samples from the

184   Ikiakpuk formation, perhaps because both the microfossils and the microcrystalline

185   limestone matrix were dark, or because fossils were generally rare. However, we

186   identified a few distinct examples in thin section, with cross sections of the coiled helices

187   visible as two parallel lines of dark circles separated by ~50 µm of micrite (Figure 6).

188   These dark circles were mineralogically distinct, as demonstrated by their dark, opaque

189   appearance against the surrounding micritic matrix and demonstrated that the

190   microfossils were preserved *in situ*.

191

192   DISCUSSION

193

194   Interpretation of pyritized structures

195

196   Coiled structures of the Ikiakpuk formation of Arctic Alaska closely resemble the

197   previously described fossil *Obruchevella* (Knoll and Ohta, 1988; Knoll, 1992;

198   Mankiewicz, 1992; Butterfield and Rainbird, 1998). The oldest *Obruchevella* were found

199   in shales of the Neoproterozoic Wynniatt Formation of arctic Canada (~800 Ma;

200   Butterfield and Rainbird, 1998), in which the three dimensional, organic-walled, coiled

201   fossils had an overall helix diameter of ~40 µm and were made up of filaments ~10 µm-

202   wide. These fossils are one component of a more diverse fossil assemblage that includes

203   other filamentous morphologies as well as acritarchs (Butterfield and Rainbird, 1998).

204   *Obruchevella* have also been identified as a component of assemblages containing other

205   organic-walled filaments in younger siliciclastic deposits that postdate the Marinoan

206   glaciation. Fossils preserved in chert in metasedimentary rocks of the Neoproterozoic

207   Baklia Formation from the Prins Karls Forland, western Svalbard, (Ediacaran in age) are

208   morphologically similar to those of the Wynniatt Formation, comprised of single

209   filaments helically coiled into cylinders (Knoll and Ohta, 1988; Knoll, 1992). The

210   Ediacaran fossils are described in two size classes: a smaller form with strand diameters

211   ~4 μm to 5 μm and cylindrical coil diameters between 25 and 30 μm, and a larger form

212   with strand diameters ~28 μm to 33 μm and cylindrical coil diameters up to 230 μm

213   (Knoll and Ohta, 1988; Knoll, 1992). Mankiewicz (1992) also described *Obruchevella*

214   from the Burgess Shale (middle Cambrian), and these have variable helix (36.4 μm to

215   71.5 μm) and filament diameters (9.1 μm to 18.2 μm). The largest fossils of the

216   Cambrian assemblages have coil and filament diameters similar to the largest

217   *Obruchevella* from the Prins Karls Forland (Knoll and Ohta, 1988; Knoll, 1992), and

218   both are nearly identical in size and shape to those of the Ikiakpuk formation.

219   Other occurrences include 2-3 μm-wide, helically coiled *Obruchevella* from the

220   pre-Sturtian Chichkan Formation of Kazakhstan preserved in chert (~800 to 750 Ma;

221   Sergeev and Schopf, 2010) and ~40 μm-wide loosely coiled *Obruchevella* in chert

222   nodules from the post-Marinoan Doushantuo Formation of China (~600-550 Ma; Zhang

223   et al., 1998; Xiao, 2004). Both of these occurrences have identical shapes to coiled

224   microfossils preserved in the Ikiakpuk formation. The previously described occurrences

225   of *Obruchevella* span ~300 My period between their first appearance Neoproterozoic

226   (~800 Ma) and those preserved in the middle Cambrian Burgess Shale (>500 Ma).

227   However, there has been a clear gap in the fossil record of *Obruchevella* between the

228   beginning of the Sturtian glaciation and end of the Marinoan glaciation. The fossils

229   described here are morphologically identical to previously described *Obruchevella,* and

230   are the first occurrence of these fossils to bridge that gap. Their presence in limestone

231   deposited during the Cryogenian non-glacial interlude shows that these cyanobacteria not

232   only survived in geographically restricted environments through the glaciations, but were

233   also an important component as primary producing organisms in some pelagic marine

234   ecosystems during or after the deglaciation.

235   The coiled structures of the Ikiakpuk formation are analogous to the range of

236   morphologies described in previous assemblages of *Obruchevella*, with tightly coiled

237   helices identical to those of the Baklia, Wynniatt and Chichkan formations (Knoll and

238   Ohta, 1988; Knoll, 1992; Butterfield and Rainbird, 1998), and loosely coiled forms

239   similar to those of the Doushantuo Formation (Zhang et al., 1998; Xiao, 2004).

240   Furthermore, coils of the Ikiakpuk formation have size ranges (strand diameters ~20 μm

241   to 30 μm and total structure diameter ~50 μm to 170 μm) comparable to the larger classes

242   of *Obruchevella* described in the Baklia Formation (Knoll and Ohta, 1988), the Wynniatt

243   Formation (Butterfield and Rainbird, 1998), and the Burgess Shale (Mankiewicz, 1992).

244   The straight and curved strands of the Ikiakpuk formation are less diagnostic than the

245   coiled structures, and may be either fragments of *Obruchevella* or remnants of other

246   filamentous bacteria with uncertain taxonomic affinities.

247   The microfossils described here as well as some previously described

248   *Obruchevella* fossils are much larger than most modern cyanobacteria, but their helically

249   coiled morphology closely resembles that of modern cyanobacteria including *Spirulina*,

250   *Cyanospira, Arthrospira*, and some species of *Anabaena* (Florenzano et al., 1985;

251   Margheri et al., 2003; Komárek and Zapomělová, 2007). All of these modern groups

252   have helically coiled trichomes that can be either loosely coiled (e.g., *Cyanospira* and

253 *Anabaena*; Florenzano et al., 1985; Komárek and Zapomělová, 2007) or tightly coiled

254 (e.g., *Spirulina*; Margheri et al., 2003). In fact, some species such as *Cyanospira*

255 *capsulata* possess a mucilaginous capsule that creates a single smooth coating over the

256 trichome with diameters up to ~20 µm (Sili et al., 2011), consistent with the size of coiled

257 structures of the Ikiakpuk formation (Figure 2).

258   Some modern filamentous algae, such as *Spirogyra, Zygnema, Mougeotia,* and

259 *Klebsormidium*, have cell diameters of >10 µm (Poulíčková et al., 2007; Mikhailyuk et

260 al., 2014), but these lack the coiled morphology characteristic of the microfossils

261 described here. In the case of *Spirogyra,* it is the chloroplast organelle that demonstrates a

262 spiraled morphology, not the filamentous organism itself, and the chloroplast has a width

263 of <10 µm (Wongsawad and Peerapornpisal, 2015), much smaller than the fossils of the

264 Ikiakpuk Formation. Filamentous sulfur oxidizing bacteria like *Beggiatoa* have similar

265 cell widths up to 200 µm, but lack any spiraled morphology (Salman et al., 2013). Some

266 strains of sulfate reducing bacteria have been described as spiraled, including some

267 species of *Desulfovibrio* and *Desulfonatronospira* (Caumette et al., 1991; Tee et al.,

268 1996; Castro et al., 2000; Sorokin and Chernyh, 2017), but these forms are rod shaped,

269 occasionally forming wavy chains (e.g., Zaarur et al., 2017). Such morphological

270 characters are entirely distinct from the long, wide, tightly coiled filaments of the

271 Ikiakpuk formation.

272   In summary, two arguments can be made in support of a cyanobacterial origin for

273 the pyritized coiled fossils described here: 1) fossils of the Ikiakpuk formation are

274 morphologically identical to the larger size classes of previously described *Obruchevella*,

275 which have been interpreted as cyanobacteria (Knoll and Ohta, 1988; Knoll, 1992;

276   Mankiewicz, 1992; Butterfield and Rainbird, 1998), and 2) these and previously

277   described *Obruchevella* are similar to modern coiled planktonic cyanobacteria

278   (Florenzano et al., 1985; Tomaselli, 1997; Tomaselli et al., 1997; Margheri et al., 2003;

279   Komárek and Zapomělová, 2007)—whose morphologies are not found among other

280   modern bacterial or eukaryotic groups.

281

282   Preservation and Depositional Environment

283

284   All microfossils described here are composed of pyrite (FeS_2; Figure 5), and

285   pyrite is also present in the insoluble residues as grains. Pyritization is an important form

286   of fossil preservation in both Proterozoic and Phanerozoic fossil assemblages (e.g.,

287   Oehler and Logan, 1977; Steiner and Reitner, 2001; Anderson et al., 2011; Wacey et al.,

288   2013; Borjigin et al., 2014). The pyrite framboids and the smooth, fine-crystalline pyrite

289   that preserves fossils in the Ikiakpuk formation (Figures 2 and 3) closely resemble

290   pyritized filamentous fossils reported in the Proterozoic McArthur H.Y.C. deposit

291   (Oehler and Logan, 1977), the Neoproterozoic Ust-Pinega Formation of Russia (Steiner

292   and Reitner, 2001) and the Ediacaran Doushantuo Formation of China (Anderson et al.,

293   2011; Borjigin et al., 2014). Still, few examples of pyritized filamentous fossils

294   interpreted as bacteria have been reported in Proterozoic sediments, and those that are

295   known are preserved in siliciclastic deposits from either before the Sturtian glaciation or

296   after the Marinoan glaciation. The fossils from the Ikiakpuk formation are the first

297   examples of preservation by pyritization in carbonates of the Cryogenian non-glacial

298   interlude, and are one of the few examples of pyritized bacteria in the fossil record.

299   This study is among one of the few three-dimensional analyses of *Obruchevella,*

300   which is largely possible due to their unique preservation by pyrite within carbonate

301   rocks. Previously described assemblages of *Obruchevella* are preserved as organic

302   remnants compressed in shales and cherts, and are therefore predominantly studied

303   petrographically, although Butterfield and Rainbird (1998) were also able to isolate three-

304   dimensional organic-walled fossils using HF dissolution in addition to their petrographic

305   analyses. The preservation of *Obruchevella* in dark, unlaminated limestone is unique for

306   this interval and rare for these fossils, and highlights an important distinction between the

307   environment in which these organisms lived and the environment in which they were

308   preserved. *Obruchevella* are the remnants pelagic photosynthetic bacteria that lived in

309   surface waters, but were preserved by pyritization in deep-water carbonates that lack

310   microbial lamination. Raman spectra reveal the presence of the D- and G-bands of fossil

311   kerogen (Figure 5), which further support an originally carbonaceous composition of the

312   structures and suggest that pyrite precipitated immediately around and within the

313   formerly organic filaments, which preserved the shape of the filaments. The preservation

314   of these organic filaments by pyrite and the occurrence of pyrite in the insoluble residues

315   not associated with the fossils suggests that the zone of sulfate reduction and sulfide

316   release was very close to the sediment-water interface, possibly extending up into the

317   water column. The organisms would have sunk to the seafloor after death, where they

318   were preserved through localized and rapid post-mortem pyritization prior to degradation

319   in the carbonate sediments.

320

321   Microbial Ecology

322

323   Microfossils preserved in the Ikiakpuk formation contribute to our growing

324 understanding of the marine realm during the Cryogenian non-glacial interlude, and

325 suggest a clear presence of primary productivity in the pelagic marine realm during this

326 greenhouse interval. The coiled structures and fragments are identical to previously

327 described *Obruchevella*, interpreted as photosynthetic cyanobacteria (Knoll and Ohta,

328 1988; Knoll, 1992; Mankiewicz, 1992; Butterfield and Rainbird, 1998). The life mode of

329 *Obruchevella* preserved in the Ikiakpuk formation is different from that of agglutinated or

330 carbonaceous benthic eukaryotes preserved in the Rasthof Formation of Namibia, the

331 Kakontwe Formation of Zambia, and the Taishir Formation of Mongolia (Bosak et al.,

332 2011a, 2012; Dalton et al., 2013; Cohen et al., 2015; Moore et al., 2017), which are

333 interpreted as eukaryotic organisms similar to testate amoebae, foraminifera, or other

334 unicellular eukaryotes or multicellular algae. Riedman *et al.* (2014) identified filamentous

335 *Siphonophycus* sp. and *Rugosoopsis tenuis* in shale deposits from the Cryogenian non-

336 glacial interlude, though the ecological niche of these organisms was not specified, and

337 other occurrences of *Siphonophycus* have been reported in benthic rather than planktonic

338 assemblages (Buick and Knoll, 1999). The fossils described here—identical to some

339 older and younger *Obruchevella*, which were previously interpreted as cyanobacteria

340 (Knoll and Ohta, 1988; Knoll, 1992; Mankiewicz, 1992; Butterfield and Rainbird,

341 1998)— provide the first direct evidence that planktonic, photosynthetic, oxygen-

342 producing organisms were present in surface waters during this interval.

343   Little is known about the recovery of the biosphere following the Sturtian

344 glaciation. The few fossil assemblages preserved in marine deposits from the Cryogenian

345   non-glacial interlude are key to understanding the response of organisms and ecosystems

346   to the hypothesized environmental conditions during this time. This is especially true for

347   fossils from the Ikiakpuk formation. *Obruchevella* first appear in the fossil record during

348   the Neoproterozoic, and were described in formations that both predate and postdate the

349   Snowball Earth events. Therefore, it follows that these organisms must have survived

350   through these events. However, to the best of our knowledge, this study provides the first

351   tangible evidence for the presence of such organisms in post-Sturtian marine ecosystems.

352   The morphology of *Obruchevella* is interpreted as diagnostically cyanobacterial, as has

353   been previously suggested (Knoll and Ohta, 1988; Knoll, 1992; Mankiewicz, 1992;

354   Butterfield and Rainbird, 1998). The presence of cyanobacteria in the Ikiakpuk formation

355   suggests that these organisms were the main primary producers in surface waters, and

356   that the overall morphological and species diversity was limited. However, further studies

357   of carbonate deposits from the Cryogenian non-glacial interlude are necessary to test the

358   hypothesis of limited diversity against the alternative hypothesis of taphonomic bias.

359

360   CONCLUSIONS

361

362   The Ikiakpuk formation of Arctic Alaska preserves fossils of photosynthetic,

363   planktonic organisms that lived during the Cryogenian non-glacial interlude. We interpret

364   fossils recovered in this study with distinctly coiled morphologies as *Obruchevella*

365   because their coiled morphology is identical to that of previously described older and

366   younger fossil occurrences of *Obruchevella* and to some modern planktonic

367   cyanobacteria such as *Spirulina*, *Cyanospira*, or *Anabaena*. Microfossils are preserved as

368 pyritized internal molds, indicating that pyrite formed inside of the cells soon after the

369 organisms died. In contrast to previously studied carbonates from this interval—including

370 the Kakontwe, Taishir and Rasthof formations, which preserve agglutinated and other

371 benthic eukaryotic organisms—the Ikiakpuk formation was deposited in a deeper water

372 setting and preserved mostly planktonic cyanobacteria. The fossil cyanobacteria

373 preserved in the Ikiakpuk formation provide the first direct evidence of photosynthetic,

374 oxygen-producing, planktonic organisms in the marine realm following the Sturtian

375 glaciation, and expand our understanding of the pelagic ecosystem and the preservational

376 conditions of deep-water settings during the Cryogenian non-glacial interlude. The

377 presence of coiled and straight filaments, and the absence of other morphologies in this

378 assemblage may indicate a reduced diversity in open marine ecosystems during this

379 interval, though further time-equivalent marine deposits are necessary to fully address

380 this hypothesis.

381

382   ACKNOWLEDGMENTS

383

391

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574

575 FIGURE CAPTIONS

576

577 FIG. 1.—Stratigraphic column of the Sadlerochit and Kikiktat Mountains and the Fourth

578   Range of Artic Alaska (Strauss et al., accepted; Macdonald et al., 2009 and

579   references therein). Samples (labeled in green as F609) come from the base of the

580   Ikiakpuk formation in the Fourth Range.

581

582 FIG. 2.—SEM images of dominant coil morphologies. Morphologies include tightly

583   coiled helices with fine crystalline granular texture (A, B, C, D), loosely coiled

584   helices with fine crystalline granular texture (E), loosely coiled helices with some

585   framboids embedded within the fine crystalline granular texture, and broken coils

586   showing solid cross sections of the strands comprising the coils (G, H).

587

588 FIG. 3.—SEM images of other morphologies. Strands are curved with uniform thickness

589   throughout the specimen and comprised of framboids (A, B), straight with

590   framboids and some areas of fine crystalline granular texture (C, D), or curved

591   and comprised of framboids that taper toward a narrow point (E, F).
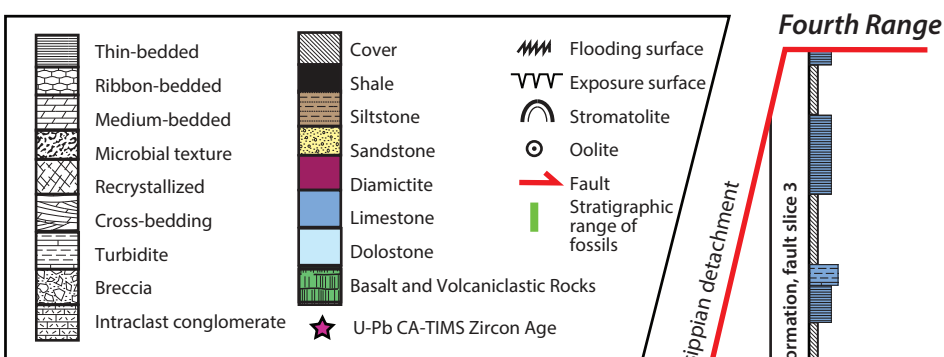
592

593   FIG. 4.—EDS chemical map of a representative coil. Chemical maps show the

594   compositional distribution of all elements present (A, B) and demonstrate a clear

595   dominance of Fe (C) and S (D) covering the structure.

596

597   FIG. 5.—Raman spectrum of a representative coil demonstrating dominant peaks at ~1348

598   cm^{-1} and ~1609 cm^{-1}, consistent with D-band and G-band Raman shift indicative

599   of organic carbon (e.g., Ferrari and Robertson, 2000; McNeil et al., 2015).

600

601   FIG. 6.—Petrographic thin section of a representative limestone of the Ikiakpuk

602   formation showing dark circles (outlined in dotted lines). These circles are rarely

603   observed in thin section due to the surrounding dark micrite, and show cross-

604   sections through the solid pyritized strands.

A

B
- 27% S/Fe
- 4% Fe/S
- 5% Fe/S

100 μm

C   Fe

100 μm

D   S

100 μm