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The end of the Ediacaran: Two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA

E.F. Smith[1], L.L. Nelson[2], M.A. Strange[3], A.E. Eyster[2], S.M. Rowland[3], D.P. Schrag[2], and F.A. Macdonald[2]
[1]Department of Paleobiology, Smithsonian Institution, PO Box 37012, MRC 121, Washington, D.C. 20013-7012, USA
[2]Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, Massachusetts 02138, USA
[3]Department of Geoscience, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, Nevada 89154-4010, USA

ABSTRACT

Evaluation of hypotheses that relate environmental to evolutionary change across the Ediacaran-Cambrian transition has been hampered by a dearth of sections that preserve both the last appearance of Ediacaran body fossils and the first appearance of *Treptichnus pedum* within carbonate-rich strata suitable for chemostratigraphic studies. Here, we report two new exceptionally preserved latest Ediacaran fossil assemblages from the Deep Spring Formation at Mount Dunfee, Nevada (USA). Further, we report these occurrences in a high-resolution carbon isotope chemostratigraphic framework, permitting correlation on a regional and global scale. The lower of the two horizons, at the base of the Deep Spring Formation, hosts a body fossil assemblage that includes *Gaojiashania,* other vermiform body fossils, and possible *Wutubus annularis* interbedded with *Cloudina* shell beds. The upper of the two fossil horizons, in the Esmeralda Member of the Deep Spring Formation, contains *Conotubus* and occurs within the basal Cambrian negative carbon isotope excursion, establishing it as the youngest Ediacaran fossil assemblage discovered to date. This is the first report of *Gaojiashania*, *Conotubus,* and *Wutubus* in Laurentia, extending the known stratigraphic ranges and biogeographic distributions of these taxa to a global scale. These data refine the relative ages of defining characteristics of the Ediacaran-Cambrian boundary and confirm that a large perturbation to the carbon cycle and surface ocean conditions coincided with the extinction of Ediacaran organisms.

INTRODUCTION

The first major radiation of macroscopic multicellular life occurred during the Ediacaran Period. Although Ediacaran organisms likely represent a diverse assemblage of eukaryotic groups—including stem- and crown-group metazoans, algae, and extinct clades with no modern representatives—they are commonly collectively referred to as the "Ediacara biota" (Xiao and Laflamme, 2009; Erwin et al., 2011; Brasier et al., 2012). Across the Ediacaran-Cambrian transition, both macroscopic soft-bodied Ediacara biota and enigmatic, tubular metazoan biota (Cai et al., 2013; Tarhan et al., 2014) disappear from the fossil record. Although it has been suggested that the apparent extinction of Ediacaran organisms is a taphonomic artifact (Gehling, 1991), the pattern of biological turnover appears to be globally reproducible through a wide range of sedimentary facies (Buatois et al., 2014). There are a few isolated reports of purported "Cambrian survivors" of Ediacaran taxa (Hagadorn et al., 2000; Jensen et al., 1998), but more taphonomic and taxonomic studies are necessary to demonstrate that they are in fact true Ediacaran holdovers (Laflamme et al., 2013).

Two general classes of hypotheses have been proposed to explain the disappearance of the Ediacaran organisms: (1) an extreme perturbation to surface environments and global geochemical cycles marked by a carbon isotope ($\delta^{13}C$) excursion triggered an extinction by generating abiotic stressors (e.g., Knoll and Carroll, 1999; Amthor et al., 2003), and (2) a growing metazoan community more gradually outcompeted Ediacaran soft-bodied non-metazoan taxa through ecological engineering and gradual biotic replacement (e.g., Erwin and Tweedt, 2012; Darroch et al., 2015). Calibrating the relative and absolute timing of changes in life and environment at this interval—the necessary framework to test these hypotheses—has been hindered by a lack of fossiliferous, carbonate-rich sections in which both paleontological and geochemical proxies can be integrated. Here we present new geological mapping, stratigraphic sections, geochemical data, and two newly discovered assemblages of Ediacaran body fossils from Mount Dunfee, Nevada (USA). These data allow us to directly relate the nadir of the multi-pronged basal Cambrian negative $\delta^{13}C$ excursion to the last appearance datum (LAD) of Ediacaran body fossils and the first appearance datum (FAD) of *Treptichnus pedum*, which defines the base of the Cambrian Period.

LITHOSTRATIGRAPHY

Ediacaran-Cambrian strata in the Great Basin of Nevada and California were deposited on the western margin of Laurentia (present coordinates) during the rift-drift transition (Armin and Mayer, 1983; Stewart, 1970), with the strata at Mount Dunfee (Figs. 1A and 1B) representing one of the most distal, carbonate-dominated sections that is preserved. The Ediacaran to lower Cambrian Deep Spring Formation consists of three members: the Dunfee (lower), Esmeralda (middle), and Gold Point (upper) Members, which are also exposed in the White-Inyo Mountains (Ahn et al., 2012; Nelson, 1962).

At Mount Dunfee, the contact between the Reed Dolomite and the overlying Deep Spring Formation has previously been placed at the transition from thickly bedded dolostone of the Reed Dolomite to distinctly bedded dolostone, limestone, and fine-grained siliciclastics of the Deep Spring Formation (Albers and Stewart, 1972). Here, because this gradational contact coincides with an irregular dolomitization front and lateral facies change, we refer to the bedded orange and gray dolostone and limestone beds above the massive, structureless dolostone as the "Reed–Deep Spring transition beds." At Mount Dunfee, these transition beds contain ooids, pisoids, oncoids, and shelly fossils in lenticular lag deposits (Gevirtzman and Mount, 1986).

We place the base of the Deep Spring Formation at a regionally distinct and easily recognizable sequence boundary (Fig. 1C). This sequence boundary is a sharp, karsted contact between a red, Fe-rich, glauconitic, peloidal limestone and a fine-grained siliciclastic facies (interbedded shale, siltstone, and sandstone) that contains mud chips, mud cracks, and syneresis cracks. The rest of the Dunfee Member consists of mixed carbonate-siliciclastic deposits representing slope to shallow subtidal settings (Gevirtzman and Mount, 1986).

The contact between the Dunfee and Esmeralda Members is marked by a pink to gray recrystallized dolostone capped by a karstic dissolution surface that is sharply overlain by green shoreface sandstone with mud cracks, interference ripples, and bed-planar trace fossils. The Esmeralda Member is 275–325 m thick and is composed of quartzitic and calcareous sandstone, stromatolitic and oolitic limestone, and minor siltstone and shale (Albers and Stewart, 1972).

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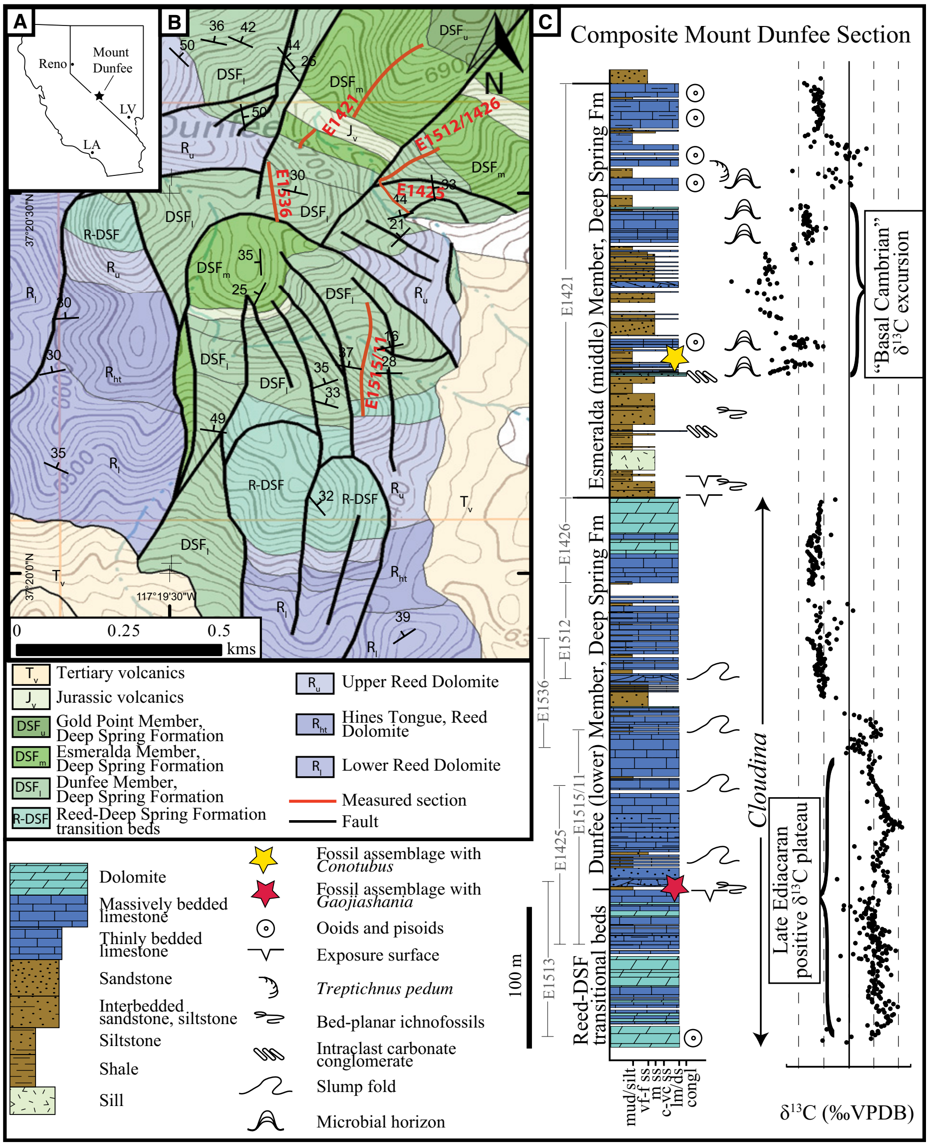

Figure 1. A: Locality map for Mount Dunfee, Nevada, USA (LA—Los Angeles, California; LV—Las Vegas, Nevada). B: Geologic map of Mount Dunfee with locations of measured sections. Section E1513 is northwest of figured map area (Base: 37°21′1.42″N, 117°19′37.85″W). C: Composite measured section with biostratigraphy and $\delta^{13}C$ chemostratigraphy for the upper Reed Dolomite and Deep Spring Formation. Stratigraphic horizons of two new Ediacaran body fossil assemblages are marked with stars. DSF—Deep Spring Formation; VPDB—Vienna Peedee belemnite. vf-f ss—very fine to fine-grained sandstone; m ss—medium-grained sandstone; c-vc ss—coarse to very coarse-grained sandstone; lm/ds—limestone and dolostone; congl—conglomerate.

CHEMOSTRATIGRAPHY

Detailed geologic mapping of Miocene down-to-the-southwest shingled normal faults in the Mount Dunfee area (Fig. 1B) and correlation of distinct marker beds enabled the construction of a composite measured section and a high-resolution $\delta^{13}C$ chemostratigraphic curve (see the GSA Data Repository[1]) of the upper Reed Dolomite through the Esmeralda Member of the Deep Spring Formation (Fig. 1C). At Mount Dunfee, the upper Reed Dolomite and lower Deep Spring Formation are characterized by a +3‰ to +4‰ $\delta^{13}C$ plateau (Fig. 1C). Above this interval, within the dolomitized and recrystallized upper ~50 m of the Dunfee Member, there is a downturn in $\delta^{13}C$ values to −2‰. The previously documented basal Cambrian negative $\delta^{13}C$ excursion (Corsetti and Kaufman, 1994) was reproduced in the middle of the Esmeralda Member, but new high-resolution data reveal additional structure to the excursion (Fig. 1C). Conglomerate with tabular carbonate intraclasts and microbial horizons A and B (Oliver and Rowland, 2002) contain $\delta^{13}C$ values as low as −6.2‰. Above this, the $\delta^{13}C$ values rise to −3‰ to −2‰ before they decrease to −9.5‰.

BIOSTRATIGRAPHY

Small shelly fossils were previously reported from the upper Reed Dolomite and the lower Dunfee Member of the Deep Spring Formation (Gevirtzman and Mount, 1986; Signor et al., 1987) and were later reinterpreted as *Cloudina* (Grant, 1990). In this study, shelly debris with circular cross-sections characteristic of *Cloudina* were discovered in the uppermost bed of the Dunfee Member, extending, in a chemostratigraphic and biostratigraphic context, the LAD of this Ediacaran index fossil (Fig. 1C). The algal fossil *Elainabella deepspringensis* occurs in brown to black siltstone above microbial horizon B and below microbial horizon C of the Esmeralda Member (Rowland and Rodriguez, 2014). The FAD of *T. pedum* occurs above the large negative $\delta^{13}C$ excursion, just a few meters below the top of the Esmeralda Member (Corsetti and Hagadorn, 2003). Additionally, two new exceptionally preserved Ediacaran body fossil assemblages were discovered in the Deep Spring Formation and are described in detail below.

Fossil Assemblage in the Dunfee Member of the Deep Spring Formation

The older of the two body fossil assemblages reported here occurs in siltstone and sandstone beds in the lowermost Dunfee Member of the Deep Spring Formation (Fig. 1C). Cast and mold impressions of annulated tubular fossils, identified as *Gaojiashania,* were discovered on multiple bedding surfaces within a 5–10-m-thick interval of strata composed of interbedded green shale, micaceous brown to green siltstone, and micaceous fine- to medium-grained sandstone (Figs. 2A and 2B). The specimens are 1.5–10 cm in length and 3–13 mm in diameter. Other fossils found in this stratigraphic interval include cast and mold impressions of possible *Wutubus annularis* (Fig. 2C), lightly pyritized compressions of smaller, tubular vermicular fossils with closed apices (Fig. 2D), and possible algal fossils. Part and counterpart slabs were collected for five *Gaojiashania* specimens. Some of the fossiliferous horizons contain <1-cm-diameter subangular to rounded mud chips. Mud cracks, syneresis cracks, and hummocky cross-stratification are present both within and above the fossiliferous interval. Small (submillimeter- to millimeter-scale) trace fossils, including *Planolites*, *Bergaueria*-like traces, and rare traces resembling *Scolicia* and *Neonereites*, occur in this same interval (Gevirtzman and Mount, 1986). Body fossils described herein were recovered from three separate fault blocks around Mount Dunfee.

To date, all reports of *Gaojiashania* are from the late Ediacaran (ca. 551–541 Ma) Dengying

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[1] GSA Data Repository item 2016307, methods, measured sections, and carbon and oxygen data tables, is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org.

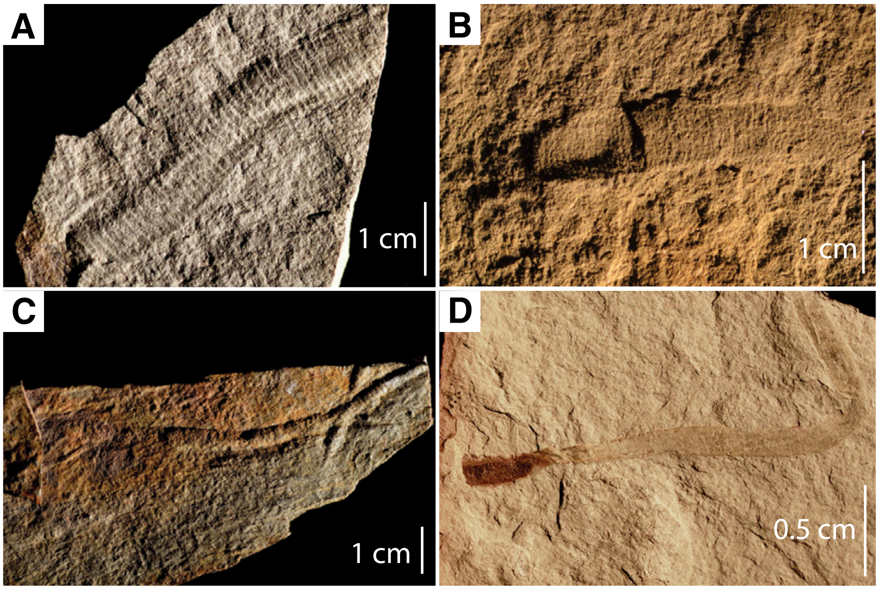

Figure 2. Photographs of fossils from the lower Dunfee Member of the Deep Spring Formation, Nevada, USA. A: Cast of *Gaojiashania* specimen preserved in siltstone. B: *Gaojiashania* specimen that preserves inner and outer fossil walls. C: Elongate, tapering, annulated fossils that we suggest should be assigned to the genus *Wutubus.* D: One of four vermicular-like body fossil specimens.

Formation (Cai et al., 2010; Lin et al., 1986) and Taozichong Formation (Hua et al., 2004) of South China. Like the specimens from South China, the Mount Dunfee specimens occur as compressed cylinders with densely spaced, transverse rings that appear to be articulated by a very thin membrane (Figs. 2A and 2B). Cai et al. (2011a) pointed to this feature as a way of distinguishing *Gaojiashania* from the late Ediacaran ribbon-shaped fossil *Shaanxilithes ningqiangensis* that is composed of serially arranged discoidal units (Meyer et al., 2012). However, more recently, Tarhan et al. (2014) interpreted the transverse ridges of *Shaanxilithes* specimens from India as representing anatomical wall thickenings of a tubular organism. On the basis of morphological characteristics, we classify the Mount Dunfee fossils as *Gaojiashania*, but acknowledge that these two fossil genera could be the same organism.

Three specimens of an additional annulated tubular taxon, which differ in size and morphology from *Gaojiashania*, also occur in the Dunfee Member assemblage. These specimens are characterized by a narrower conical termination and are similar in size and morphology to *Wutubus annularis* specimens from the Shibantan Member (correlative with the Gaojiashan Member) of the Dengying Formation of South China (Chen et al., 2014) (Fig. 2C).

Fossil Assemblage in the Esmeralda Member of the Deep Spring Formation

The upper of the two fossiliferous horizons (Fig. 1C) at Mount Dunfee occurs in the middle part of the Esmeralda Member of the Deep Spring Formation in shale and siltstone beds between microbial horizons B and C (Oliver and Rowland, 2002). These fossils consist of narrow conical tubes with transverse annulations (Figs. 3A and 3B). The diameter of these tubular fossils is ~1 mm and the length of articulated specimens ranges from 0.5 to 3 cm. Cross-sections of the fossils are circular, and the narrow end of these fossils is tapered and closed (Fig. 3A). Non-uniform curvature is present in some of these fossils, and many of the specimens are characterized by funnel-in-funnel structure that is characteristic of the family Cloudinidae (Figs. 3A and 3B). These fossils are commonly stained orange or red, in contrast to the black, brown, or green matrix of the host siltstone and shale, most likely reflecting oxidation of a pyrite pseudomorph remnant of the original fossil wall. This same stratigraphic interval also contains the multicellular algae *Elainabella deepspringensis* (Rowland and Rodriguez, 2014).

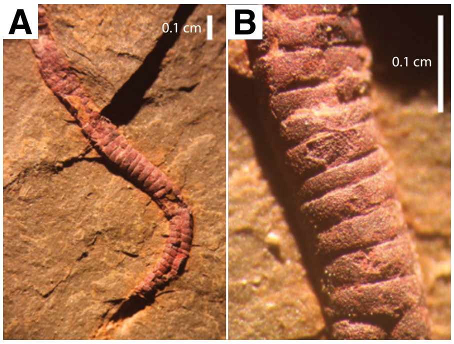

Figure 3. Photographs of pyritized *Conotubus* specimen from the Esmeralda Member of the Deep Spring Formation, Nevada, USA. A: *Conotubus* specimen that exhibits bending and high-relief preservation. B: High-resolution photograph of the same specimen that shows funnel-in-funnel structure.

Based on morphological similarity, we classify these annulated tubular fossils as *Conotubus*, which, like *Gaojiashania*, until now has been described only from the Gaojiashan Lagerstätte in South China (Cai et al., 2011a; Hua et al., 2007). The pyritization of the Dunfee specimens is also similar to that of the *Conotubus* fossils in South China (Cai et al., 2012; Schiffbauer et al., 2014). Like *Cloudina*, *Conotubus* is characterized by tubular morphology with nested cylindrical or funnel-shaped units, but what distinguishes the two genera is that *Cloudina* are interpreted to have been biomineralized (Grant, 1990), whereas *Conotubus* are either weakly biomineralized or non-biomineralized (Hua et al., 2007). The combination of non-uniform bends and the high relief of some of the fossil specimens described herein (Fig. 3A) suggests that the original wall could have been lightly calcified or composed of a resistant biomolecule such as chitin. Due to similarities in morphology and interpreted epibenthic life mode, *Conotubus* has been interpreted as a potential evolutionary precursor to *Cloudina* (Cai et al., 2011b; Hua et al., 2007). The data presented here, however, establish an inverse biostratigraphic relationship between *Conotubus* and *Cloudina,* in which *Conotubus* appears ~100 m above the LAD of *Cloudina* (Fig. 1C).

DISCUSSION

Two new, exceptionally preserved late Ediacaran body fossil assemblages at Mount Dunfee compose the only known Ediacaran Lagerstätten in the southwestern United States. Discovery of these fossil assemblages expands the biogeographic distributions and stratigraphic ranges of the tubular fossils *Gaojiashania*, *Conotubus,* and *Wutubus,* adding another late Ediacaran fossil locality to the global record, and specifically, one dominated by tubular metazoans. Furthermore, at Mount Dunfee, the biostratigraphic range of *Gaojiashania* overlaps with that of *Cloudina*, instead of occurring exclusively below *Cloudina* as it does in South China (Cai et al., 2010).

The two competing models for the cause of the end-Ediacaran extinction—an exogenous shock to surface environments or more gradual biotic replacement of soft-bodied Ediacaran organisms (e.g., erniettomorphs, rangeomorphs) by tubular metazoans—are not mutually exclusive, and earlier stages of biotic replacement could have preceded an ultimate extinction event. However, the data set presented here shows that the nadir of the $\delta^{13}C$ excursion, the LAD of Ediacaran tubular fossils, and the FAD of *T. pedum*, which defines the Precambrian-Cambrian boundary, all occur within ~100 m of stratigraphy. The large δ^{13}C excursion likely records a major perturbation to the carbon cycle through the addition of isotopically light carbon to the ocean-atmosphere system, and possibly concomitant acidification of the surface ocean. The data presented here represent the tightest relationship documented to date between the negative δ^{13}C excursion and biological turnover at the Ediacaran-Cambrian boundary, consistent with an environmental disturbance eliminating the last of the Ediacaran biota and paving the way for the Cambrian radiation.

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