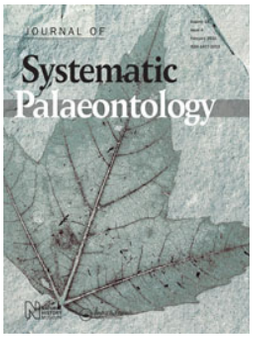


Journal of Systematic Palaeontology

ISSN: 1477-2019 (Print) 1478-0941 (Online) Journal homepage: https://www.tandfonline.com/loi/tjsp20

A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA

Tara Selly, James D. Schiffbauer, Sarah M. Jacquet, Emily F. Smith, Lyle L. Nelson, Brock D. Andreasen, John Warren Huntley, Michael A. Strange, Gretchen R. O'Neil, Casey A. Thater, Natalia Bykova, Michael Steiner, Ben Yang & Yaoping Cai

To cite this article: Tara Selly, James D. Schiffbauer, Sarah M. Jacquet, Emily F. Smith, Lyle L. Nelson, Brock D. Andreasen, John Warren Huntley, Michael A. Strange, Gretchen R. O'Neil, Casey A. Thater, Natalia Bykova, Michael Steiner, Ben Yang & Yaoping Cai (2020) A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA, Journal of Systematic Palaeontology, 18:4, 357-379, DOI: 10.1080/14772019.2019.1623333

To link to this article: https://doi.org/10.1080/14772019.2019.1623333

Published online: 22 Jul 2019.

Journal of Systematic Palaeontology, 2020
Vol. 18, No. 4, 357–379, http://dx.doi.org/10.1080/14772019.2019.1623333

A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA

Tara Selly[a,b]*, James D. Schiffbauer[b,a]*, Sarah M. Jacquet[b], Emily F. Smith[c], Lyle L. Nelson[c], Brock D. Andreasen[d,b], John Warren Huntley[b], Michael A. Strange[e], Gretchen R. O'Neil[f], Casey A. Thater[b], Natalia Bykova[g], Michael Steiner[h], Ben Yang[i] and Yaoping Cai[j]

[a]*X-ray Microanalysis Core Facility, University of Missouri, Columbia, Missouri 65211, USA;* [b]*Department of Geological Sciences, University of Missouri, Columbia, MO 65211, USA;* [c]*Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MA 21218, USA;* [d]*College of Agriculture, Food and Natural Resources, University of Missouri, Columbia, MO 65211, USA;* [e]*Department of Geoscience, University of Nevada, Las Vegas, NV 89154, USA;* [f]*Department of Geosciences, North Dakota State University, Fargo, North Dakota 58108, USA;* [g]*Trofimuk Institute of Petroleum Geology and Geophysics, Siberian Branch Russian Academy of Sciences, Novosibirsk 630090, Russia;* [h]*Fachbereich Geowissenschaften, Institut für Geologische Wissenschaften, Freie Universität Berlin, Berlin 12449, Germany;* [i]*Institute of Geology, Chinese Academy of Geological Sciences Baiwanzhuang Road 26, Beijing 100037, People's Republic of China;* [j]*Early Life Institute, State Key Laboratory of Continental Dynamics, and Department of Geology, Northwest University, Xi'an 710069, People's Republic of China*

(Received 11 November 2018; accepted 16 May 2019)

Owing to their temporal position during the decline of the classic Ediacara biota and the appearance of the more recognizable metazoans of the Cambrian Period, the terminal Ediacaran (~551–539 Ma) assemblages of tubular fossil forms hold potential to improve understanding of biotic turnover near the end of the Ediacaran Period. Cloudinid taxa, including the terminal Ediacaran index fossil *Cloudina*, are the most well studied of these Ediacaran tubular forms due to their global palaeogeographical distribution. Recent reports revealed ecosystems of tubicolous organisms from the Great Basin region, Nevada, USA, and assigned taxa to such genera as *Conotubus*, *Gaojiashania* and *Wutubus*, well known from contemporaneous Chinese deposits. Appreciating the role that these organisms may have played in the evolutionary history of metazoans and recognizing their potential global distribution, however, requires careful taxonomic study. Here, we detail pyritized fossils from the Deep Spring and Wood Canyon formations of Esmeralda and Nye counties, Nevada, USA, respectively. Our investigation focused on the most abundant tubular taxon from the Nevada sites, which was previously generically assigned to *Conotubus*. While outwardly similar in morphology to this Gaojiashan taxon, our investigation determines that those fossils previously figured as *Conotubus* are instead two distinct taxa. The first represents a new species of *Saarina* – *Saarina hagadorni* sp. nov. – a genus previously known only from the East European platform, and the second is established as a novel genus and species, *Costatubus bibendi* gen. et sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:pub:CC391194-FF96-4BDF-B9B2-E4361DA64A5B

Keywords: Nevada; Ediacaran; tubular fossils; cloudinids; *Saarina*; *Costatubus*

Introduction

The final ~12 million years of the Ediacaran Period (*c*. 551–539 Ma; Linnemann *et al*. 2019) represent a fulcrum in the evolution of complex multicellular eukaryotes, marking a transition between the peak diversity of the classic Ediacara biota and the subsequent rise of nearly all modern metazoan phyla during the Cambrian. This interval is characterized by a reduced diversity of earlier Ediacaran forms, with only a few representative rangeomorphs, arboreomorphs and erniettomorphs (Laflamme *et al*. 2013; Darroch *et al*. 2015), and an increased diversity of organisms with broadly cylindrical or tubular morphologies (called the 'wormworld fauna' by Schiffbauer *et al*. 2016). While these small, tubular fossils of the terminal Ediacaran may not look as charismatic as those from either earlier Ediacaran assemblages or post-'Cambrian Explosion' lagerstätten, they bore witness to several key ecological and environmental events at the dawn of animals (Fike *et al*. 2006; Marshall 2006; Schiffbauer *et al*. 2016; Darroch *et al*. 2018).

The cosmopolitan distribution and stratigraphical range of the terminal Ediacaran tubular fauna during the decline of the classic Ediacara biota (Darroch *et al*. 2015, 2016, 2018; Schiffbauer *et al*. 2016) is a direct reflection of their ecological success and plasticity (e.g. Germs 1972; Cai *et al*. 2014; Cortijo *et al*. 2015; Smith

*Corresponding authors. Emails: sellyt@missouri.edu schiffbauerj@missouri.edu

Published online 22 Jul 2019

et al. 2017; Warren *et al*. 2017). Their ecological success in the changing benthic ecological landscape can likely be attributed to several evolutionarily advantageous characteristics – foremost of which may have been their ability to biomineralize, even if only weakly (providing no structural support) to lightly (providing improved structural integrity). The biological construction of external shells at least impeded attacks from another novel group of organisms during this interval – drilling predators (Bengtson & Yue 1992; Hua *et al*. 2003, 2005). Given their pivotal position in the evolution of biologically mediated mineralization at the dawn of diverse metazoan life, these tubular taxa may have served as an evolutionary bridge across the Ediacaran–Cambrian transition (e.g. Yang *et al*. 2016; Han *et al*. 2017; Cai *et al*. 2017, 2019). Indeed, numerous biomineral tube-builders, similar in outward appearance and potentially phylogenetically related, are known from small shelly deposits of the early Cambrian, including *Feiyanella manica* Han *et al*., 2017, *Multiconotubus chinensis* Cai *et al*., 2017, *Rajatubulus costatus* (Mambetov in Missarzhevsky & Mambetov, 1981), and various others (e.g. Yang *et al*. 2016; Cai *et al*. 2019).

The most renowned of the Ediacaran shell-builders, *Cloudina* Germs, 1972, is an index fossil of the terminal Ediacaran owing to its cosmopolitan distribution and relatively high preservational potential. The cloudinids, more generally, are a group of tubular fossils characterized by multi-layered construction and repeating growth units, usually described as 'funnel-in-funnel' units, or collars. While the terminology 'cloudinid' should refer specifically to members of the Family Cloudinidae Hahn & Pflug, 1985 (including the genera *Cloudina* and *Conotubus* Zhang & Lin in Lin *et al*., 1986), its usage in the literature has also included form-taxa which may fit under the diagnosis for the family, but have not been taxonomically assigned as such. This previous inexact usage of the term 'cloudinid', conflating taxonomy and morphology, has led to some confusion in the literature as to what can be definitively called a cloudinid, taxonomically *sensu stricto*, versus a tubular fossil with cloudinid-like morphology. Thus, to follow suit with other Ediacaran morphological groupings (Xiao & Laflamme 2009), we here introduce the informal term 'cloudinomorphs' to represent this group of form-taxa, and suggest that future systematic revision may focus on better understanding the phylogenetic history of these organisms.

While *Cloudina* may have had the broadest palaeogeographical distribution of these form-taxa, new reports of tubular fossils from the south-western USA (Smith *et al*. 2016, 2017) are reinvigorating discussions on the biostratigraphical and ecological significance of cloudinomorphs in the terminal Ediacaran. With initial reports of a diverse tubular fauna, including specimens generically, but loosely, assigned to *Conotubus*, *Gaojiashania* Yang, Zhang & Lin in Lin *et al*., 1986 and *Wutubus* Chen *et al*., 2014, from south-central Nevada (Smith *et al*. 2016, 2017), the onus now shifts towards providing a thorough taxonomic assessment of these fossils to better understand their relationship to other terminal Ediacaran tubular forms. Herein, from these Nevada sites, we provide formalized and detailed descriptions of two distinct nested tubular taxa.

Locality, geological setting and taphonomy

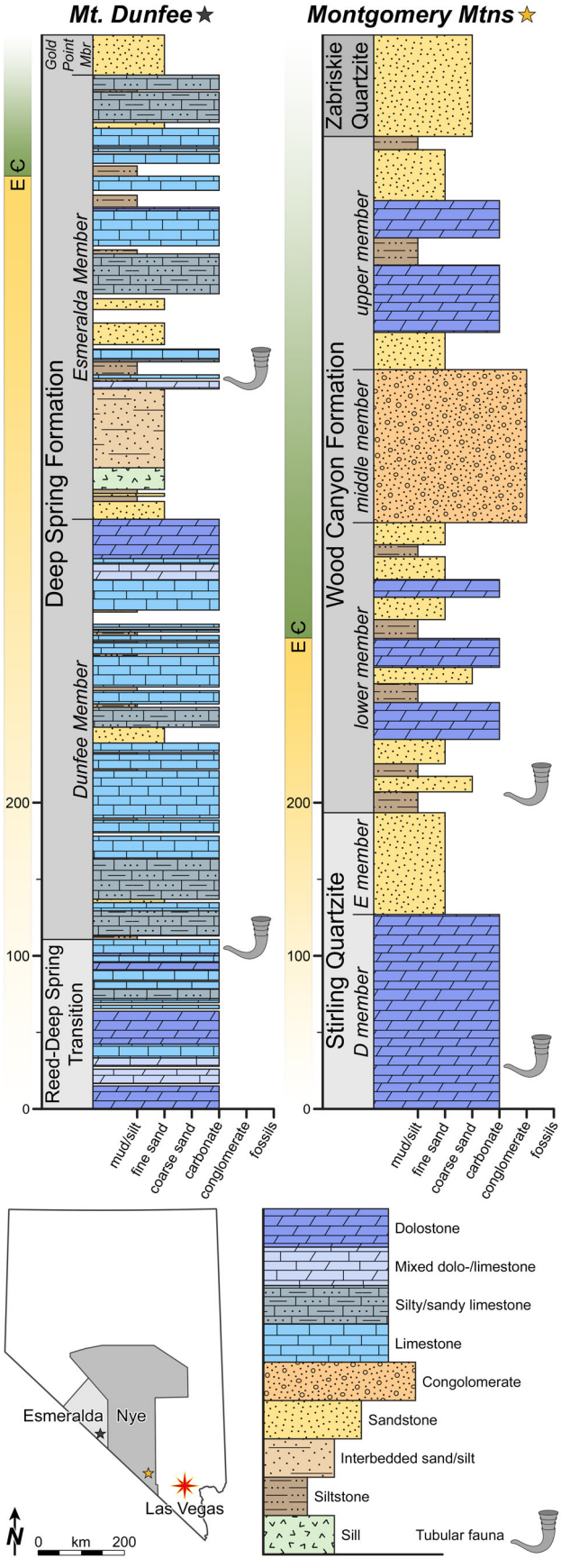
Tubicolous fossils were collected from both float material and *in situ* strata from the south-central Nevada Deep Spring and Wood Canyon formations. Deep Spring Formation fossils specifically came from two separate fault blocks of the Esmeralda Member at Mount Dunfee, Esmeralda County, and Wood Canyon Formation materials were collected from five fault blocks of the lower member at the Montgomery Mountains site, Nye County (Fig. 1).

Mount Dunfee

The Mount Dunfee fossil site is located *c*. 5 km to the east of Gold Point, Nevada, on the north-eastern side of Mount Dunfee proper. The fossils reported herein are specifically found in the lower portion of measured section E1421 of Smith *et al*. (2016) within the Esmeralda Member of the Deep Spring Formation. This locality is one of the most distal, carbonate-dominated sections of terminal Ediacaran–lower Cambrian strata preserved in the Great Basin (Stewart 1970).

Underlying the Deep Spring Formation are the Reed-Deep Spring transitional beds, as defined by Smith *et al*. (2016) to represent a gradational contact complicated by a dolomitization front and lateral facies change. In the White-Inyo Mountains, the upper member of the Reed Dolomite contains shelly fragments that were initially identified as *Wyattia* Taylor, 1966, which were later synonymized with *Cloudina* (Grant 1990).

The Deep Spring Formation comprises three members: the Dunfee, Esmeralda and Gold Point members (Albers & Stewart 1962; McKee & Moiola 1962; Nelson 1962; Ahn *et al*. 2012; Smith *et al*. 2016). The Dunfee Member consists of limestone, dolostone, siltstone, calcareous sandstone and quartzite, representative of slope to shallow subtidal settings (Gevirtzman & Mount 1986). Throughout the region, numerous shelly fossils have been reported from carbonates of the



Dunfee Member, including the tenuous hyolith *Salanytheca* sp., and tubular forms *Spinulitheca billingsi* Syssoviev, 1962, *Nevadatubulus dunfeei* Signor *et al*., 1987, *Coleolella* sp. (although later synonymized with *Nevadatubulus* by Signor *et al*. 1987), *Sinotubulites cienegensis* McMenamin, 1985 and *Cloudina* sp. (Cloud & Nelson 1966; Nelson & Durham 1966; Signor *et al*. 1983). While variably classified with each original report, the majority of these tubular taxa have since been synonymized with *Cloudina* sp. by Grant (1990).

The contact between the Dunfee and Esmeralda members is marked by an easily recognizable contact between pink to white recrystallized dolostone with an uppermost karstic dissolution surface and sharply overlying shoreface-intertidal sandstone to siltstone with bed-planar trace fossils (Stewart 1970; Smith *et al*. 2016). The Esmeralda Member is composed of quartzose and calcareous sandstone, stromatolitic and oolitic limestone, and minor amounts of siltstone and shale (Albers & Stewart 1972; Smith *et al*. 2016). The middle Esmeralda Member is fossiliferous, containing the tubicolous forms reported here (Smith *et al*. 2016), the putative algal fossil *Elainabella deepspringensis* Rowland & Rodriguez, 2014, and horizontal trace fossils, including possible worm burrows (Cloud & Nelson 1966; Stewart 1970; Rowland & Rodriguez 2014). The tubicolous fossils, including both smooth walled and funnel-in-funnel pyritized fossils, are found within the siltstones in the middle Esmeralda Member (Fig. 1; Smith *et al*. 2016). Near the top of the Esmeralda Member, the Ediacaran–Cambrian boundary is marked by the first occurrence of the trace fossil *Treptichnus pedum* Seilacher, 1955, which correlates well with the Basal Cambrian Carbon Isotope Excursion (BACE; Corsetti & Hagadorn 2000; Ahn *et al*. 2012; Smith *et al*. 2016).

Montgomery Mountains

The Montgomery Mountains site is located *c*. 3 km south-west of Johnnie, Nevada. The Wood Canyon Formation overlies the Stirling Quartzite and is divided into three informal members (lower, middle and upper), with the Ediacaran–Cambrian boundary placed within the lower member. The fossil materials reported herein were recovered 15–20 m below the boundary (Fig. 1).

The Stirling Quartzite is composed primarily of quartz arenite with minor amounts of conglomerate, siltstone

Figure 1. Stratigraphy of the Mt. Dunfee locality (black star in lower map inset), Esmeralda County, Nevada and the Montgomery Mountains locality (yellow star in lower map inset), Nye County, Nevada (after Smith *et al*. 2016, 2017).

and carbonate, which record deposition in a shoreface environment (Fedo & Prave 1991; Stewart 1970; Wertz *et al*. 1982). This unit has been divided into five informal members, A–E (Stewart 1966), and *Cloudina* sp. has been reported from carbonate materials in the D member in the Funeral Mountains, although these specimens are poorly preserved and potentially problematic (Langille 1974; Smith *et al*. 2017). The carbonate-rich C and D members are thought to be correlative to the Reed Dolomite from Mount Dunfee (Stewart 1966; Stewart 1970).

The lower member of the Wood Canyon Formation principally consists of interbedded siltstone and sandstone, deposited in shallow marine environments within three shallowing-upward parasequences that are capped by dolostone marker beds (Stewart 1970; Diehl 1974; Smith *et al*. 2017). The tubular fossils reported herein were recovered from the first of these parasequences, within a ~5 m siltstone to shale interval below the first dolostone marker. Ediacaran body fossils that have been previously described from the lower member include *Swartpuntia* Narbonne *et al*., 1997, erniettomorphs (Horodyski 1991; Smith *et al*. 2017), and several distinct tubular variants including *Archaeichnium* sp., *Cloudina* sp., *Corumbella* sp. and *Onuphionella* sp. (Hagadorn & Waggoner 2000, figs 3.5–3.10, 5.1–5.7; Smith *et al*. 2017). Stratigraphically higher in the lower member, above the second dolostone marker bed, the first appearance datum of *Treptichnus pedum* and the occurrence of other Cambrian trace fossils have been reported (Stewart 1970; Corsetti & Hagadorn 2000; Hagadorn & Waggoner 2000).

Fossil preservation

The majority of specimens collected from the Deep Spring and Wood Canyon formations are preserved through light to pervasive pyritization, much like those of the Gaojiashan Lagerstätte (Cai & Hua 2007; Cai *et al*. 2012). Fossils appear rusty orange to red in coloration, within light green to light brown to dark grey siltstones and silty to clayey mudstones. Many of the Nevada tubular fossils have been heavily weathered, indicated by the presence of framboidal iron oxide/oxyhydroxide pseudomorphs. Despite the degree of weathering, anatomical features, including tube structures and funnel rims, are still present and can be used in taxonomic identification of these fossils.

Material and methods

Tubular body fossils from 149 collected siltstone slabs were morphologically evaluated to assess the taxonomic composition and diversity of the Deep Spring and Wood Canyon assemblages. Samples were photomicrographed under standard optical microscopy using a Nikon SMZ1500 binocular microscope. Selected specimens (n = 10) with clear, distinguishable morphologies were further characterized using X-ray and electron microscopic imaging (μCT and SEM, respectively) at the University of Missouri X-ray Microanalysis Core facility. SEM analyses were conducted using both a five-segment high-definition backscattered electron detector for Z-contrast compositional imaging, and a cascade current variable pressure secondary electron detector for topographic imaging, both equipped on a Zeiss Sigma 500 VP scanning electron microscope. μCT analyses were conducted using a Zeiss Xradia 510 Versa.

A total of 185 individual specimens with identifiable morphologies were measured and classified. Though the vast majority of specimens could be identified as cloudinomorphs based on their nested and repeating structural units, fossils lacking distinct features – i.e. simple, smooth-walled tubes and those with poor preservational quality – could not be confidently classified and were therefore removed from further analyses. Height and width of repeating units were measured from scaled photographs using Fiji freeware (Schindelin *et al*. 2012). For each sample, the maximum (apertural) and minimum (apical) widths were assessed from the apertural-most repeating unit. In addition, from a random subsample of each taxon, interapertural spacing (i.e. the height of each funnel-unit) along with maximum funnel width was assessed through the full length of the sample. The dimensions of Nevada specimens were compared to fossils with broadly similar morphologies, including: (1) collections of the Gaojiashan Lagerstätte, housed at the Early Life Institute, Northwest University, Xi'an, China; and (2) rephotographed holotype material of saarinids from Gatchina, Russia (Sokolov 1965, 1967; Gnilovskaya 1996). Body size distributions of these tubicolous taxa were compared through two-dimensional kernel density plots (width *vs* apertural spacing). These analyses were conducted in R freeware (Version 3.4.1 [2017-06-30] – 'Single Candle') with the ggplot2 package (Wickham 2009).

Designated holotype and paratype specimens from the novel species and genus described herein are reposited at the Smithsonian Institution (USNM). Other samples are held at the home institutions of the collectors, including the University of Missouri, Johns Hopkins University, and the University of Nevada, Las Vegas.

Systematic palaeontology

General information

The cloudinomorphs are typically millimetric tubular fossils constructed by nested, repeating, collared cylindrical units – commonly referred to as 'funnel-in-funnel' structures or collars. Representative taxa include the mineralized type genus *Cloudina* and the weakly to non-mineralized *Conotubus* (Conway Morris *et al*. 1990; Grant 1990; Chen & Sun 2001; Cai *et al*. 2011, 2017). The cloudinomorph group expands, however, to include other comparable form-taxa, most of which have previously been left in open nomenclature above the genus level. Future systematic revision of taxa including *Saarina* Sokolov, 1965, *Rajatubulus* Yang *et al*., 2016, *Multiconotubus* and *Feiyanella* may consider the appropriateness of placement within the cloudinomorphs, although a thorough taxonomic revision of the group is beyond the scope of the current paper.

The cloudinomorphs are known to share some morphological similarity with the Saarinidae Sokolov, 1965. Unlike the conventional treatment of the cloudinids, the saarinids are defined as thin-walled, likely nonmineralized tubes, typically preserved via pyritization or organic carbonaceous compression. However, in the case of the type genus *Saarina*, originally designated under Saarinidae Sokolov, 1965, this taxon clearly has a comparable morphology to the cloudinomorphs, such as the genus *Cloudina*, notably their shared construction by collared, funnel-shaped, repeating units. In addition, cloudinids such as *Conotubus* are commonly preserved via pyritization and organic carbonaceous compression (Cai *et al*. 2012; Schiffbauer *et al*. 2014). Thus, we believe it appropriate to consider this genus within the broader cloudinomorphs.

While comparable tubular morphotypes are common in the late Ediacaran through early Cambrian, members of the cloudinomorphs are primarily distinguishable by their characteristic multilayered and nested tubular construction with smooth inner walls. This construction is distinct from tubes that lack family level (and higher) taxonomic assignment, including the lamellar *Sinotubulites* Chen, Chen & Qian, 1981, the transversely annulated *Sinospongia* Chen in Chen & Xiao, 1992; the four-fold annulated *Corumbella* Hahn *et al*., 1982; and the cross-walled *Ramitubus* Liu *et al*., 2008, *Sinocyclocyclicus* Xue *et al*., 1992, *Quadratitubus* Xue *et al*., 1992 and *Crassitubus* Liu *et al*., 2008. Although some reports have indicated cloudinomorph-like fossils from the early Cambrian (Vidal *et al*. 1994; Salak & Lescinsky 1999; Zhuravlev *et al*. 2009, 2012; Yang *et al*. 2016), the cloudinomorphs are broadly differentiated from Cambrian small shelly fauna, such as the non-segmented hyoliths, the trifold symmetric anabaritids, the rod-constructed conulariids, and the shallow cup-shaped nested laminae of *Spygoria* Salak and Lescinsky, 1999 (Conway Morris & Chen 1990; Bengtson & Conway Morris 1992; Ivantsov & Fedonkin 2002; Malinky & Skovsted 2004; Malinky *et al*. 2009).

Terminology used for the description of cloudinomorphs herein broadly follows that of Cai *et al*. (2011, 2017), and is based principally on external visible and measurable morphological features. We have compiled a list of these morphological characteristics that may be useful for identifying cloudinomorphs and other similar tubular forms (Table 1).

Our investigation focused on the most abundant tubular taxon from the Nevada sites, which was previously generically assigned to *Conotubus* by Smith *et al*. (2016, 2017). These tubes have not been without internal complication, however, as the same specimen figured in Smith *et al*. (2016) as *Conotubus* was later refigured as *Gaojiashania* by Darroch *et al*. (2018). This is further compounded by the fact that the original type material of *Conotubus* had been thought lost, and a neotype was designated as a result by Cai *et al*. (2011). The *Conotubus* neotype shows some similarity with the Nevada tubicolous remains, but does not show the typical surface ornamentation of funnel-like segments as seen in the syntypes of Zhang and Lin (Lin *et al*. 1986). However, one of the syntypes of *Conotubus* has been rediscovered and it is now clear that the Nevada tubicolous fossils previously regarded as *Conotubus* by Smith *et al*. (2016) or *Gaojiashania* by Darroch *et al*. (2018) instead comprise two distinct taxa, neither of which are identifiable as *Conotubus*.

The higher level taxonomy and phylogeny of the cloudinomorphs remains largely unresolved, with interpretations ranging from algae (Beurlen & Sommer 1957; Tarhan *et al*. 2018) to eumetazoa (Germs 1972; Glaessner 1976; Hahn & Pflug 1985; Conway Morris *et al*. 1990; Grant 1990; Chen & Sun 2001; Hua *et al*. 2005; Cortijo *et al*. 2010; Vinn & Zatoń 2012). Owing to this uncertainty, systematic descriptions are focused on the genus level and below.

Incertae sedis

Genus ***Saarina*** Sokolov, 1965 emend.

Type species. *Saarina tenera* Sokolov, 1965 from the Rovno Horizon, Gatchina borehole number 13, Russia.

Diagnosis. After Sokolov (1965, 1967), translated by N. Bykova. Minor differences between the 1965 (p. 91) and 1967 (p. 203) diagnoses are here merged. "Tubes were likely very thin and do not show signs of chitinization, sculpture preserved through pyritization of the

Table 1. Distinguishing characteristics of select Ediacaran–Cambrian cloudinomorphs and other comparable cylindrical taxa. In composition, preservation of non-mineral forms is denoted in [brackets], where ker = kerogenization, py = pyritization and ph = phosphatization. An asterisk* in 'external features' notes that the structure indicated is only present in some species, not all, within the given genus.

Taxon		Original composition	External shape (apex to aperture)	Construction	Spacing of repeating unit	Open/closed repeating unit	Closed terminal apex	External features	Branching observed	Internal features	Reference
Cloudinomorphs	*Cloudina*	Biomineral	Conical	Adjacent funnels nested	Variable	Open	Yes	Transverse annulations*, thickened apical and apertural funnel rims	Yes	Smooth lumen	Cai *et al.* (2017)
	Conotubus	Weakly biomineral to non-mineral [Ker/Py]	Conical	Adjacent funnels nested	Irregular	Open	Yes	Transverse annulations, thickened apical and apertural rims	–	Smooth lumen	Cai *et al.* (2011)
	Costatubus	Weakly biomineral to non-mineral [Py]	Cylindrical	Adjacent barrels slightly nested	Uniform	Open	–	Smooth barrels	–	Smooth lumen	This report
	Feiyanella	Not reported [Ph]	Conical	Partially to fully nested cones	–	Closed base, open aperture	Yes?	Wrinkled cones	Yes	Transverse ridges, wrinkles	Han *et al.* (2017)
	Multiconotubus	Biomineral	Conical	Fully nested cones	–	Closed base, open aperture	Yes	Smooth cones	–	Smooth lumen	Cai *et al.* (2017)
	Rajatubulus	Biomineral	Cylindrical	Adjacent funnels slightly nested	Uniform	Open	–	Smooth funnels, strongly flared apertures	–	Cross-walls	Yang *et al.* (2016)
	Saarina	Non-mineral [Ker/Py]	Conical	Adjacent funnels nested	Uniform	Open	Partially?	Transverse wrinkles*, flared to furled apertures	–	Smooth lumen	This report; Gnilovskaya (1996)
Other cylindrical forms	*Annulatubus*	Not reported	Cylindrical	Undulatory, lunate annular ridges	Uniform	Open?	–	Fine transverse laminations	–	–	Carbone *et al.* (2015)
	Corumbella	Biomineral to non-mineral	Polyhedral, pyramidal, quadrangular	Adjacent rings slightly nested, helical	Uniform	Open	Attachment structures?	Smooth, angular rings	–	Internal septa	Babcock *et al.* (2005); Pacheco *et al.* (2015)
	Fusinia	Not reported	Cylindrical	Subrectangular serial units	Uniform	Closed?	Attachment structures	Concentric wrinkles	Yes	–	Droser & Gehling (2008)
	Gaojiashania	Non-mineral [Ker/Py]	Cylindrical	Ring and flexible bucket	Variable	Open	–	Transverse annuli	–	–	Cai *et al.* (2013)
	Rugatotheca	Biomineral	Cylindrical, conical	Corrugated cylinder	–	Open	–	Annular rugae, wrinkled cylinder	–	Transverse and longitudinal wrinkles	Yang *et al.* (2016)
	Sabellidites	Non-mineral [Ker]	Cylindrical	Fibrous cylinder	–	Open	–	Furrows, wrinkled cylinder	–	Smooth lumen	Moczydłowska *et al.* (2014)
	Sekwitubulus	Not reported	Cylindrical	Rigid, annular ridges	Uniform	Open?	Tentaculate disc	Fine perpendicular lineations	–	–	Carbone *et al.* (2015)
	Shaanxilithes	Non-mineral [Ker]	Ribbon-like	Stacked lensoids or discs	Uniform	Closed?	–	–	–	Smooth lumen	Meyer *et al.* (2012)
	Sinotubulites	Biomineral	Cylindrical, prismatic	Fully nested, multilayered cylinders	–	Open	–	Transverse corrugations, longitudinal ridges*	–	Smooth lumen	Cai *et al.* (2015)
	Somatohelix	Non-mineral	Cylindrical	Sinuous tube, helical	–	Open	Yes?	Smooth?	–	Smooth?	Sappenfield *et al.* (2011)
	Vendoconularia	Non-mineral	Conical, hexagonal	Transverse ridges	Uniform	Open	Yes	Fine linear, striated thickenings	–	Longitudinal bands	Ivantsov & Fedonkin (2002); Van Iten *et al.* (2005)
	Wutubus	Not reported	Conical	Uniserial inflated ring-like annulae	Uniform	Open?	Strong basal taper	Smooth annulae	–	–	Chen *et al.* (2014)

organic membrane. Tubes are large, up to 2–7 mm in width. Funnel-like segmentation is regular with a clear and sharp edge. Lower Cambrian of the East European platform, late Precambrian(?) of Tian Shan. Three species are known."

Emendment from Gnilovskaya (1996, p. 548): "The receptacle of the organism is tubular; at its initial stage it is ampullaceous, distinctly articulated, and modeled on funnels closely inserted into one another. The outlines of the lateral margins of funnels in different species may be direct, convex, or concave. The receptacle of the organism was originally organic; its surface pyritized after fossilization."

Type species *S. tenera* Sokolov, 1965. After Sokolov (1967, p. 203), translated by N. Bykova: "Tubes are constructed as dense funnels with clear and relatively thicker edges. Edges form roll-like structures, sometimes coupled. Tube diameter is approximately 3.5–5.0 mm, the distance between funnel edges (segments) is 0.5–0.7 mm."

Emended diagnosis. Straight, curving, or abruptly bent slightly conical tube. Tubes developed regularly spaced funnel-shaped collars. Apertural ends open, with distinctly thickened rim at apertural edge. Lateral shape of funnel-like units variable. Tube wall shows no evidence of original biomineralization, or of branching. Interior lumen of tube smooth.

Dimensions. Tubes reach up to *c.* 75 mm in length, aperture diameter constrained to less than *c.* 5 mm, interapertural spacing is consistent at less than *c.* 1 mm.

Remarks. *Saarina* is defined by an organic walled tube composed of regularly spaced funnel-like collared units. Showing the common funnel-like collared construction of the cloudinomorphs, *Saarina* displays no indications of biomineralization, branching, budding, internal septa or cross-walls. These characteristics differentiate *Saarina* from other genera, including the biomineralized and sometimes branching *Cloudina* (Grant 1990; Hua *et al*. 2007) and the irregularly spaced funnel-like transversely annulated units of *Conotubus* (see Cai *et al*. 2011, fig. 3 for examples). *Saarina* is further differentiated from other coeval and outwardly similar tubes, such as the non-nested *Gaojiashania* (Cai *et al*. 2010, 2013), the ribbon-like *Shaanxilithes* Xing, Yue & Zhang in Xing *et al*., 1984, the multi-layered *Feiyanella*, and the multi-layered, cone-in-cone *Multiconotubus*.

Saarina hagadorni sp. nov.
(Figs 2A–F, 3, 4)

2017 *Conotubus* (Zhang & Lin); Smith, Nelson, Tweedt, Zeng & Workman: 7, fig. 4a.

Diagnosis. Straight or sinuous, slightly conical form; tube circular to oval in cross-section. Tube gently tapers from terminal aperture to base. Constructed of collared, funnel-like units. Repeating units are singular funnels, nested at apertural end, with regular interapertural spacing between successive funnel rims. Apertural ends of funnels are open, with conspicuously thickened apertural rims; apical rims absent. Funnels flare outward toward apertural rim, exterior of funnel unit concave. Exterior and interior of funnel units appear smooth; transverse annulations, wrinkle textures, septa or cross walls are absent. Tube may show sections defined by abrupt bending or change in orientation. Tube wall non-biomineralized.

Derivation of name. *Saarina hagadorni* sp. nov. is named in honour of palaeontologist and sedimentologist Dr James W. Hagadorn. Hagadorn's work on Ediacaran sections and fossils, including tubular fossils, in the South-West USA was influential for this study.

Holotype. USNM-E1636_009_B13, partially preserved (Figs 2A, 3A–D), from E1421 fault block float, Deep Spring Formation at Mt. Dunfee locality, Esmeralda County, Nevada, USA.

Paratypes. USNM-WCF_005_01, full specimen (Figs 2B, 3E) from Montgomery Mountains section of the Wood Canyon Formation, Nye County, Nevada, USA; USNM-MS_DS_12_3, partial specimen (Fig. 2D), from 5 m thick siltstone block from lower Esmeralda Member, Deep Spring Formation at Mt. Dunfee locality, Esmeralda County, Nevada, USA; USNM-N1601_FL_007_A4, partial specimen (Fig. 2E), from Montgomery Mountains section of the Wood Canyon Formation, Nye County, Nevada, USA.

Hypodigm. Total number of collected specimens identified = 88.

Occurrence. The late Ediacaran Wood Canyon and Deep Spring formations in south-central Nevada, USA.

Description. Tubes of *S. hagadorni* sp. nov. range from *c.* 1–75 mm in length and up to *c.* 4 mm in aperture diameter (Table 2). Funnels display a thickened, flared lip or rim at apertural opening (Figs 3B, C, 4A), although no apical rims are apparent. Spacing between consecutive apertural rims, as a measure of visible funnel height, is constrained to less than *c.* 1 mm. Interapertural spacing increases as funnels widen. Funnel-like units are smooth, lacking ornament, septa, cross walls and transverse annulations (Fig. 4B). Interior lumen of the tube also appears smooth (Fig. 4B, C). Tubes are circular-to-ovoid in cross-sectional shape, partly compressed in cross-section (Fig. 4D). In

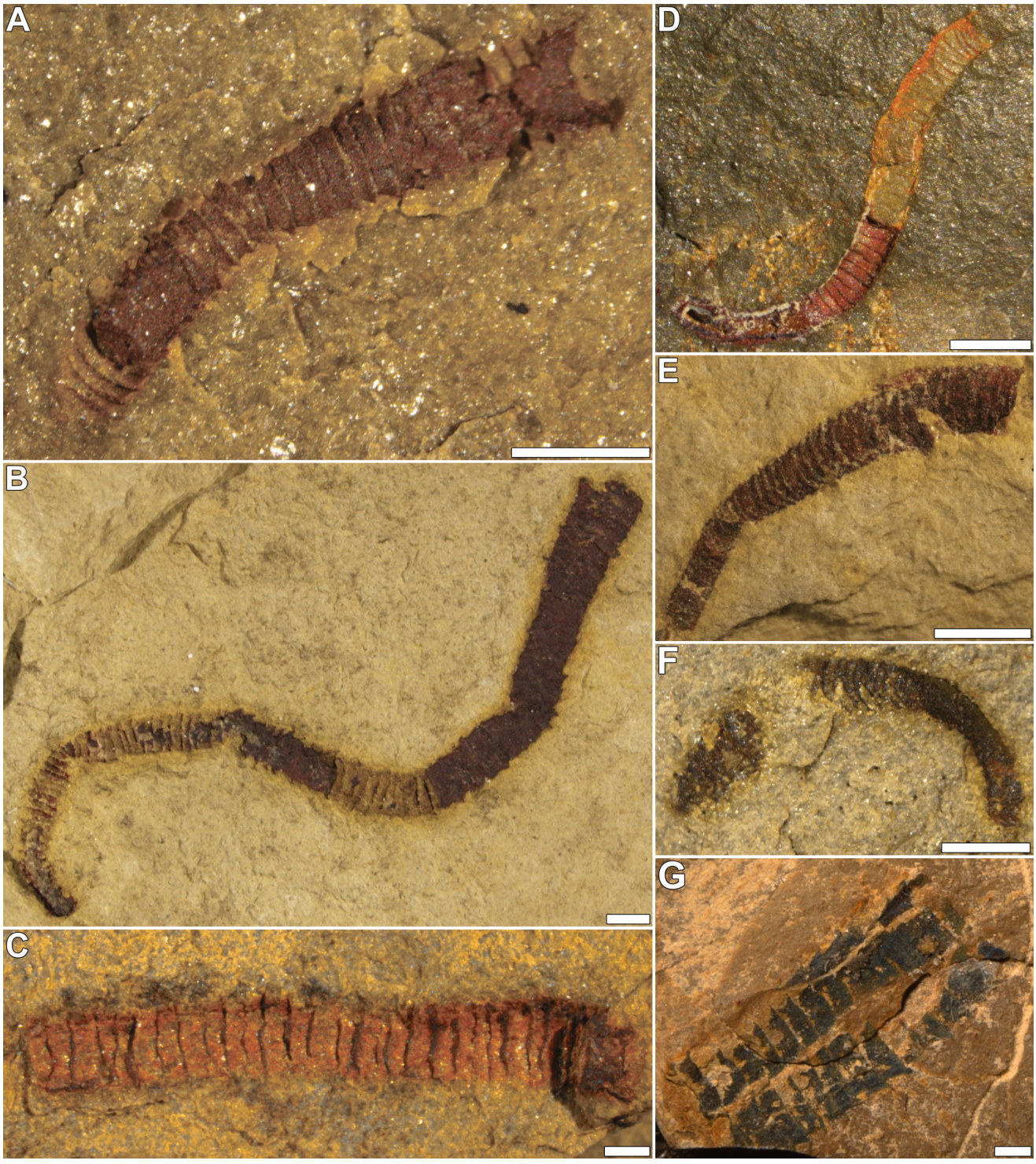
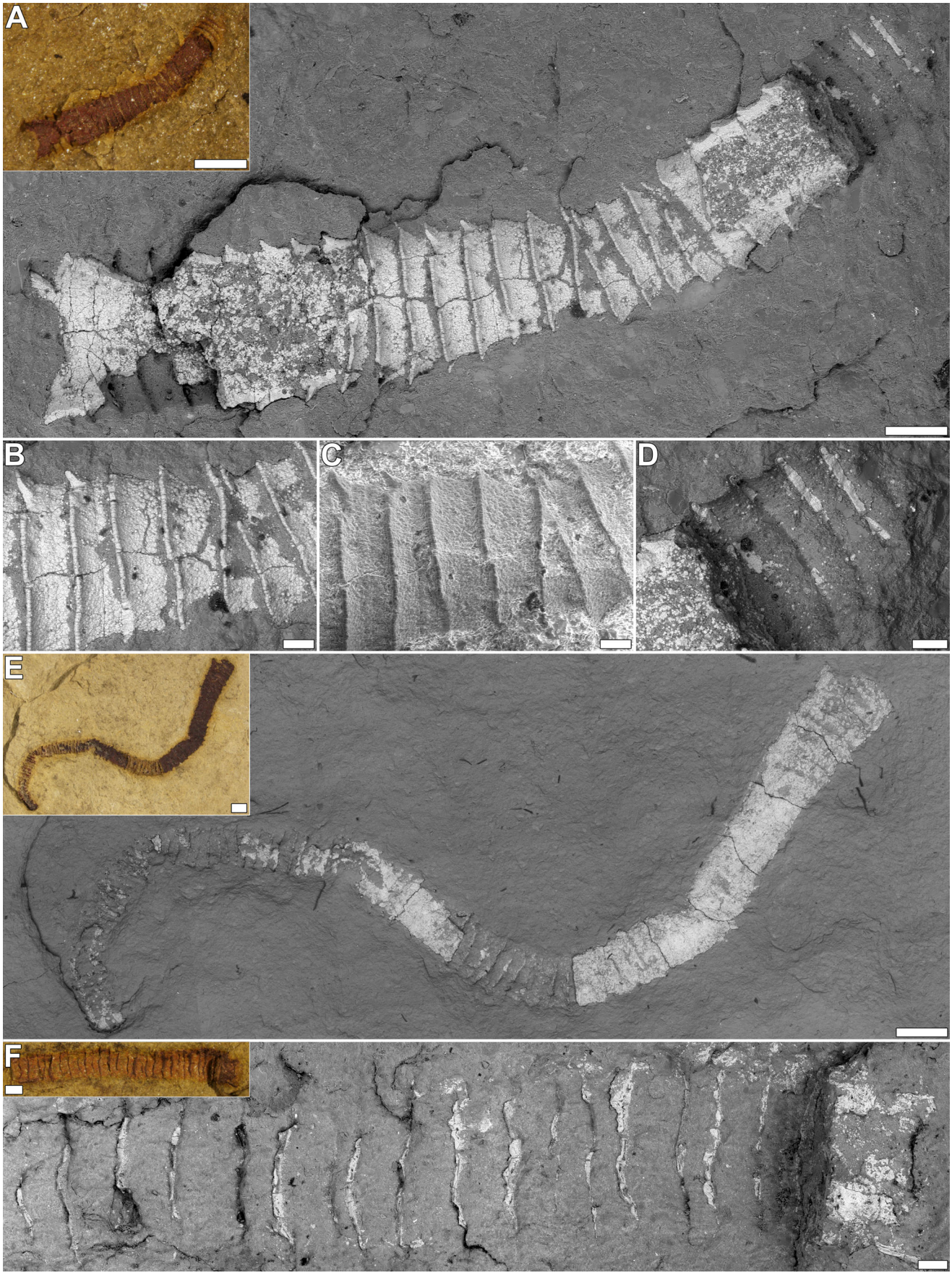


Figure 2. Photomicrographs of *Saarina* from Nevada localities (A–F) and the East European platform (G) for comparison. **A,** holotype of *Saarina hagadorni* sp. nov., sample USNM-E1636_009_B13. **B,** paratype, sample USNM-WCF_005_01. **C,** external mould with pyritized funnel rim flares, sample USNM-E1630_10_B1. **D, E,** paratypes of *Saarina hagadorni* sp. nov., samples USNM-MS_DS_12_3 and USNM-N1601_FL_007_A4, respectively. **F,** pyritized compression showing funnel rim imbrication, sample USNM-E1630_026_B2. **G,** holotype of *Saarina juliae*, rephotographed from Gnilovskaya (1996). All scale bars = 1 mm.


A
B
C
D
E
F

compacted specimens, rims are consistently imbricated. Tubes show no apparent indications of original biomineralization, as shown by plastic deformation; brittle fracture absent. Specimens are predominantly preserved as three-dimensionally pyritized tubes (or iron oxyhydroxides due to weathering), or pyritized but compressed tubes (Fig. 2F), with rarer examples of external moulds (Fig. 2C). Preservation of complete tubes is presumed to be uncommon.

Remarks. The two most morphologically similar fossil taxa to *S. hagadorni* sp. nov. are *Saarina juliae* Gnilovskaya, 1996 (Fig. 2G) and *Conotubus hemiannulatus* Zhang & Lin in Lin *et al*., 1986.

With respect to *C. hemiannulatus*, neither *S. hagadorni* sp. nov. reported here nor *C. hemiannulatus* from the Gaojiashan Lagerstätte show strong evidence of original biomineralization of their tube walls, as supported by flexible or plastic, but not brittle, deformation. These two species additionally lack septa, cross walls, and any other internal structures. However, *S. hagadorni* sp. nov. also lacks external, transverse annulations, a feature known in the best-preserved examples of *C. hemiannulatus* (Cai *et al*. 2011, fig. 3D, E). We acknowledge that the preservation of the Nevada material, as compared to that of the Gaojiashan, may be of lower taphonomic quality, but even the best-preserved *S. hagadorni* sp. nov. with very clearly defined apertural funnel rims show no further indication of exterior funnel ornament (Fig. 3A–D). Moreover, the collared funnel-like units in *S. hagadorni* sp. nov. flare more widely as compared to *Conotubus*. Further, *C. hemiannulatus* possesses thickened apical funnel rims which appear as faint annuli in the preserved tubes (Cai *et al*. 2011, fig. 3D), and on occasion doubly annulated apertural rims (Cai *et al*. 2011, fig. 3C), neither of which are observed in *S. hagadorni* sp. nov. In *C. hemiannulatus*, funnel rims and annulation are typically better developed in the anterior, apertural end of the tube as compared to the generally smoother posterior, apical end of the tube (Cai *et al*. 2011, fig. 3A). Comparatively, while funnel annulations are absent entirely in *S. hagadorni* sp. nov., apertural funnel rims are well defined and conspicuous throughout the length of its tube (Figs 2B, 3E). *Saarina hagadorni* sp. nov. also shows regular funnel spacing, from rim to nested funnel rim, as opposed to *C. hemiannulatus*, which demonstrates irregular spacing (Cai *et al*. 2011, fig. 3A). In terms of size comparisons of the measured specimens, *S. hagadorni* sp. nov. shows a more constrained distribution in maximum funnel width, typically exhibiting narrower tubes as compared to *C. hemiannulatus* (Table 2; Fig. 9A). The width range of *S. hagadorni* sp. nov. would have more comfortably fit within a previously recognized species of *Conotubus*, *C. mimicus*, but this species has been reconciled as an ontogenetic variant of *C. hemiannulatus* – specifically representing only the protoconch, or embryonic cone (*sensu* Cai *et al*. 2011).

The comparison of *S. hagadorni* sp. nov. to *S. juliae*, however, is not as well delineated. Principally, this is because the latter has been described and figured only once previously, with four specimen photographs in the original publication (Gnilovskaya 1996, fig. 1 а–г). The holotype from Gnilovskaya (1996) has now been refigured herein (Fig. 2G). In terms of similarities, both taxa are preserved via pyritization of an originally organic conotubular tube composed of flared funnel-like, collared, repetitive units. They can, however, be differentiated in several regards (the following characters of *S. juliae* are taken from the description of Gnilovskaya 1996). Considering size metrics, both *S. hagadorni* sp. nov. and *S. juliae* share comparable maximum tube widths (*c.* 3.9 mm *vs c.* 4.7 mm, respectively; Table 2), but with so few figured specimen of *S. juliae*, it is not possible to predict the size range for this species. On the other hand, the majority of *S. hagadorni* sp. nov. specimens are much narrower, falling between *c.* 0.5 and 1.5 mm in width. A comparable pattern is observed in the interapertural spacing of funnel units (Fig. 9A), such that the larger *S. juliae* has wider spacing between funnel rims (*c.* 0.7 mm) versus that of *S. hagadorni* sp. nov. (*c.* 0.2 mm). Further, *S. juliae* has a substantially smaller preserved length in the previously published specimen (*c.* 18 mm *vs c.* 75 mm here), although the overall length of this taxon is limited by their discovery in boreholes rather than outcrop. Nonetheless, total lengths for either species are likely fragmental and not taxonomically informative.

More robust morphological and preservational distinctions include the following: (1) *Saarina juliae* shows smoother sinuousity as compared to *S. hagadorni* sp. nov., which shows abrupt changes in tube growth direction (Fig. 2A, B, E) – more comparable to *C.*

Figure 3. SEM with light microscopy inserts of *Saarina hagadorni* sp. nov. **A–D,** holotype; **A,** backscattered electron image (BSE) mosaic (same sample as Fig. 2A, rotated *c.* 180°); **B,** detailed view of thickened apertural rim morphology in BSE; **C,** detailed view of thickened apertural rim morphology in secondary electron image (SE; same view as B); **D,** BSE of apertural rim detail in mouldic section or tube preservation. Note that thickened apertural rims are broken and remain within mouldic preservation. **E,** paratype of *Saarina hagadorni* sp. nov., BSE image mosaic (sample USNM-WCF_005_01, also figured in Fig. 2B). **F,** mouldic preservation showing isolated thickened apertural rims, BSE imaging (same sample as Fig. 2C). All scale bars = 1 mm.

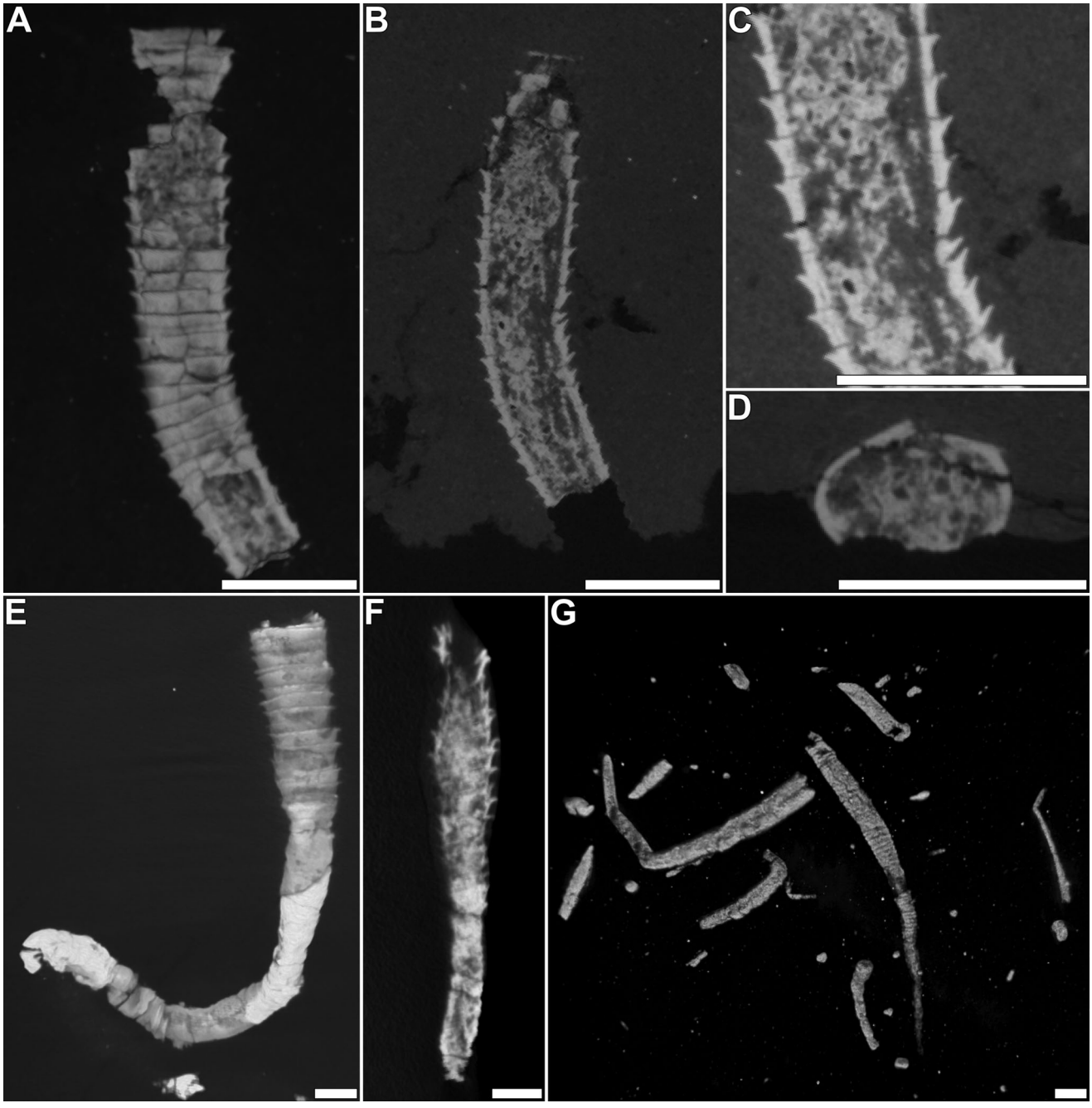


Figure 4. Tomographic μCT slices and volume renders of *Saarina hagadorni* sp. nov. **A–D,** holotype; **A,** 3D render of external tube wall; **B,** longitudinal 2D slice; **C,** longitudinal 2D slice detail of tube cross-section, showing funnel flare and smooth internal lumen; **D,** latitudinal 2D slice of the tube, showing subrounded/compressed cross-section. **E–F,** 3D renders of rock-enclosed specimens. Note presence of presumed rounded/curled apical termination in **E** and subtle funnel furl in **F. G,** 3D render of abundant rock-enclosed specimens. All scale bars = 1 mm.

hemiannulatus (Cai *et al*. 2011, fig. 6); (2) *Saarina juliae* in some specimens illustrates a much stronger tapering of the tube from anterior to posterior (Gnilovskaya 1996, fig. 1а, б, г), whereas *S. hagadorni* sp. nov. shows only minor taper (Fig. 2); (3) the funnels of *Saarina hagadorni* sp. nov. illustrate consistent and moderate concave-outward flare (Figs 2, 3). This is distinct from the pronounced, but less consistent, furl in *S. juliae* (Gnilovskaya 1996, fig. 1а–в), exhibiting enrolled apertural funnel rims; (4) the apertural rims of *Saarina hagadorni* sp. nov. funnels are conspicuously thickened (Fig. 3A–D), whereas no thickening is observed in *S.*

juliae; (5) *Saarina juliae* is described as having a smooth posterior portion composed of cup units, which is not apparent in *S. hagadorni* sp. nov. (Fig. 2B); (6) *Saarina juliae* appears to have indications of tube flexibility prior to pyritization, including some minor twisting of the tube structure as well as transverse wrinkling (Gnilovskaya 1996, fig. 1б), which are absent in *S. hagadorni* sp. nov.; and (7) although described as three-dimensionally preserved, *S. juliae* appears in all figured specimens (Gnilovskaya 1996, fig. 1 а–г) to have been compressed before pyritization (Fig. 2G), as opposed to the true three-dimensional nature of *S. hagadorni* sp. nov. in nearly all specimens. This latter feature, as well as the minor twisting and transverse wrinkling in *S. juliae*, may be taphonomically induced features such that post-burial onset of pyritization in *S. hagadorni* sp. nov. took place much more rapidly and thus retained three-dimensionality. Alternatively, this could indicate a higher level of inherent tube rigidity in *S. hagadorni* sp. nov., albeit still an organic walled vessel. We believe that these differences, in sum, justify the description of a new species designation within the genus *Saarina*.

Genus ***Costatubus*** gen. nov.

Derivation of name. From Latin, *costa*, rib, and *tubus*, pipe, with reference to the ribbed appearance of the exterior tube walls characteristic of this genus.

Type species. *Costatubus bibendi* gen. et sp. nov. (Figs 5A, B, 6, 7) from the Deep Spring Formation, Mount Dunfee locality, Esmeralda County, Nevada, USA.

Diagnosis. Tube straight or sinuous with open aperture. Tube wall constructed stout, stacked, exteriorly convex barrel-shaped units. In cross-section units are slightly crescentic to allantoid, ends pointed or rounded towards the interior of tube. Barrel-shaped units slightly overlap at adjacent interface, each unit inset at a mitred joint yielding indentations on exterior surface. Tube shows little-to-no taper, does not branch or split, or show surface annulations.

Remarks. While its small size and similar preservation could easily lead to confusion with the newly described *S. hagadorni* sp. nov., especially via simple optical examination, microscopic investigation reveals a distinct morphology of *Costatubus* gen. nov. that cannot be readily accommodated in any contemporaneous genus. *Costatubus* gen. nov. exhibits stout barrel-shaped, non-flaring construction with stacked repeating units – i.e. 'barrel-in-barrel'. The tube construction of this new genus with non- to lightly mineralized exoskeletons differs from the prominent members of the cloudinomorphs, such as the biomineralized funnel-shaped construction of *Cloudina* (Conway Morris *et al*. 1990), the non-mineralized funnel-shaped units of *Saarina* and *Conotubus*, which display overlapping and flared collars unlike that of *Costatubus* gen. nov. This new genus differs from other morphologically similar genera as well, including the tubes with ring-like thickenings of the late Ediacaran *Gaojiashania* and the transversely annulated, multilayered and non-segmented tube of the early Cambrian *Hyolithellus*.

Costatubus bibendi sp. nov.
(Figs 5–7)

2016 *Conotubus* – generic assignment only; Smith *et al*.: 913, fig. 3A, B.
2016 *Conotubus* – generic assignment only; Smith *et al*. in Schiffbauer: 976, fig. 1.
2018 *Gaojiashania* – generic assignment only; Darroch *et al*.: 2, fig. 1i.

Diagnosis. As for genus.

Dimensions. Lengths range up to *c.* 43 mm, with aperture diameters ranging up to *c.* 6.5 mm. Barrel-shaped units with height ranging up to *c.* 1 mm. By individual, visible barrel-shaped units have consistent heights.

Derivation of name. Derived from Latin, genitive case of *bibendum*, meaning to be drunk. Bibendum is the adopted name of the 'Michelin Tyre Man' symbol of the Michelin company, designed to be an anthropomorphic stack of tyres. Used here to denote the 'stack of tyres' morphology of the species.

Holotype. USNM-MS_DS_12, part and counterpart (A/B) of a single specimen (Figs 5A, B, 6, 7), from E1421 fault block float, Deep Spring Formation at Mount Dunfee locality, Esmeralda County, Nevada, USA.

Paratypes. USNM-DS_12 (Fig. 5C) and USNM-DS_34 (Fig. 5D), from E1421 fault block float, Deep Spring Formation at Mount Dunfee locality, Esmeralda County, Nevada, USA.

Hypodigm. Total number of collected specimens identified = 97.

Occurrence. The late Ediacaran Wood Canyon and Deep Spring formations in south-central Nevada, USA.

Description. Tubes typically range from *c.* 1–43 mm in length, which may record only fragmental length; unit aperture diameters *c.* 0.1–6.5 mm, *c.* 0.1–6 mm in apex diameter, and *c.* 0.1–1 mm in unit height (Table 2; Fig. 9A, C). Where barrel-shaped units overlap, there is a slight indentation at the joint, which gives rise to the ribbed appearance of the tube (Figs 5A, 6B). No distinct rims or collars are present on barrel units, although fine

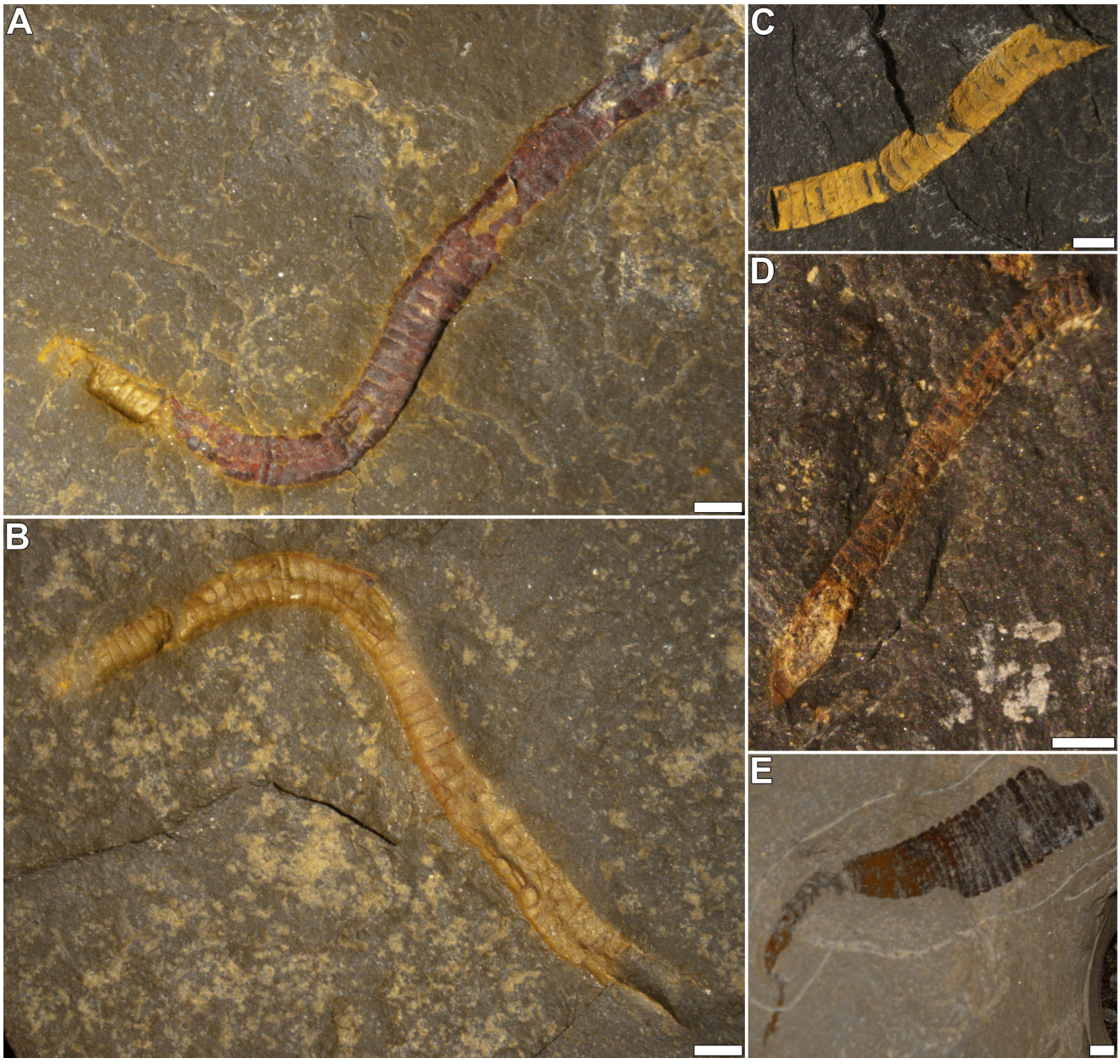


Figure 5. Photomicrographs of *Costatubus bibendi* gen. et sp. nov. from Nevada localities and the East European platform (E) for comparison. **A, B,** holotype part (rephotographed from Smith *et al*. 2016) and counterpart, sample USNM-MS_DS_12. **C,** paratype, sample USNM-DS_12. **D,** paratype, sample USNM-DS_34. **E,** holotype of *Costatubus kirsanovi*, rephotographed from Gnilovskaya 1996. All scale bars = 1 mm.

sediment accumulation between barrels at joint indentations may yield a rim-like appearance. In latitudinal cross-section, complete tubes are circular in shape (Fig. 7D). Compression-related ovality is rare; burial compression yields brittle fracture and tube collapse (Figs 6C, D, 7E). In longitudinal cross-section, walls of individual barrel units are crescentic to allantoid (Fig. 7B). Cross-sections of the barrel wall show a typically sharp apical end which comes to a terminal point and intersects in a mitred joint with the adjacent barrel unit which together form a stacked tubular construction (Fig. 7C). Tubes do not possess septa, cross walls, or show evidence of transverse annulations (Fig. 7B).

Remarks. Specimens of *C. bibendi* gen. et sp. nov. are preserved as pyritized (or iron oxy-hydroxides, due to weathering) tubes, with the vast majority illustrating three-dimensionality. Some examples of pyritized

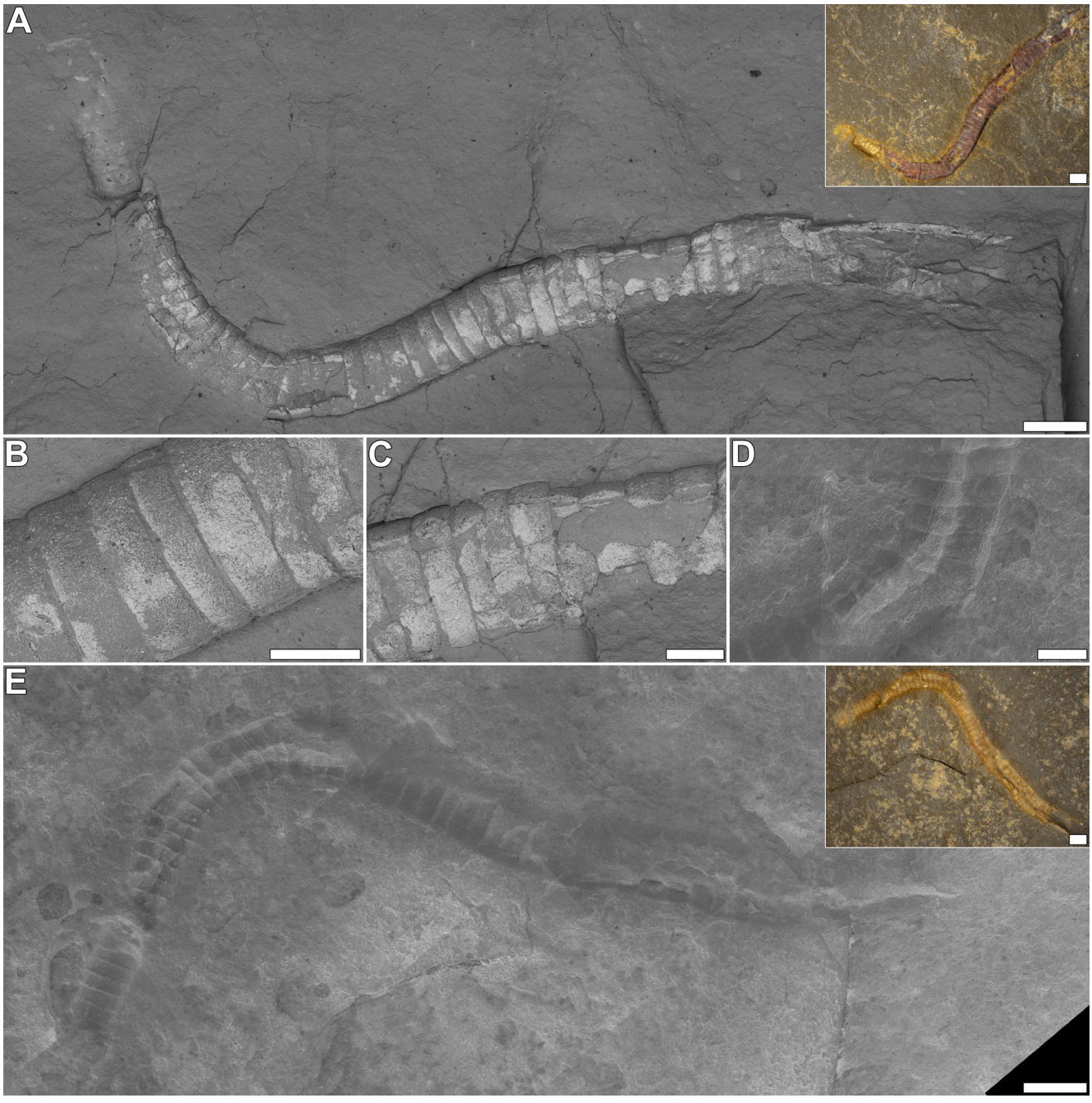


Figure 6. SEM with light microscopy inserts of *Costatubus bibendi* gen. et sp. nov. holotype part and counterpart from the Deep Spring Formation, Nevada. **A,** holotype part in mixed signal BSE:SE (same sample as Fig. 5A). **B,** detail of barrel morphology in mixed signal BSE:SE. **C,** detail of brittle fracture of the tube in mixed signal BSE:SE. **D,** detail of brittle fracture/tube collapse, in SE. **E,** holotype counterpart in SE mosaic (same sample as Fig. 5B). All scale bars = 1 mm.

compressions (Fig. 5C) and external moulds (Fig. 5E) are present. In most compacted specimens, barrels experience longitudinal brittle fracture and tube collapse, but otherwise show little distortion.

While numerous tube constructions have been reported from the late Ediacaran, the stacked barrel-shaped units represent a novel construction, which warrants the erection of a new genus. *Costatubus bibendi* gen. et sp. nov. is distinguishable from other species within the cloudinomorphs by its barrel-shaped elements, as opposed to funnels or conical tubes (see reconstructions of *S. hagadorni* and *C. bibendi* in Fig. 8).

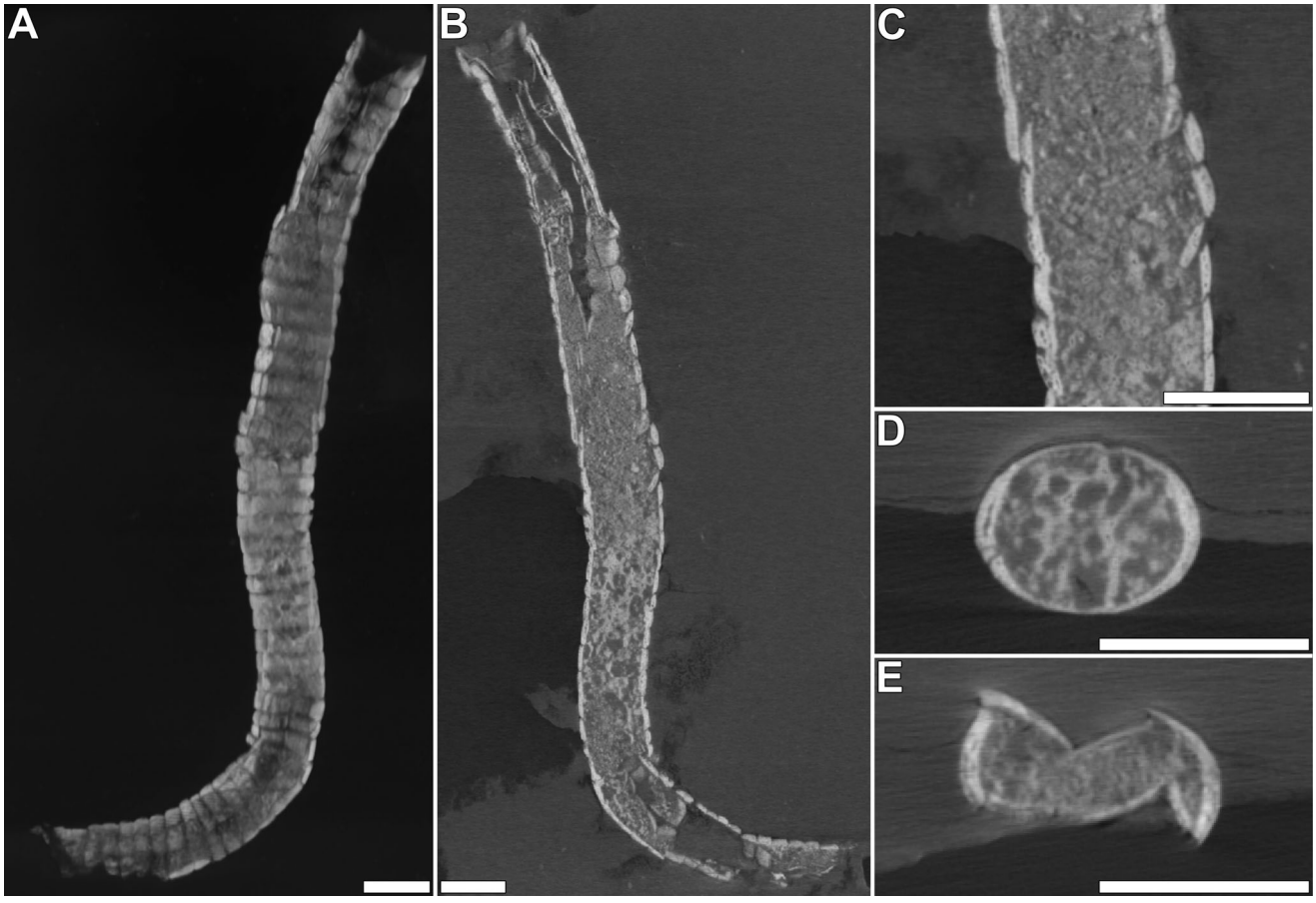


Figure 7. Tomographic μCT slices and volume renders of *Costatubus bibendi* gen. et sp. nov. holotype. **A,** 3D render of external tube wall. **B,** longitudinal 2D slice. **C,** longitudinal 2D slice detail of tube cross-section, showing allantoid to crescentic barrel wall cross-sections. **D,** latitudinal 2D slice, showing circular cross-section. **E,** latitudinal 2D slice showing brittle fracture and tube collapse. All scale bars = 1 mm.

Other late Ediacaran to early Cambrian tubes express similar morphologies to this taxon. One species of *Saarina*, *S. kirsanovi* Gnilovskaya, 1996, appears outwardly to share this barrel-in-barrel morphology (Gnilovskaya 1996, fig. 1 д, е; holotype refigured herein, Fig. 2H), but there are several key differences. First, the figured specimens of *S. kirsanovi* are uniformly flattened, and are described as composed of weakly convex arched cone units. Visualizing their cone unit wall structure is not possible. Secondly, *S. kirsanovi* is described as 'very elastic' owing to the presence of transverse wrinkles/folds. This is in stark contrast to the highly rigid tubes of *C. bibendi* gen. et sp. nov. Lastly, *S. kirsanovi* shows significant tapering of the tube, as measured on the holotype, a ratio of *c.* 7:1 from tube aperture to apex reported by Gnilovskaya (1996). Comparatively, *C. bibendi* gen. et sp. nov. shows minimal tapering (Fig. 5). *Costatubus bibendi* gen. et sp. nov. can also be easily differentiated from other tubular forms. For example, the terminal Ediacaran *Gaojiashania cyclus* Yang, Zhang & Lin in Lin *et al*., 1986 exhibits an inverse construction of rigid rings connected by concave, presumably flexible 'buckets' (Cai *et al*. 2013, fig. 4). While *Wutubus annularis* Chen *et al*., 2014 and potentially *Sekwitubulus annulatus* Carbone *et al*., 2015 display a similar 'stack of tyres' construction, there are no details on the serial nature of these tubes or their construction, and both possess holdfast structures (Carbone *et al*. 2015, fig. 3; Chen *et al*. 2014, fig. 5). Cambrian tubes such as *Hyolithellus* Billings, 1871 show remarkably similar traits to *C. bibendi* gen. et sp. nov., including tube diameter, original biomineralization, and comparable longitudinal brittle deformation. While similar, *Hyolithellus* differs in its tube wall thickness, which gradually increases towards the apex, external surface ribbed annulations, and densely laminated internal structure (Skovsted & Peel 2011, fig. 2).

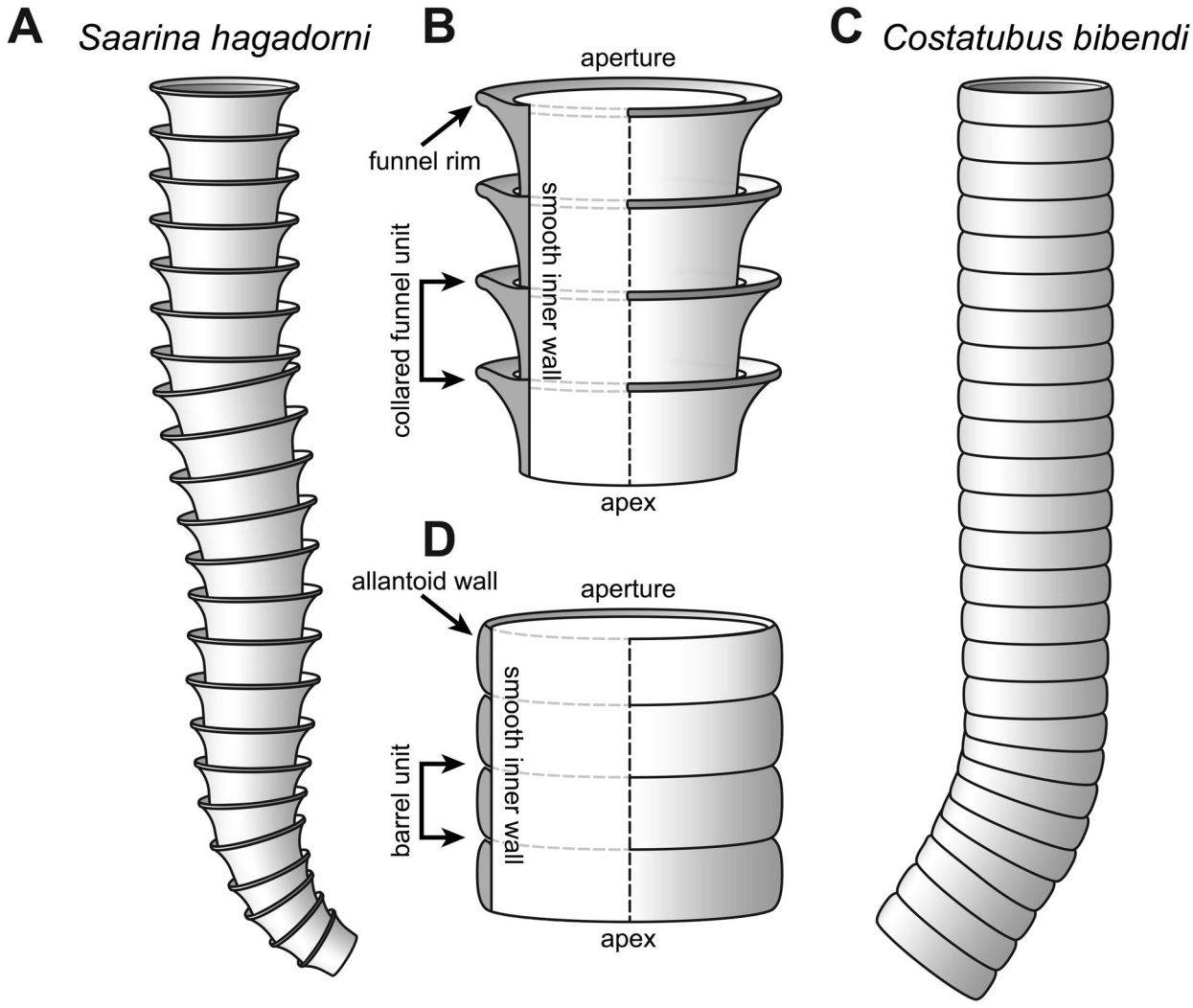


Figure 8. Schematic tube reconstruction of *Saarina hagadorni* sp. nov. (**A,** external morphology; **B,** detailed cross-section construction) and *Costatubus bibendi* gen. et sp. nov. (**C,** external morphology; **D,** detailed cross-section construction).

Costatubus kirsanovi (Gnilovskaya, 1996)
(Fig. 5E)

1996 *Saarina kirsanovi* Gnilovskaya: 549, fig. 1 д [d], e.

Remarks. *Saarina kirsanovi*, much like the newly erected genus *Costatubus* gen. nov., exhibits stout barrel-shaped, non-flaring construction with stacked repeating units – i.e. 'barrel-in-barrel' construction. Whereas the other two described species of *Saarina*, *S. juliae* as figured herein (Fig. 2G) and *S. tenera* (Sokolov 1967, fig. 2 1a), both show repeating collared funnel-like tube constructions, the placement of *S. kirsanovi* within the same genus is viewed as tenuous. Therefore, even with potential differences in recalcitrance of the tube wall structure between the rigid *Costatubus bibendi* and the presumably more malleable *Saarina kirsanovi*, we here propose transferal of *S. kirsanovi* to the new genus *Costatubus* gen. nov. based on the shape of their repeating unit structure. Differences delineating *C. bibendi* and *C. kirsanovi* to justify retaining two species within this new genus include the significantly stronger tube taper and wider barrel-unit per height ratios exhibited in *C. kirsanovi* (Table 2; Fig. 9A).

Discussion

Morphometrics

As the width of the anterior-most repeating unit was a consistent and observable feature, it serves as a proxy for body size for all identifiable tubicolous taxa (Table 2).

Table 2. Summary statistics of maximum width (mm) of anterior-most repeating unit of tubicolous taxa from Nevada, China and Russia.

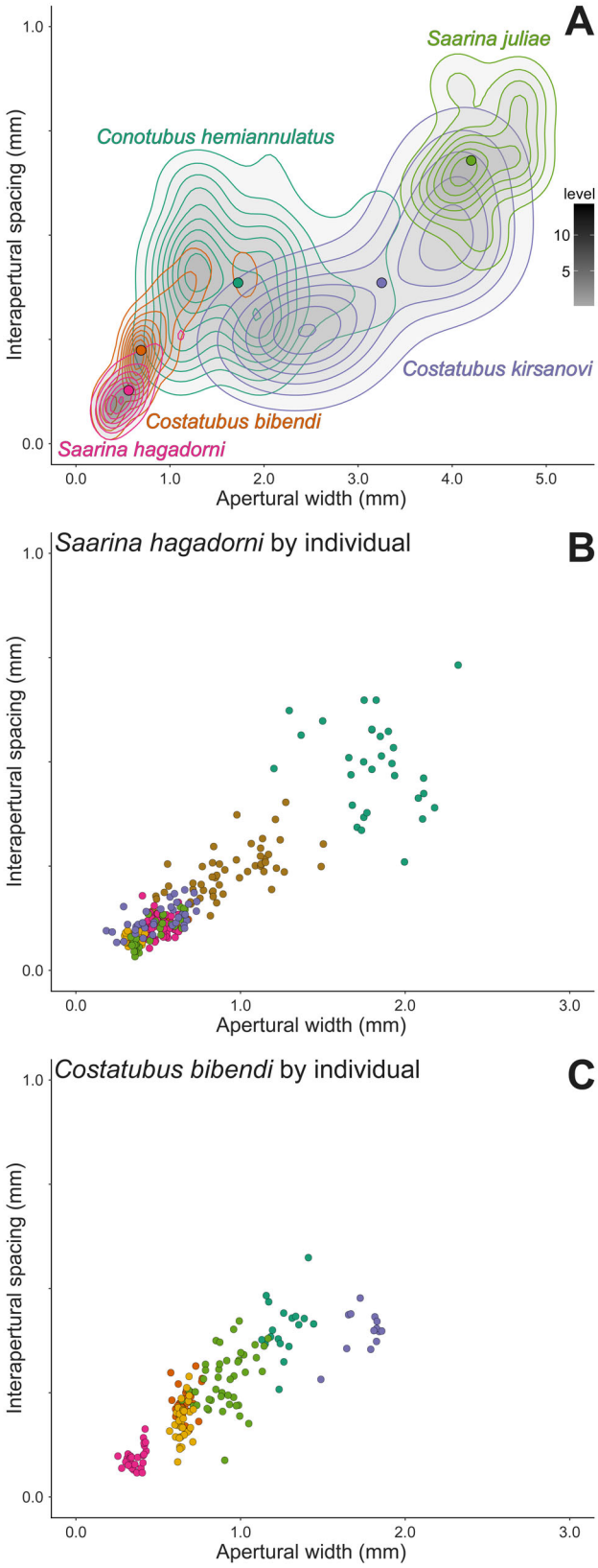
	n	Min	Median	Max	SD
Saarina hagadorni sp. nov. (NV)	88	0.253	0.739	3.921	0.674
Costatubus bibendi gen. et sp. nov. (NV)	97	0.217	1.091	6.363	1.397
Conotubus hemiannulatus (China)	1975	0.382	2.855	13.736	2.256
Saarina juliae (Russia)	1		4.736		
Costatubus kirsanovi (Russia)	1		4.151		

For comparison, Table 2 and Figure 9A also include the same metric from morphologically comparable taxa, *C. hemiannulatus* from the Gaojiashan Lagerstätte, and *S. juliae* and *C. kirsanovi* from the East European platform. From a randomly selected subset of our best-preserved samples, in each case including the designated holotype, we assessed the maximum width of each repeating unit and its corresponding interapertural spacing along the entire length of the specimen (Fig. 9B, C). As is observable here, while the Nevada taxa show significant overlap, their distributions are distinct from either *C. hemiannulatus, S. juliae* or *C. kirsanovi*, the distributions of which are less well constrained. This separation, along with morphological distinction, further supports our designation of *S. hagadorni* sp. nov. as a new species and *Costatubus* gen. nov. as a new genus. By individual both Nevada taxa show a general positive correlation between unit width and interapertural spacing. As *S. hagadorni* sp. nov. illustrates tapering of its tube, its funnel width by individual has a broader range than barrel width in *Costatubus* gen. nov. by individual (Fig. 9B, C, respectively). A possible alternative interpretation, specifically with regard to *S. juliae* and *S. hagadorni* sp. nov. given the seemingly linear trend that evolves from the observation of their funnel width by interapertural spacing (Fig. 9A), is that *S. hagadorni* represents an earlier ontogenetic stage of *S. juliae* – potentially explained as a taphonomic sorting effect in the Nevada sites versus the (limited) Russian materials. That no larger *S. hagadorni* tubes are recovered, but larger less well-defined tubes on the same scale as *S. juliae* are observed in the Nevada sites, may be an argument against this alternative hypothesis, albeit equivocal. However, we suggest that the morphological differences observed in the Nevada specimens indeed justify the establishment of a new species within *Saarina* at this time, but further investigation may be warranted.

Biomineralization and life mode

The two tubular taxa described here from south-central Nevada illustrate differences in their original tube construction, not just from the perspective of morphological structure but also from inferences of their original composition. Tubes of *C. bibendi* gen. et sp. nov. display brittle fracture, a feature interpreted here as evidence of a notably more robust and potentially lightly mineralized tube wall *in vivo*. However, the pyritization process responsible for the preservation of these tubes, compounded by later weathering diagenesis, overprinted any evidence of this taxon's original mineralogy. Thus, it follows that alternative explanations should be evaluated. One such alternative could be that the tube wall of *Costatubus* gen. nov. was pyritized very rapidly after burial, but before sediment compaction and lithification. Later compaction could have then produced the observed fracture. This brittle fracturing, however, is only seen in *Costatubus* gen. nov. specimens, and not observed in any *S. hagadorni* sp. nov., which instead show plastic deformation and moderate ovality imposed by compression. In order for the compaction fracture argument to be valid, it would follow that *S. hagadorni* sp. nov. is pyritized less rapidly, such that its tube wall was still malleable upon sediment compaction and lithification. Given that these two taxa are found within the same fossil horizons, it seems that the most parsimonious explanation requires a distinction in the inherent rigidity of their tube walls. Further, it is observed in *S. juliae*, which is also preserved largely via pyritization, that the tubes are compressed with indications of transverse wrinkling and twisting. Assuming *S. hagadorni* sp. nov. and *S. juliae* share comparable tube wall composition and robustness, *S. hagadorni* sp. nov. does not possess a rigid, mineralized tube wall – and that the three-dimensionality of its tubes in the Nevada localities are a result of rapid pyritization. If the interpretation of *Saarina* possessing a non-mineral tube is correct, the differences observed in the structural integrity of *Costatubus* gen. nov. tubes suggest a more robust original tube histology, potentially ranging from a thicker or more rigid organic composition through light, structurally relevant biomineralization.

There is only minor, perhaps parallel evidence to evaluate the possible life mode of *S. hagadorni* sp. nov. Comparison of the funnel-in-funnel and sinuous tube nature of *S. hagadorni* sp. nov. to other organic-walled cloudinomorphs could suggest that these organisms experienced an initial recumbent growth phase during earlier ontogeny before growing vertically from the



seafloor (Cai *et al*. 2011). This would serve to increase the stability of the tube as it grew larger, helping it maintain an upright orientation and elevating its apertural end for feeding purposes. The sharp changes in growth direction observed on some specimens may indicate rejuvenation from partial burial or event sedimentation that had knocked the tube over – effectively righting the tube back to a vertical position – similar to that inferred from *C. hemiannulatus* (Cai *et al*. 2011). *Costatubus bibendi* gen. et sp. nov. and its previously unreported tube structure, on the other hand, provides no means for evaluating life mode. We could only speculate based on comparison to other morphologically comparable forms whether *C. bibendi* gen. et sp. nov. is recumbent, akin to *Gaojiashania* (Cai *et al*. 2013), or upright, like *Hyolithellus* (Skovsted & Peel 2011). Further investigation into the community dynamics of these co-occurring taxa may be able to reveal additional details on their life mode and autecology.

Palaeogeography and depositional setting

With the discovery and taxonomic classification of *S. hagadorni* sp. nov. and *C. bibendi* gen. et sp. nov., we expand our understanding of diversity of the terminal Ediacaran tubular fauna. In order to understand the broader context and significance of this diversity, it is important to recognize both the palaeogeographical and palaeoenvironmental distributions of the cloudinomorphs. These organisms have reported occurrences in China (Chen *et al*. 1981, 2008; Ding *et al*. 1992; Zhang & Hua 2000; Chen & Sun 2001; Yang *et al*. 2016; Cai *et al*. 2017), Mexico (McMenamin 1985; Sour-Tovar *et al*. 2007), the south-western USA (Taylor 1966; Mount *et al*. 1983; Signor *et al*. 1983, 1987; Smith *et al*. 2016, 2017), Namibia (Germs 1972; Grant 1990; Grotzinger *et al*. 2000), Kazakhstan (Yang *et al*. 2016), Spain (Cortijo *et al*. 2010; Zhuravlev *et al*. 2012), Oman (Conway Morris *et al*. 1990), Brazil (Walde *et al*. 2015; Adorno *et al*. 2017), the East European platform (Gnilovskaya 1996; Sokolov 1965, 1967), the Siberian platform (Kontorovich *et al*. 2009; Terleev *et al*. 2011; Zhuravlev *et al*. 2012), and Paraguay (Warren *et al*. 2011, 2017), among other localities (see summary in

Figure 9. Body size cross-plots of tubicolous taxa. **A,** kernel density plots of apertural width versus interapertural spacing, by species. Large, black-outlined points represent median value of measured specimens. **B,** scatterplot of apertural width versus interapertural spacing of *Saarina hagadorni* sp. nov., by individual. Individual specimens are plotted in different colours. **C,** scatterplot of apertural width versus interapertural spacing of *Costatubus bibendi* gen. et sp. nov., by individual. Individual specimens are plotted in different colours.

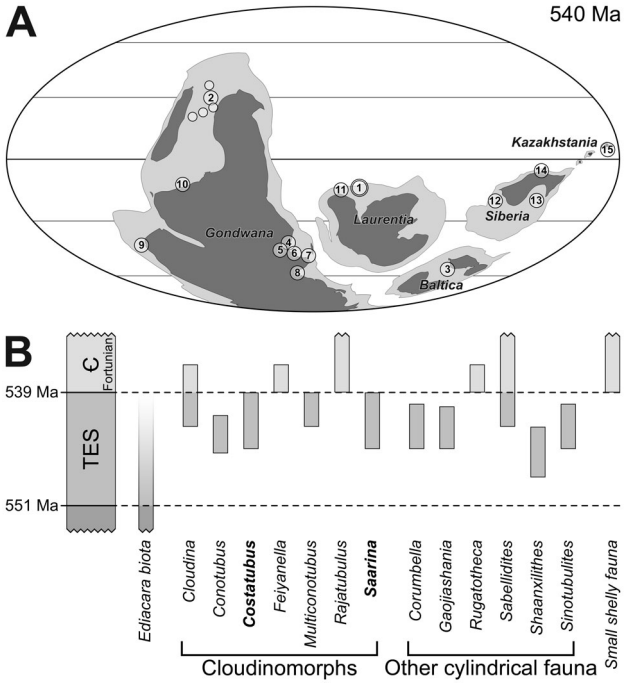


Figure 10. A, palaeogeographical reconstruction at 540 Ma using G-Plates. Numbered circles indicate localities where broader cloudinomorphs have been reported. Localities: 1, Nevada; 2, Gaojiashan (and other Chinese localities [small hollow circles]); 3, Baltica/East European platform; 4. Namibia; 5, Paraguay; 6, Uruguay; 7, Argentina; 8, Brazil; 9, Spain; 10, Oman; 11, Mexico; 12–14, Siberian and Mongolian localities; 15. Kazakhstan. **B,** generalized temporal constraints of broader cloudinomorphs and other Ediacaran–Cambrian tube-like forms.

Cai *et al*. 2017). Viewing the palaeogeographical distribution of the currently recognized cloudinomorph sites (Fig. 10, reconstructed from G-Plates), the Nevada localities examined here sat on the northern shelf margin of Laurentia and are definitively tropical. Tubular faunas known from Oman, Mexico, Kazakhstan, Siberia and Mongolia are of comparable palaeolatitudes. However, other localities, such as those from China, the East European platform and South America, are distributed within temperate palaeolatitudes. Whereas other terminal Ediacaran fossils, such as *Namacalathus* Grotzinger *et al*., 2000, have been interpreted to show latitudinal/climatic preference (Warren *et al*. 2017), the same cannot be observed for the broader cloudinomorphs. Nonetheless, while broad in palaeolatitudinal range, all of these localities were deposited in shallow shelf environments, but there are differences between the facies recorded. For instance, the Gaojiashan, dominated by obrution deposits of limestones and fine-grained siliciclastics (Cai *et al*. 2010), appears to be a comparatively deeper water setting, below storm wave base – although the obrution-deposited nature of these fossils may indicate transport from a shallower setting. The Nevada localities, on the other hand, are comparatively shallower settings. The fossils of the Mount Dunfee locality are contained within finer-grained siliciclastics, specifically silts between stromatolites and ooid shoals, bounded by coarser sands above and below. The Wood Canyon fossils sit in a shallower palaeoenvironment, within ∼ 5 m of silt beds also bounded by abundant sandstones (Fig. 1). These discussions of facies emplacement is undoubtedly cursory at present, but provide an interesting avenue for follow-up studies to consider potential facies dependence of the broader cloudinomorphs. In sum, the addition of these new taxa broadens the known diversity of the cloudinomorphs, and perhaps provides further utility for the use of wormworld faunal components as index taxa for the terminal Ediacaran – potentially pertinent in forthcoming attempts to establish Series- and Stage-level subdivisions of the Ediacaran Period (Xiao *et al*. 2016).

Conclusions

Our investigation of terminal Ediacaran tubular fossils from Nevada resulted in the establishment of two novel species. The first taxon, *Saarina hagadorni* sp. nov., features the characteristic regularly spaced, flared funnel-in-funnel, non-mineralized tube morphology of *Saarina* Sokolov, 1965, as described from the East European platform. We have designated the Nevadan representatives as a new species based on multiple morphological and preservational distinctions from previously reported species (Gnilovskaya 1996). In addition, a new taxon, *Costatubus bibendi* gen. et. sp. nov., is designated herein for its novel tubular construction, consisting of very regular, stout and tight units, appearing like barrel-shaped repeating segments – here denoted as 'barrel-in-barrel' morphology.

With the addition of a new species of *Saarina* in the form of *Saarina hagadorni* sp. nov. from a Laurentian locality, we expand the distribution of this genus to a new palaeocontinent. In addition, the new genus described here increases the diversity and morphological disparity of the terminal Ediacaran tubicolous fauna. In sum, the addition of these novel taxa to the widespread occurrences of the cloudinomorphs can augment the global picture of a prevalent and diverse tubular fauna in the shallow seas of the terminal Ediacaran Period. Continuing investigation of the tubular biota in the south-western USA may provide further insights into the evolution of biomineralization and the increasing ecosystem complexity of non Ediacara-type taxa prior to the Ediacaran–Cambrian boundary.

Acknowledgements

The authors wish to thank the members of the Ediacaran Subcommission of the International Commission on Stratigraphy for their useful discussion and assistance in the field; and also acknowledge Elena Golubkova (Institute of Precambrian Geology and Geochronology Russian Academy of Sciences) for providing new photographs of *Saarina juliae* and *Saarina kirsanovi* holotypes. TS, JDS, SMJ and JWH acknowledge the financial support of the University of Missouri College of Arts & Science Dean's Office and the John Roy Barker and Mary Smith Barker Faculty Enhancement Fund. JDS, BDA and CAT are supported by the National Science Foundation EAR CAREER-1652351; JDS and TS are supported by EAR/IF-1636643. EFS was supported by the Smithsonian Institution Peter Buck Fellowship, the Palaeontological Society Research Grant-PA-RG201703, and the NASA Astrobiology Institute Lewis and Clark Fund for Exploration and Field Research in Astrobiology. MAS would like to thank Jeremy Strange, Nate Strange and Greg Parsegov for assistance collecting at Mount Dunfee. NB is supported by the Russian Science Foundation (RSF #17-17-01241). BY is supported by the National Natural Science Foundation of China (No. 41502020). YC is supported by the Strategic Priority Research Program of Chinese Academy of Sciences (No. umc-XDB26010104). Fossils were collected under Paleontological Resources Use Permit No. N-94103, Bureau of Land Management, Nevada State Office.

ORCID

James D. Schiffbauer http://orcid.org/0000-0003-4726-0355
Sarah M. Jacquet http://orcid.org/0000-0001-6673-4929
Emily F. Smith http://orcid.org/0000-0001-9260-9355

References

Adorno, R. R., **do Carmo, D. A.**, **Germs, G.**, **Walde, D. H.**, **Denezine, M.**, **Boggiani, P. C.**, **Sousa e Silva, S. C.**, **Vasconcelos, J. R.**, **Tobias, T. C.** & **Guimaraes, E. M.** 2017. *Cloudina lucianoi* (Beurlen & Sommer, 1957), Tamengo Formation, Ediacaran, Brazil: taxonomy, analysis of stratigraphic distribution and biostratigraphy. *Precambrian Research*, **301**, 19–35.

Ahn, S. Y., **Babcock, L. E.** & **Hollingsworth, J.** 2012. Revised stratigraphic nomenclature for parts of the Ediacaran-Cambrian Series 2 succession in the southern Great Basin, USA. *Memoirs of the Association of Australasian Palaeontologists*, **42**, 105–114.

Albers, J. P. & **Stewart, J. H.** 1962. Precambrian (?) and Cambrian stratigraphy in Esmeralda County, Nevada. *USGS Professional Paper*, **1**, 24–27.

Albers, J. P. & **Stewart, J. H.** 1972. *Geology and mineral deposits of Esmeralda County, Nevada*. Mackay School of Mines, University of Nevada, 88 pp.

Babcock, L. E., **Grunow, A. M.**, **Sadowski, G. R.** & **Leslie, S. A.** 2005. *Corumbella*, an Ediacaran-grade organism from the Late Neoproterozoic of Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**(1–2), 7–18.

Bengtson, S. & **Conway Morris, S.** 1992. Early radiation of biomineralizing phyla. Pp. 447–481 in J. H. Lipps & P. W. Signor (eds) *Origin and early evolution of the Metazoa*. Plenum, New York, USA.

Bengtson, S. & **Yue, Z.** 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science*, **257**, 367–369.

Beurlen, K. & **Sommer, F. W.** 1957. Observações estratigráficas e paleontológicas sôbre o calcário Corumbá. *Boletim de Geologia e Mineralogia-DNPM*, **168**, 1–47.

Billings, E. 1871. Proposed new genus of Pteropoda [*Hyolithellus*]. *Canadian Naturalist and Geologist*, **6**, 240.

Cai, Y. & **Hua, H.** 2007. Pyritization in the Gaojiashan Biota *Chinese Science Bulletin*, **52**(5), 645–650.

Cai, Y., **Hua, H.**, **Xiao, S.**, **Schiffbauer, J. D.** & **Li, P.** 2010. Biostratinomy of the late Ediacaran pyritized Gaojiashan Lagerstätte from southern Shaanxi, South China: Importance of event deposits. *Palaios*, **25**, 487–506.

Cai, Y., **Schiffbauer, J. D.**, **Hua, H.** & **Xiao, S.** 2011. Morphology and paleoecology of the late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan Lagerstätte of southern Shaanxi Province, South China. *Precambrian Research*, **191**, 46–57.

Cai, Y., **Schiffbauer, J. D.**, **Hua, H.** & **Xiao, S.** 2012. Preservational modes in the Ediacaran Gaojiashan Lagerstätte: pyritization, aluminosilicification, and carbonaceous compression. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **326–328**, 109–117.

Cai, Y., **Hua, H.** & **Zhang, X.** 2013. Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte. *Precambrian Research*, **224**, 255–267.

Cai, Y., **Hua, H.**, **Schiffbauer, J. D.**, **Sun, B.** & **Yuan, X.** 2014. Tube growth patterns and microbial mat-related lifestyles in the Ediacaran fossil *Cloudina*, Gaojiashan Lagerstätte, South China. *Gondwana Research*, **25**, 1008–1018.

Cai, Y., **Cortijo, I.**, **Schiffbauer, J. D.** & **Hua, H.** 2017. Taxonomy of the late Ediacaran index fossil *Cloudina* and a new similar taxon from South China. *Precambrian Research*, **298**, 146–156.

Cai, Y., **Xiao, S.**, **Hua, H** & **Yuan, X.** 2015. New material of the biomineralizing tubular fossil Sinotubulites from the late Ediacaran Dengying Formation, South China. *Precambrian Research*, **261**, 12–24.

Cai, Y., **Xiao, S.**, **Li, G.** & **Hua, H.** 2019. Diverse biomineralizing animals in the terminal Ediacaran Period herald the Cambrian explosion. *Geology*, **47**, 380–384.

Carbone, C. A., **Narbonne, G. M.**, **Macdonald, F. A.** & **Boag, T. H.** 2015. New Ediacaran fossils from the uppermost Blueflower Formation, northwest Canada: disentangling biostratigraphy and paleoecology. *Journal of Paleontology*, **89**(2), 281–291.

Chen, M. & **Xiao, Z.** 1992. Macrofossil biota from upper Doushantuo Formation in eastern Yangtze Gorges, China. *Acta Palaeontologica Sinica*, **31**(5), 513–529.

Chen, M., **Chen, Y.** & **Qian, Y.** 1981. Some tubular fossils from Sinian–Lower Cambrian boundary sequences, Yangtze Gorge. *Bulletin, Tianjin Institute of Geology and Mineral Resources*, **3**, 117–124.

Chen, Z. & **Sun, W.** 2001. Late Sinian (tubular) metazoan fossils: *Cloudina* and *Sinotubulites* from southern Shaanxi. *Acta Micropalaeontologica Sinica*, **18**(2), 180–202.

Chen, Z., **Bengtson, S.**, **Zhou, C.**, **Hua, H.** & **Yue, Z.** 2008. Tube structure and original composition of *Sinotubulites*: shelly fossils from the late Neoproterozoic in southern Shaanxi, China. *Lethaia*, **41**, 37–45.

Chen, Z., **Zhou, C.**, **Xiao, S.**, **Wang, W.**, **Guan, C.**, **Hua, H.** & **Yuan, X.** 2014. New Ediacara fossils preserved in marine limestone and their ecological implications. *Scientific Reports*, **4**, 4180. doi:10.1038/srep04180

Cloud, P. E. & **Nelson, C. A.** 1966. Phanerozoic–Cryptozoic and related transitions: New evidence. *Science*, **154**, 766–770.

Conway Morris, S. & **Chen, M.** 1990. Tommotiids from the Lower Cambrian of South China. *Journal of Paleontology*, **64**(2), 169–184.

Conway Morris, S., **Mattes, B.** & **Chen, M.** 1990. The early skeletal organism *Cloudina*: new occurrences from Oman and possibly China. *American Journal of Science*, **290**, 245–260.

Corsetti, F. A. & **Hagadorn, J. W.** 2000. Precambrian–Cambrian transition: Death Valley, United States. *Geology*, **28**(4), 299–302.

Cortijo, I., **Mus, M. M.**, **Jensen, S.** & **Palacios, T.** 2010. A new species of *Cloudina* from the terminal Ediacaran of Spain. *Precambrian Research*, **176**, 1–10.

Cortijo, I., **Mus, M. M.**, **Jensen, S.** & **Palacios, T.** 2015. Late Ediacaran skeletal body fossil assemblage from the Navalpino anticline, central Spain. *Precambrian Research*, **267**, 186–195.

Darroch, S. A. F., **Sperling, E. A.**, **Boag, T. H.**, **Racicot, R. A.**, **Mason, S. J.**, **Morgan, A. S.**, **Tweedt, S.**, **Myrow, P.**, **Johnston, D. T.**, **Erwin, D. H.** & **Laflamme, M.** 2015. Biotic replacement and mass extinction of the Ediacara biota. *Proceedings of the Royal Society of London B*, **282**, 1–10.

Darroch, S. A. F., **Boag, T. H.**, **Racicot, R. A.**, **Tweedt, S.**, **Mason, S. J.**, **Erwin, D. H.** & **Laflamme, M.** 2016. A mixed Ediacaran-metazoan fossil assemblage from the Zaris Sub-basin, Namibia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **459**, 198–208.

Darroch, S. A. F., **Smith, E. F.**, **Laflamme, M.** & **Erwin, D. H.** 2018. Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution*, **33**, 653–663.

Diehl, P. 1974. Stratigraphy and sedimentology of the Wood Canyon Formation, Death Valley area, California. *Guidebook: Death Valley Region, California and Nevada: California Division of Mines and Geology Special Report*, **106**, 37–48.

Ding, L., **Zhang, L.**, **Li, Y.** & **Dong, J.** 1992. *The study of the Late Sinian–Early Cambrian biotas from the northern margin of the Yangtze Platform*. Scientific and Technical Documents Publishing House, Beijing, 156 pp.

Droser, M. L. & **Gehling, J. G.** 2008. Synchronous aggregate growth in an abundant new Ediacaran tubular organism. *Science*, **319**, 1660–1662.

Fedo, C. M. & **Prave, A. R.** 1991. Extensive Cambrian braidplain sedimentation: Insights from the southwestern USA Cordillera. Pp. 227–235 in J. Cooper & C. Stevens (eds) *Paleozoic paleogeography of the Western United States-II*. Pacific Section SEPM, Tulsa, Oklahoma.

Fike, D. A., **Grotzinger, J. P.**, **Pratt, L. M.** & **Summons, R. E.** 2006. Oxidation of the Ediacaran ocean. *Nature*, **444**, 744–747.

Germs, J. G. B. 1972. New shelly fossils from the Nama Group, South West Africa. *American Journal of Science*, **272**, 752–761.

Gevirtzman, D. A. & **Mount, J. F.** 1986. Paleoenvironments of an earliest Cambrian (Tommotian) shelly fauna in the southwestern Great Basin, USA. *Journal of Sedimentary Research*, **56**(3), 412–421.

Glaessner, M. F. 1976. A new genus of late Precambrian polychaete worms from South Australia. *Transactions of the Royal Society of South Australia*, **100**(3), 169–170.

Gnilovskaya, M. 1996. New saarinids from the Vendian of Russian Platform. *Doklady Akademii Nauk*, **348**, 89–93.

Grant, S. W. F. 1990. Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *American Journal of Science*, **290-A**, 261–294.

Grotzinger, J. P., **Watters, W. A.** & **Knoll, A. H.** 2000. Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology*, **26**(3), 334–359.

Hagadorn, J. W. & **Waggoner, B. M.** 2000. Ediacaran fossils from the southwestern Great Basin, United States. *Journal of Paleontology*, **74**(2), 349–359.

Hahn, G. & **Pflug, H. D.** 1985. Polypenartige Organismen aus dem Jung-Praekambrium (Nama-Gruppe) von Namibia. Polyp-like organisms from the upper Precambrian Nama Group of Namibia. *Geologica et Palaeontologica*, **19**, 1–13.

Hahn, G., **Hahn, R.**, **Leonardos, O.**, **Pflug, H. D.** & **Walde, D.** 1982. Körperlich erhaltene Scyphozoen-Reste aus dem Jungpräkambrium Brasiliens. *Geologica et Palaeontologica*, **16**, 1–18.

Han, J., **Cai, Y.**, **Schiffbauer, J. D.**, **Hua, H.**, **Wang, X.**, **Yang, X.**, **Uesugi, K.**, **Komiya, T.** & **Sun, J.** 2017. A *Cloudina*-like fossil with evidence of asexual reproduction from the lowest Cambrian, South China. *Geological Magazine*, **154**(6), 1294–1305.

Horodyski, R. 1991. Late Proterozoic megafossils from southern Nevada. Pp. 163 in *Geological Society of America Abstracts with Programs*, San Diego, CA.

Hua, H., **Pratt, B. R.** & **Zhang, L.** 2003. Borings in *Cloudina s*hells: Complex predator-prey dynamics in the terminal Neoproterozoic. *Palaios*, **18**, 454–459.

Hua, H., **Chen, Z.**, **Yuan, X.**, **Zhang, L.** & **Xiao, S.** 2005. Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*. *Geology*, **33**(4), 277–280.

Hua, H., **Chen, Z.** & **Yuan, X.** 2007. The advent of mineralized skeletons in Neoproterozoic Metazoa: new fossil evidence from the Gaojiashan Fauna. *Geological Journal*, **42**, 263–279.

Ivantsov, A. Y. & **Fedonkin, M. A.** 2002. Conulariid-like fossil from the Vendian of Russia: a metazoan clade across the Proterozoic/Palaeozoic boundary. *Palaeontology*, **45**(6), 1219–1229.

Kontorovich, A., **Sokolov, B.**, **Kontorovich, V.**, **Varlamov, A.**, **Grazhdankin, D.**, **Efimov, A.**, **Klets, A.**, **Saraev, S.**,

Terleev, A. & **Belyaev, S. Y.** 2009. The first section of vendian deposits in the basement complex of the West Siberian petroleum megabasin (resulting from the drilling of the Vostok-3 parametric borehole in the Eastern Tomsk region). *Doklady Earth Sciences*, **425**(1), 219–222.

Laflamme, M., **Darroch, S. A. F.**, **Tweedt, S. M.**, **Peterson, K. J.** & **Erwin, D. H.** 2013. The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat? *Gondwana Research*, **23**, 558–573.

Langille, G. 1974. Problematic calcareous fossils from the Stirling Quartzite. Pp. 204–205 in *Funeral Mountains, Inyo County, California: Geological Society of America Abstracts with Programs*, Geological Society of America, Boulder, CO.

Lin, S., **Zhang, Y.**, **Zhang, L.**, **Tao, X.** & **Wang, M.** 1986. Body and trace fossils of metazoa and algal macrofossils from the upper Sinian Gaojiashan Formation in southern Shaanxi. *Geology of Shaanxi*, **4**(1), 9–17.

Linnemann, U., **Ovtcharova, M.**, **Schaltegger, U.**, **Gärtner, A.**, **Hautmann, M.**, **Geyer, G.**, **Vickers-Rich, P.**, **Rich, T.**, **Plessen, B.** & **Hofmann, M.** 2019. New high-resolution age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion. *Terra Nova*, **31**, 49–58.

Liu, P., **Xiao, S.**, **Yin, C.**, **Zhou, C.**, **Gao, L.** & **Tang, F.** 2008. Systematic description and phylogenetic affinity of tubular microfossils from the Ediacaran Doushantuo Formation at Weng'an, South China. *Palaeontology*, **51**(2), 339–366.

Malinky, J. M. & **Skovsted, C. B.** 2004. Hyoliths and small shelly fossils from the Lower Cambrian of North-East Greenland. *Acta Palaeontologica Polonica*, **49**(4), 551–578.

Malinky, J. M., **Eriksson, M. E.** & **Ahlberg, P.** 2009. 'Mediterranean Province' hyoliths from the middle Cambrian and Upper Ordovician of Sweden. *GFF*, **131**(4), 281–291. https://www.tandfonline.com/loi/sgff20

Marshall, C. R. 2006. Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Sciences*, **34**, 355–384.

McKee, E. & **Moiola, R.** 1962. Precambrian and Cambrian rocks of south-central Esmeralda County, Nevada. *American Journal of Science*, **260**(7), 530–538.

McMenamin, M. A. S. 1985. Basal Cambrian small shelly fossils from the La Cienega Formation, Northwestern Sonora, Mexico. *Journal of Paleontology*, **59**(6), 1414–1425.

Meyer, M., **Schiffbauer, J. D.**, **Xiao, S.**, **Cai, Y.** & **Hua, H.** 2012. Taphonomy of the late Ediacaran enigmatic ribbon-like fossil *Shaanxilithes*. *Palaios*, **27**, 354–372.

Missarzhevsky, V. & **Mambetov, A.** 1981. Stratigraphy and fauna of Cambrian and Precambrian boundary beds of Maly Karatau. *Trudy Akademii Nauka SSSR, Moscow*, **326**, 1–92.

Moczydłowska, M., **Westall, F.** & **Foucher, F.** 2014. Microstructure and biogeochemistry of the organically preserved Ediacaran metazoan *Sabellidites*. *Journal of Paleontology*, **88**(2), 224–239.

Mount, J. F., **Gevirtzman, D. A.** & **Signor, P. W.** 1983. Precambrian–Cambrian transition problem in western North America: Part I. Tommotian fauna in the southwestern Great Basin and its implications for the base of the Cambrian System. *Geology*, **11**(4), 224–226.

Narbonne, G. M., **Saylor, B. Z.** & **Grotzinger, J. P.** 1997. The youngest Ediacaran fossils from southern Africa. *Journal of Paleontology*, **71**(6), 953–967.

Nelson, C. A. 1962. Lower Cambrian–Precambrian succession, White-Inyo Mountains, California. *Geological Society of America Bulletin*, **73**(1), 139–144.

Nelson, C. & **Durham, J. W.** 1966. *Guidebook for field trip to Precambrian–Cambrian succession White-Inyo Mountains*, *California*. Geological Society of America, Boulder, CO, 17pp.

Pacheco, M. L. A. F., **Galante, D.**, **Rodrigues, F.**, **de M. Leme, J.**, **Bidola, P.**, **Hagadorn, J. W.**, **Stockmar, M.**, **Herzen, J.**, **Rudnitzki, I. D.**, **Pfeiffer, F.** & **Marques, A. C.** 2015. Insights into the skeletonization, lifestyle, and affinity of the unusual Ediacaran fossil *Corumbella*. *PLoS ONE*, **10**(3), e0114219. doi:10.1371/journal.pone.0114219

Rowland, S. M. & **Rodriguez, M. G.** 2014. A multicellular alga with exceptional preservation from the Ediacaran of Nevada. *Journal of Paleontology*, **88**, 263–268.

Salak, M. & **Lescinsky, H. L.** 1999. *Spygoria zappania* new genus and species, a *Cloudina*-like biohermal metazoan from the Lower Cambrian of central Nevada. *Journal of Paleontology*, **73**(4), 571–576.

Sappenfield, A., **Droser, M. L.** & **Gehling, J. G.** 2011. Problematica, trace fossils, and tubes within the Ediacara Member (South Australia): redefining the Ediacaran trace fossil record one tube at a time. *Journal of Paleontology*, **85**(2), 256–265.

Schiffbauer, J. D. 2016. The age of tubes: a window into biological transition at the Precambrian– Cambrian boundary. *Geology*, **44**(11), 975–976.

Schiffbauer, J. D., **Xiao, S.**, **Cai, Y.**, **Wallace, A. F.**, **Hua, H.**, **Hunter, J.**, **Xu, H.**, **Peng, Y.** & **Kaufman, A. J.** 2014. A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. *Nature Communications*, **5**. doi:10.1038/ncomms6754

Schiffbauer, J. D., **Huntley, J. W.**, **O'Neil, G. R.**, **Darroch, S. A. F.**, **Laflamme, M.** & **Cai, Y.** 2016. The latest Ediacaran wormworld fauna: setting the ecological stage for the Cambrian explosion. *GSA Today*, **26**, 4–11.

Schindelin, J., **Arganda-Carreras, I.**, **Frise, E.**, **Kaynig, V.**, **Longair, M.**, **Pietzsch, T.**, **Preibisch, S.**, **Rueden, C.**, **Saalfeld, S.** & **Schmid, B.** 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods*, **9**(7), 676.

Seilacher, A. 1955. Spuren und fazies im Unterkambrium. Pp. 373–399 in O.H. Schindewolf and A. Seilacher (ed.) *Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan)*. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse der Akademie der Wissenschaften und der Literatur Mainz, Mainz, Germany.

Signor, P. W., **McMenamin, M. A.**, **Gevirtzman, D. A.** & **Mount, J. F.** 1983. Two new pre-trilobite faunas from western North America. *Nature*, **303**, 415–418.

Signor, P. W., **Mount, J. F.** & **Onken, B. R.** 1987. A pre-trilobite shelly fauna from the White-Inyo region of eastern California and western Nevada. *Journal of Paleontology*, **61**(3), 425–438.

Skovsted, C. B. & **Peel, J. S.** 2011. *Hyolithellus* in life position from the lower Cambrian of North Greenland. *Journal of Paleontology*, **85**(1), 37–47.

Smith, E. F., **Nelson, L. L.**, **Strange, M. A.**, **Eyster, A. E.**, **Rowland, S. M.**, **Schrag, D. P.** & **Macdonald, F. A.**

2016. The end of the Ediacaran: two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA. *Geology*, **44**, 911–914.

Smith, E., **Nelson, L.**, **Tweedt, S.**, **Zeng, H.** & **Workman, J. B.** 2017. A cosmopolitan late Ediacaran biotic assemblage: new fossils from Nevada and Namibia support a global biostratigraphic link. *Proceedings of the Royal Society of London B*, **284**. doi:10.1098/rspb.2017.0934

Sokolov, B. S. 1965. The most ancient Early Cambrian deposits and sabelliditids. Pp. 78–91 in B. S. Sokolov (ed.) *All-Union Syposium on paleontology of Precambrian and Early Cambrian*. Akad Nauk SSSR, Novosibirsk. [In Russian.]

Sokolov, B. S. 1967. Drevneyshiye pognofory [The oldest Pogonophora]. *Doklady Akademii Nauk SSSR*, **177**(1), 201–204. [English translation, pp. 252–255.]

Sour-Tovar, F., **Hagadorn, J. W.** & **Huitrón-Rubio, T.** 2007. Ediacaran and Cambrian index fossils from Sonora, Mexico. *Palaeontology*, **50**, 169–175.

Stewart, J. H. 1966. Correlation of Lower Cambrian and some Precambrian strata in the southern Great Basin, California and Nevada. *US Geological Survey Professional Paper*, **550**, C66–C72.

Stewart, J. H. 1970. *Upper Precambrian and Lower Cambrian strata in the southern Great Basin California and Nevada*. Geological Survey Professional Paper **620**. United States Government Printing Office, Washington, DC, 206 pp.

Syssoiev, V. 1962. *Cambrian hyolithids of the northern slope of the Aldan Shield*. Izd-vo Akademii Nauk SSSR, Moscow, Russia, 63 pp.

Tarhan, L. G., **Droser, M. L.**, **Cole, D. B.** & **Gehling, J. G.** 2018. Ecological expansion and extinction in the Late Ediacaran: weighing the evidence for environmental and biotic drivers. *Integrative and Comparative Biology*, **58**, 688–702.

Taylor, M. E. 1966. Precambrian mollusc-like fossils from Inyo County, California. *Science*, **153**, 198–201.

Terleev, A. A., **Postnikov, A. A.**, **Tokarev, D. A.**, **Sosnovskaya, O. V.** & **Bagmet, G. N.** 2011. *Cloudina–Namacalathus–Korilophyton* association in the Vendian of the Altay-Sayan Foldbelt (Siberia). Pp. 96–98 in *Proceedings of the International Conference on Neoproterozoic Sedimentary Basins: stratigraphy, geodynamics and petroleum potential*.

Van Iten, H., **de Moraes Leme, J.**, **Coelho Rodrigues, S.** & **Guimaraes Simoes, M.** 2005. Reinterpretation of a conulariid-like fossil from the Vendian of Russia. *Palaeontology*, **48**(3), 619–622.

Vidal, G., **Palacios, T.**, **Gamez-Vintaned, J. A.**, **Balda, M. A. D.** & **Grnat, S. W. F.** 1994. Neoproterozoic–early Cambrian geology and palaeontology of Iberia. *Geological Magazine*, **131**(6), 729–765.

Vinn, O. & **Zatoń, M.** 2012. Inconsistencies in proposed annelid affinities of early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences. *Carnets de Géologie*, **2012**(3), 39–47.

Walde, D. H., **do Carmo, D. A.**, **Guimarães, E. M.**, **Vieira, L. C.**, **Erdtmann, B. -D.**, **Sanchez, E. A.**, **Adorno, R. R.** & **Tobias, T. C.** 2015. New aspects of Neoproterozoic–Cambrian transition in the Corumbá region (state of Mato Grosso do Sul, Brazil). *Annales de Paléontologie*, **101**, 213–224.

Warren, L. V., **Fairchild, T. R.**, **Gaucher, C.**, **Boggiani, P. C.**, **Poire, D. G.**, **Anelli, L. E.** & **Inchausti, J. C.** 2011. *Corumbella* and in situ *Cloudina* in association with thrombolites in the Ediacaran Itapucumi Group, Paraguay. *Terra Nova*, **23**(6), 382–389.

Warren, L. V., **Quaglio, F.**, **Simões, M. G.**, **Gaucher, C.**, **Riccomini, C.**, **Poiré, D. G.**, **Freitas, B. T.**, **Boggiani, P. C.** & **Sial, A. N.** 2017. *Cloudina-Corumbella-Namacalathus* association from the Itapucumi Group, Paraguay: increasing ecosystem complexity and tiering at the end of the Ediacaran. *Precambrian Research*, **298**, 79–87.

Wertz, W. E. 1982. Stratigraphy and sedimentology of the Stirling Quartzite, Death Valley area, California and Nevada. Pp. 165–170 in J.D. Cooper, L.A. Wright, and B.W. Troxel, *Geology of selected areas in the San Bernardino Mountains, Western Mojave Desert, and southern Great Basin, California: Volume and guidebook for field trip*. Death Valley Publishing, Shoshone, CA.

Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York.

Xiao, S. & **Laflamme, M.** 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology and Evolution*, **24**, 31–40.

Xiao, S., **Narbonne, G. M.**, **Zhou, C.**, **Laflamme, M.**, **Grazhdankin, D. V.**, **Moczydłowska-Vidal, M.** & **Cui, H.** 2016. Towards an Ediacaran time scale: problems, protocols, and prospects. *Episodes*, **39**(4), 540–555.

Xing, Y., **Ding, Q.**, **Luo, H.**, **He, T.** & **Wang, Y.** 1984. The Sinian–Cambrian Boundary of China. *Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences*, **10**, 1–262.

Xue, Y. -S., **Tang, T. -F.** & **Yu, C. -L.** 1992. Discovery of the oldest skeletal fossils from upper Sinian Doushantuo Formation in Weng'an, Guizhou, and its significance. *Acta Palaeontologica Sinica*, **31**(5), 530–539.

Yang, B., **Steiner, M.**, **Zhu, M.**, **Li, G.**, **Liu, J.** & **Liu, P.** 2016. Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: implications for chronostratigraphy and metazoan evolution. *Precambrian Research*, **285**, 202–215.

Zhang, L. & **Hua, H.** 2000. Late Sinian tubular shell fossils and their significance. *Acta Palaeontologica Sinica*, **3**, 326–333.

Zhuravlev, A. Y., **Vintaned, J. A. G.** & **Ivantsov, A. Y.** 2009. First finds of problematic Ediacaran fossil *Gaojiashania* in Siberia and its origin. *Geological Magazine*, **146**(5), 775–780.

Zhuravlev, A. Y., **Liñán, E.**, **Gámez Vintaned, J. A.**, **Debrenne, F.** & **Fedorov, A. B.** 2012. New finds of skeletal fossils in the terminal Neoproterozoic of the Siberian Platform and Spain. *Acta Palaeontologica Polonica*, **57**, 205–224.

Associate Editor: Ken Johnson