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IT'S A TRAP!: MODERN AND ANCIENT HALITE AS LAGERSTÄTTEN

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ABSTRACT: Chemical sediments, such as bedded halite (NaCl), are strongly influenced by environmental conditions during deposition and, if unaltered, may preserve microorganisms, microfossils, and organic compounds for hundreds of millions of years. Recent studies show that halite is an excellent repository for organic materials, as well as a variety of environmental data. Halite is a perfect trap. Due to its rapid growth, parent brine, gas, crystals of other minerals, and any organic material are encased within primary fluid inclusions or as solid inclusions along growth bands. These inclusions function as "snapshot" repositories of the hydrosphere, atmosphere, lithosphere, and biosphere. However, organic material in halite is still relatively unknown in the sedimentological and paleontological communities. Here, we present highlights of preservation in halite to showcase the diversity of life that has been documented within it. We also discuss: 1) the properties of halite that give it such excellent preservation potential, 2) the challenges to and strategies for studying organic material in halite, 3) preservation in other salt minerals such as gypsum, and 4) implications for astrobiological research. Recommendations for the future study of organic material in halite include collaboration amongst chemical sedimentologists, paleontologists, and microbiologists.

INTRODUCTION

A long-lived assumption is that evaporites (aka chemical sediments) contain no fossils. For this reason, most sedimentologists and paleontologists have neglected to consider the possibility that bedded halite and salt minerals may contain evidence of life. However, a variety of biological material has been documented in modern and ancient halite, as well in its parent surface waters. Here, in this review paper, we highlight representative organic material in halite from the scientific literature, as well as report some of our new findings. The overarching objective of this paper is to make a case that bedded halite and other salt minerals should indeed be targeted for combined paleontological and sedimentological study.

Fossilization in chemical sediments, such as bedded halite, is different from fossilization in siliciclastic and most carbonate rocks because the fossils are trapped within individual crystals. As halite crystals grow rapidly from surface brines in salt lakes, lagoons, or oceans, either as bottom-growth or cumulate crystals (Fig. 1; see Lowenstein and Hardie 1985 for more details about halite growth), they tend to entrap any objects in their path. There are two ways that this happens. The first way is as a simple growth of halite around solids. In the field at modern saline lakes, this can be seen in the form of halite-encrusted fences, driftwood, and insects. As halite grows around these solids, it quickly "buries" them *in situ* as solid inclusions in the halite. Pollen grains and spores are examples of smaller solid inclusions in halite. The second style of fossilization occurs as fluids containing organic material are enclosed in the crystals. As halite grows, its outermost crystal surface is not perfectly flat, but is instead characterized by step-like patterns due to the cleavage of the mineral. Halite's three planes of cleavage equal to 90° results in a growth surface of cubic protrusions and indentations. The indentations commonly are grown over by

new halite, sealing the parent brine in a cubic pocket (Fig. 1). These primary fluid inclusions form *in situ* during growth of the crystal and comprise growth bands (Dellwig 1955; Roedder 1982, 1984; Goldstein and Reynolds 1994). Besides parent surface brine, these primary fluid inclusions can contain other liquids, air or other gases, accidental daughter crystals, microorganisms, organic compounds, and other organic material. As such, fluid inclusions in halite may serve as microhabitats for communities of microorganisms and organic compounds (Lowenstein et al. 2011).

HOW TO STUDY LIFE IN SALT MINERALS

Halite from modern saline environments, recent halite from shallow subsurface cores, and ancient halite from subsurface cores, as well as from subsurface mine walls, all have the potential to host organic material. Bedded halite likely has the highest concentration of biological material. However, some diagenetic halite may also yield organic material, although this is not the focus of this review paper.

Organic material can be studied in numerous ways. Petrography of intact bedded halite enables *in situ* optical observations and some non-destructive geochemical analyses, such as laser Raman spectroscopy. In contrast, extraction methods permit detailed morphological and biological analyses for some biological material. For other biological material, especially microorganisms, extraction enables identifications to genus and species level.

Petrographic methods for the documentation of organic material in halite are relatively straightforward and inexpensive. We prepare samples by cleaving halite with a razor blade along cleavage planes into chips that are ∼ 1–2 mm thick. Alternately, thick sections (up to 1 cm thick) of halite cut and prepared with limited use of water and heat are another easy way to conduct petrography (Andeskie et al. 2018; Benison 2019). Transmitted-light microscopy with
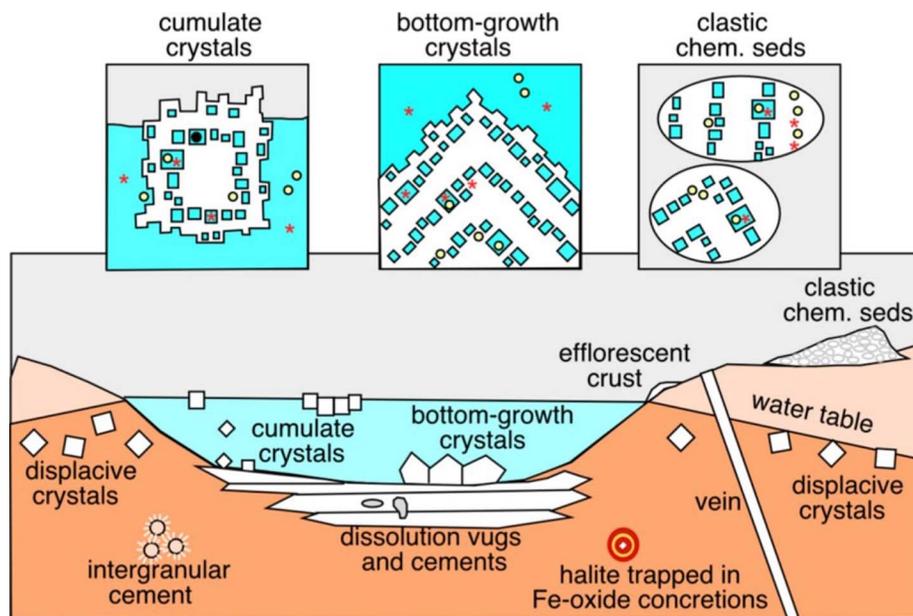
FIG. 1.—Schematic cross-section displaying types of bedded halite and their modes of entrapment of organic material. Bottom-growth crystals, cumulate crystals, clastic halite, and efflorescent crusts are all types of bedded halite. Halite that precipitates in saline surface waters makes beds of halite that include bottom-growth crystals (aka chevrons and cornets) and/or cumulate crystals. Surface saline waters and associated gas, solids, and/or organic material (red stars and yellow circles) are encased within crystals as halite rapidly grows around them, making primary fluid inclusions and solid inclusions along growth bands. Another type of bedded halite lithology, clastic chemical sedimentary rocks, are composed of grains of physically reworked bottom-growth and/or cumulate crystals; they retain growth bands of primary fluid and solid inclusions in their interiors. A fourth type of bedded halite, efflorescent crusts, are composed of tiny salt crystals that form upon desiccation of surface water. Fluid inclusions in efflorescent crusts are too small to effectively study, so are not included in this paper. Diagenetic halite, such as displacive crystals and cements that grow from groundwaters, or halite that is a replacement or recrystallized phase, are also not considered in this review paper.

long-working-distance objectives at magnifications up to 2000× allows *in situ* imaging of objects as small as 1 µm within halite crystals. Reflected light can help identify some organic material, especially plant material. UV-vis light microscopy (in the 330–450 nm wavelength range) can be used to determine any fluorescent response of organic material (Conner and Benison 2013; Benison 2019; Schreder-Gomes et al. 2022). This study of *in situ* objects within halite crystals also precludes most concerns about possible contamination.

Extraction methods, such as dissolution of the halite host by distilled water and/or acids, are used to release solid organic material, particularly for palynological analysis (e.g., Gibson and Bodman 2021). Bulk halite dissolution can also be used to release inclusion fluids to be used for isolation, enrichment, and culturing of microorganisms (e.g., Fish et al. 2002; Jaakkola et al. 2016; Thompson et al. 2021). Bulk halite has been analyzed with gas chromatography for identification of lipids (e.g., Sanchez-García et al. 2018). Targeted extraction by microsyringe of individual fluid inclusions for biological studies has also been used for microbiological analysis (Mormile et al. 2003; Vreeland et al. 2000, 2007). Fluid inclusions to be sampled by microsyringe need to be relatively large (approximately 100 µm), and care should be taken to confirm primary origin of the fluid inclusions.

Size and morphological characteristics of suspect organic material can be described and compared to appearances of known prokaryotes, algae, fungi, pollen grains and spores, plant cuticle, insects, and arthropods. After characterizing morphological and optical features of organic material, we can use analytical instruments to determine chemical composition. For example, laser Raman spectroscopy detects disordered graphite composition of organisms and specific organic compounds such as beta-carotene within fluid inclusions (Benison et al. 2008; Conner and Benison 2013; Winters et al. 2013; Jehlička and Oren 2013; Karmanocky and Benison 2016). Laser Raman spectroscopy, like petrography, targets microfossils and organic material *in situ* and nondestructively. The ionic bonds of halite make it a particularly attractive material

for Raman spectroscopic analysis because this method detects only covalent bonds. Therefore, Raman spectra have no background "noise" from the halite host crystal. More secondary methods, including scanning electron microscopy, can be used to image surface textures on potential microfossils once exposed. However, scanning electron microscopy, which can image only the outer surface textures of solids, cannot be used to image microfossils within fluid inclusions or as solid inclusions within crystals.

DIVERSITY OF LIFE TRAPPED IN HALITE

Biological data from halite most typically includes two sources of organisms and organic material: the halophilic and halotolerant organisms living in the surface brines and the organic material carried into the surface brines by wind or water transport. This makes halite an exceptional repository for organic material because it serves as a trap for both a local and regional sample of the depositional setting. This allows for interpretations to be made about both the habitability of the saline surface waters and the surrounding landscape. Here, we showcase a variety of the life preserved within bedded halite over geological timescales. Table 1 summarizes types of organisms found in halite from various geologic time periods.

The preservation of microorganisms in modern to recent halite has informed the search for organic material in ancient halite. However, larger organisms have been found encrusted and encased in halite. A variety of vertebrate and invertebrate remains have been discovered at hypersaline lakes in northern Chile and Western Australia, including an entire vicuña skeleton (Fig. 2A), an echidna, a snake (Fig. 2B), a frog (Fig. 2C), a centipede (Fig. 2D), and beetles (Fig. 2E; Benison 2019). Invertebrates have also been observed as solid inclusions inside modern bedded halite from Western Australia and include a whole mosquito (Fig. 2F), insect fragments, and a scorpion.

TABLE 1.—*Summary of life documented in halite from throughout geologic time, as discussed in this paper.*

	Archaea	Bacteria	Algae	Fungi	Palynomorphs	Plant Cellulose	Arthropods
Modern	x	x	x	x	x	x	x
Cenozoic	x	x	x		x	x	
Mesozoic	x	x	x		x	x	
Paleozoic	x	x	x	x	x	x	x
Precambrian	x	x	x		not yet evolved	not yet evolved	not yet evolved

Plant remains and fossils are more common compared to animal remains. Leaves of the grass *Spinifex* have been observed coated in halite on desiccated Lake Brown and Twin Lake West (Fig. 2G; Western Australia; Benison 2019). Plant remains are also known to be covered in secondary halite growth in Iranian karst caves; seeds and spider webs have been found encrusted (Filippi et al. 2011). The most common fossil plant remains found in halite, however, are their reproductive vectors, pollen grains and spores. The term fossil here is subjective. Pollen grains and spores are composed of the highly recalcitrant biopolymer sporopollenin, which promotes its preservation over geological timescales. Although there is no mineral replacement, the organic material in the pollen grains and spores has degraded; therefore, they are referred to as fossils. Fragments of plant cuticle representing tracheids and phytodebris are also common.

Evaporite palynologists, those who study palynomorphs (microscopic plant, fungal, and animal structures) recovered from evaporites, have been assessing the preservation potential of halite since the early 1900s (e.g., Lück 1913; Reissinger 1938). The earliest reports investigated Permian and Triassic halite from Europe and Permian and Jurassic halite from North America. Following these studies, pollen grains and spores have been extracted from Miocene evaporites from Italy and Poland (Kirchheimer 1950; Balteş 1967; Pertescu et al. 1999; Pertescu and Bican-Brişan 2005; Durska 2016, 2017, 2018; Machado et al. 2023), Triassic halite from across Europe (Potonié and Klaus 1954; Leschik 1956; Grebe 1957; Déak 1959; Stuhl 1962; Freudenthal 1964; Kłowska and Dowgiałło 1964; Visscher 1966; Dybová-Jachowicz 1974), Permian and Jurassic halite of North America (Jux 1961; Kirkland 1969; Rueger 1996), Permian and Triassic halite of Austria and Germany (Klaus 1953a, 1953b, 1955a, 1955b, 1963, 1964, 1970, 1972), and late Devonian–early Carboniferous halite of Kazakhstan (Varencov et al. 1964). Although evaporites have been studied for more than a century, historically they have been regarded as a poor preserver of palynological data. However, in the last five years, advances in dissolution techniques that use less host halite and return a higher yield of palynomorphs (Gibson and Bodman 2021; Machado et al. 2023) are helping palynologists realize the value of evaporites. The fossil assemblages recovered from halite provide insight into the vegetation associated with some of the most extreme environments on Earth, those characterized by wide ranges of aridity, temperature, salinity, and pH. As palynomorphs are a highly valuable tool for reconstructing continental paleoenvironments and paleoclimate, the palynological record, in concert with the fluid inclusion record within bedded halite may make continental evaporites a significant sink of paleoecology, paleoenvironment, and paleoclimate data.

Recent botanical data from halite highlights its excellent preservation potential. For example, cellulose fibers have been recovered from Permian halite (Griffith et al. 2008). Exceptionally well-preserved three-dimensional pollen grains (Fig. 3A), plant cuticle (Fig. 3B, C), and fungi (Fig. 3D, E) from the Permian Zechstein Group of the UK show that halite is a superior repository for microfossils compared to most other lithologies (Gibson and Wellman 2021; Gibson and Bodman 2021; Gibson 2022). Petrographic examinations of thin sections and thick sections of halite from the Permian Nippewalla Group (Kansas, U.S.A.) and the Permian Opeche Shale (North Dakota, U.S.A.) have revealed *in situ* pollen grains (Fig. 3F), plant cuticle with visible stomata (Fig. 3G, H), phytodebris, and organic fibers (Fig. 3I) trapped as solid inclusions in halite. Plant cuticles with visible cellular structures have also been observed as solid inclusions in chips of modern lake halite from Western Australia (Fig. 3J, K). Petrographic observations of Permian halite from the Upper Pechora Basin of Russia and in Miocene halite have documented pollen grains and cyanobacteria inside primary fluid inclusions (Shanina et al. 2018; Galamay 2018).

Fungal remains have been recovered from halite. In Permian halite from the Zechstein Group, *Callimothallus*-type epiphytic fungi (Family Microthyraceae; Fig. 3D) and *Chaematomium*-like fungi (Family Chaetomiaceae; Fig. 3K) have been recovered using dissolution techniques (Gibson and Bodman 2021; Gibson 2022). Cultures from halite from Western Australian lakes have yielded both extremophilic and common fungi (Benison et al. 2023). We have also seen *in situ* assorted fungal remains in thin sections and chips of modern halite crystals from Lake Magic, Western Australia (Fig. 3L).

Prokaryotes and algae have been detected in halite using combined optical, chemical, and biological methods. Optical petrography shows that microorganisms are situated within primary fluid inclusions and as solid inclusions along growth bands in bottom-growth crystals (chevrons and cornets) and cumulate crystals of bedded halite (Figs. 1, 4). Microorganisms can be seen under plane-transmitted light and through fluorescent responses to UV-vis light (Fig. 4; e.g., Lowenstein et al. 2011; Benison 2013; Conner and Benison 2013). Prokaryotes (bacteria and archaea) appear as 1–2 μm, typically bright and high-relief, clear spheres and rods. Under UV-vis light, prokaryotes fluoresce pale green or blue-green. In contrast, most algae appear as 3–10 μm, yellow, green, or brown dimpled spheres, ovals, or "football" shapes, and fluoresce blue (Fig. 4A–C; e.g., Lowenstein et al. 2011; Conner and Benison 2013). Some algae have flagella (Fig. 4A). It is common to find multiple algal and prokaryotic cells together in single fluid inclusions (Fig. 4C, H).

Clusters of microorganisms and Ca-sulfate crystals, informally called "hairy blobs," are easily detected optically in modern halite from Western Australia, as well as in Permian halite from Kansas and North Dakota (Fig. 4J; Benison et al. 2008; Jagniecki and Benison 2010, 2013). Hairy blobs are found as solid inclusions, as well as within some fluid inclusions. They appear as spiky black objects in transmitted light, up to 1.5 mm in diameter, and fluoresce blue and green in response to UV-vis light. SEM images show morphologies such as bumpy textures on crystal surfaces, meniscus textures between crystals, and hollow rod shapes that are consistent with microbial features (Benison et al. 2008). The black "hairs" are commonly in contact with clear crystals of gypsum and/or anhydrite; some hairs are wrapped around the crystals, and some hairy blobs have a tiny crystal at the end of a single hair.

Microorganisms in halite have been known for the past several decades. Some of the earliest mentions of organic material in halite rely on petrographic observations (e.g., Dombrowski 1963; Reiser and Tasch 1960). More commonly, bulk extractions by dissolution, followed by culturing and, more recently, DNA sequencing, have been done, with a focus on prokaryotes (e.g., Norton and Grant 1988; McGenity et al. 2000). However, recent advances have been made by combining sedimentological observations in the field, fluid inclusion petrography, water geochemistry, and microbiology. In Saline Valley (California, U.S.A.), prokaryotes and algae

FIG. 2.—Vertebrate, invertebrate, and plant remains encrusted in halite from modern acid saline environments. **A)** Vicuña skeleton encrusted in halite and gypsum at Salar Gorbea, Chile. **B)** Dead snake. **C)** Dead frog. **D)** Dead centipede on an acid lake sandflat in Western Australia. **E)** Beetle trapped in halite at Twin Lake West, Western Australia. KCB observed the beetle land on the halite crust and become encased in halite as the crystals rapidly grew. **F)** Mosquito trapped as a solid inclusion in halite from Lake Aerodrome, Western Australia. **G)** *Spinifex* grass coated in halite from Twin Lake West, Western Australia.
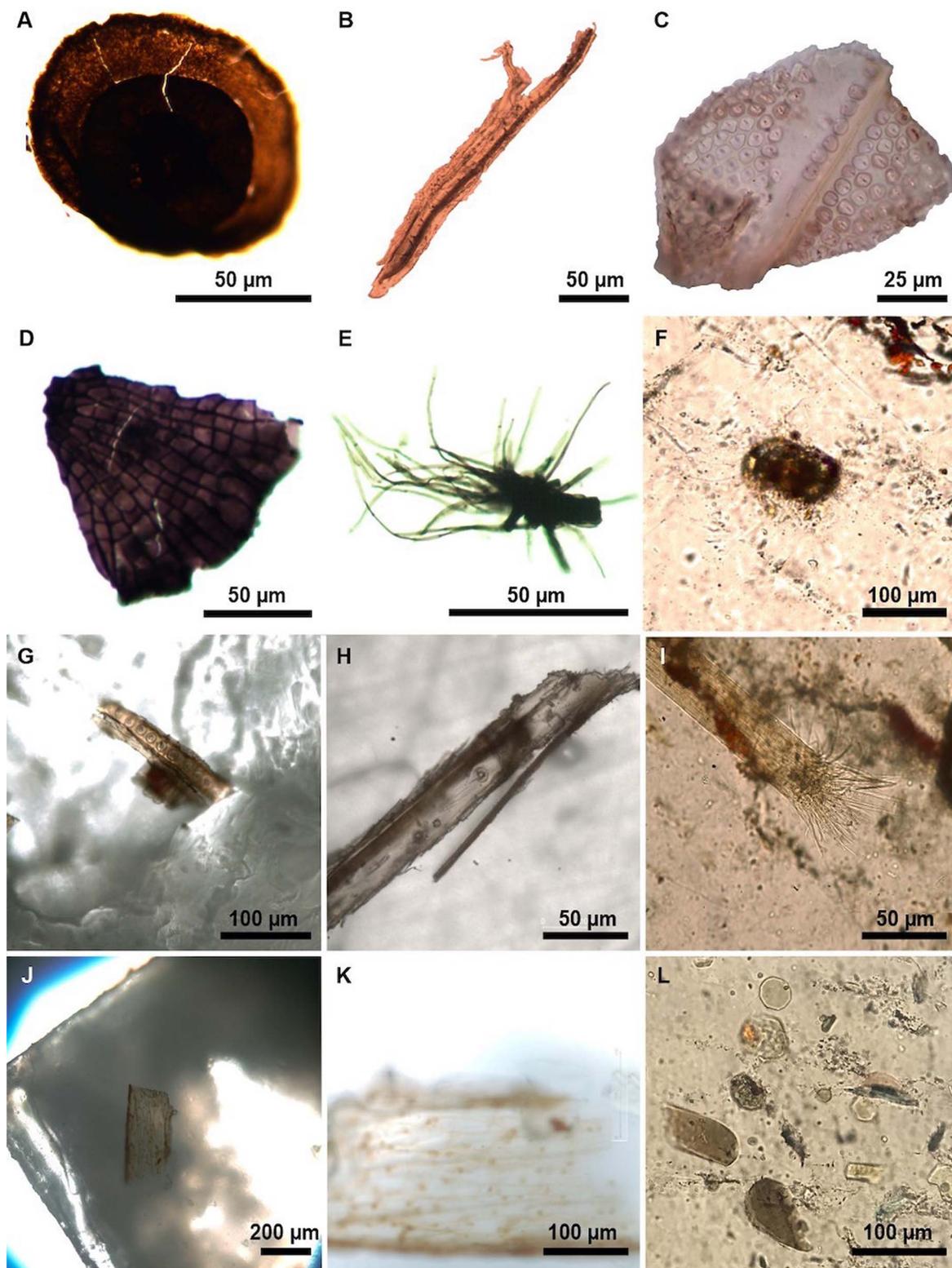
FIG. 3.—Palynological remains from evaporites imaged as recovered specimens and *in situ* in thin sections or thick chips of halite. **A)** Monosaccate pollen grain species *Nuskoisporites dulhuntyi* recovered from Permian halite from the Billingham Anhydrite Formation (SM11 1382.12 m) of northeast England. **B)** Gymnospermous plant tracheid recovered from Permian halite from the Fordon Evaporite Formation (SM11 1465.92 m) of northeast England. **C)** Plant cuticle with visible stomata preserved in 3-D recovered from Permian halite from the Sherburn Anhydrite Formation (SM11 1304.14 m) of northeast England. **D)** *Callimothallus*-type fungi (Family Microthyraceae) recovered from halite from the Billingham Anhydrite Formation (SM11 1394.88 m) of northeast England. **E)** *Chaematomium*-type fungi (Family Chaetomiaceae)

have been observed in both modern lake waters and their halite precipitates (Schubert et al. 2009a). Core samples of older bedded halite counterparts from the subsurface of Saline Valley and Death Valley host primary fluid inclusions containing prokaryotes and algae (Schubert et al. 2009b; Lowenstein et al. 2011). Guided by petrographic observations, culturing was conducted on extractions of both targeted single fluid inclusions and bulk halite composed of multiple primary fluid inclusions. DNA analyses on these same samples confirm the same species of archaea as cultures (Sankaranarayanan et al. 2014). Halite as old as 150 ka yielded genus- and species-level identifications, including halophilic archaea genera *Halorubrum*, *Natronomonas*, and *Haloterrigena*, halophilic bacteria *Halobacterium salinarum*, and the algal genus *Dunaliella* (Mormile et al. 2003; Schubert et al. 2010a, 2010b; Lowenstein et al. 2011; Sankaranarayanan et al. 2014). Another example, from modern ephemeral acid-saline lakes and halite in Western Australia, show similar preservation. Lake Magic waters contain prokaryotes, algae, and fungi. Here, archaea are rare and bacteria are far less diverse and abundant than algae and fungi (Zaikova et al. 2018). Transmitted-light and UV-vis petrography of primary fluid inclusions in chevron halite from Lake Magic suggest prokaryotes and the halophilic algae *Dunaliella*; analysis of suspect microbes show Raman spectra consistent with disordered graphite, recognized as confirmation of past life (Pasteris and Wopenka 2003; Conner and Benison 2013). Halite from Death Valley, Saline Valley, and Western Australia all have organic compounds in association with microbes. Organic compounds appear as red, orange, and yellow solids or liquids within fluid inclusions (Fig. 4B1, C1). Fluorescent response to UV-vis light commonly shows pinks and purples (Fig. 4B2, C2). Laser Raman analyses of these organic compounds has confirmed the presence of beta-carotene and other carotenoids (Conner and Benison 2013; Winters et al. 2013).

Microorganisms found inside fluid inclusions in ancient halite are morphologically very similar to those found in modern surface brines (e.g., Schubert et al. 2009a). Genus- and species-level identifications have been made in halite from the Mesozoic and Paleozoic (e.g., Norton and Grant 1988; Norton et al. 1993; Vreeland et al. 2000; Fish et al. 2002; Stan-Lotter et al. 1999, 2002). For example, the genome of *Halobacterium noricense*-related archaea has been isolated from 123 Ma halite (Jaakkola et al. 2016). The DNA of haloarchaea and the genus *Halobacterium* have been extracted from 11–425 Ma halite (Fish et al. 2002) and 23, 121, and 419 Ma salts (Park et al. 2009).

Numerous kinds of microorganisms have been observed co-occurring in primary fluid inclusions with organic compounds. For example, primary fluid inclusions in Triassic halite from Northern Ireland contain abundant microorganisms and organic compounds (Fig. 4F). Halite from the Permian of Kansas has yielded prokaryotes and yellow algae, as well as organic compounds (Fig. 4G–I). Halite much older than Permian can contain organic material. Primary fluid inclusions in Neoproterozoic halite from Western Australia host prokaryotes, algal cells, and globules of organic compounds (Fig. 4K–M; Schreder-Gomes et al. 2022).

Organic compounds found in halite inside primary fluid and as solid inclusions include carotenoids, waxes, and other hydrocarbons, as well as glycerol, chlorophyll, lipids, cellulose, and DNA. These may represent the products of metabolism, the decomposed remains of microorganisms, or be abiotic in origin. Some organic compounds can be detected using a combination of plane transmitted light and UV-vis light. Carotenoids and long-chain hydrocarbons fluoresce pink, purple, light blue, orange, red, yellow, or white, and simple liquid hydrocarbons, such as methane, fluoresce bright blue (Conner and Benison 2013; Winters et al. 2013; Karmanocky and Benison 2016; Benison 2019). Organic crystalline solids are typically amorphous in shape and appear clear, pale yellow, green, orange, and/or brown in plane-transmitted light with a faint fluorescence under UV-vis light (Lowenstein et al. 2011). Liquid organic compounds can be found enveloping algae and air bubbles and exhibit white, blue to blue-green, or pale orange to red fluorescent responses under UV-vis light. Other organic compounds, such as lipids (n-alkanes, n-alkanols, isoprenoids, steroids, hopanoids) and functionalized hydrocarbons (n-fatty acids, n-aldehydes), have been found in Miocene and Permian halite (Sanchez-García et al. 2018; Isaji et al. 2019; Cockell et al. 2020).

DISCUSSION

Communities in Fluid Inclusions

Some studies have compared microorganisms in modern saline environments with those trapped in halite precipitating from those brines (e.g., Schubert et al. 2009a). Results show that at least some of these microorganisms from the environment also exist in primary fluid inclusions. For example, Lake Magic in Western Australia hosts rare archaea, uncommon bacteria, and abundant and diverse algae, including *Dunaliella*, and fungi. Primary fluid inclusions in bedded halite collected from Lake Magic host prokaryotes, abundant *Dunaliella*, and fungi (Benison et al. 2022; Conner and Benison, 2013; Zaikova et al. 2018). To date, nothing identified in the fluid inclusions has not also been identified in parent surface brines. However, these studies have not been comprehensive; for example, fungi have been the focus of only limited recent studies.

Primary fluid inclusions in halite contain the same waters of the environment from which the host mineral precipitated. Because bedded halite grows rapidly from saline surface brine, at the minutes–hours scale, the primary fluid inclusions are entrapped pockets of that surface water. When seen in fluid inclusions in modern and ancient halite, numerous types of microorganisms, along with organic compounds, are typically found together in the same inclusions. Recent studies have demonstrated biological relationships amongst prokaryotes and algae, associated with organic compounds such as beta-carotene and glycerol, within individual fluid inclusions in halite from Death Valley and Saline Valley (California, U.S.A.; Schubert et al. 2010a; Lowenstein et al. 2011). Furthermore, they suggest that biological activity could continue within individual fluid inclusions after entrapment. The production of organic compounds (e.g., glycerol) by algae may provide prokaryotes with an energy source (Lowenstein et al. 2011). In addition, decomposed algae may be another energy source for prokaryotes (Schubert et al 2010a). This may explain how microbial communities can persist over geologic time scales in bedded halite (Schubert et al 2009b; Lowenstein et al. 2011). Therefore, these fluid inclusions are essentially microhabitats.

The Preservation Potential of Bedded Halite

Halite is an exceptional material for preserving organic material. It: 1) precipitates rapidly at the Earth's surface, 2) insulates from air and light-element gases, such as hydrogen and oxygen, and 3) partially blocks UV radiation.

←

recovered from the Permian the Permian Fordon Evaporite Formation (SM4 1438.07 m) of northeast England. **F)** Coniferous pollen grain observed in thin section in modern halite from Twin Lake West, Western Australia. **G)** Plant cuticle with visible stomata *in situ* in thin sections of the Permian Nippewalla Group of Kansas, U.S.A. (Rebecca K Bounds #1 borehole), and **H)** *in situ* in thin sections from the Permian Opeche Shale of North Dakota, U.S.A. (Gulf Romanysyn OP7497). **I)** Possible cellulose fibers *in situ* in thin section of modern halite from Twin Lake West, Western Australia. **J)** Plant cuticle *in situ* in modern chevron halite crystal from Twin Lake West, Western Australia. **K)** Plant cuticle with visible cellular structures in modern chevron halite crystal from Twin Lake West, Western Australia. **L)** Various fungal remains *in situ* in thin section from modern chevron halite crystal from Twin Lake West, Western Australia.

Fig. 4.—Images of microorganisms and organic compounds in modern and ancient halite. Unless otherwise indicated, images are shown in transmitted plane light. **A)** Yellow algae with flagellum in primary fluid inclusion from Lake Gounter, Western Australia. Photo courtesy of M. Timofeeff. **B1)** Yellow algal cell in primary fluid inclusion from Lake Gounter, Western Australia. **B2)** Same view as in part B1 in UV-vis light. Pink fluorescence indicates beta-carotene coating algal cell. **C1)** Primary fluid inclusion from Lake Magic, Western Australia, hosting three dimpled pale yellow *Dunaliella* algal cells, small cocci prokaryotes (one in focus), and a bright yellow globule. **C2)** Same view as C1 in UV-vis light. Blue fluorescence of three algal cells, green fluorescence of prokaryote, and pink and purple fluorescence of carotenoids.

Rapid burial is credited as an important prerequisite for fossilization. In the case of chemical sediments, such as bedded halite, rapid precipitation replaces burial by sediments. Halite chevrons and cumulates grow rapidly as a geological phenomenon, especially during evapocentration in shallow saline lakes and lagoons. The rapid growth causes pockets of brine to be trapped along cleavage-plane indentations and form primary fluid inclusions. In many evaporative environments, chevron and cornet halite crystals are characterized by cloudy, inclusion-rich growth bands, which typically form during afternoons and clear, inclusion-poor growth bands, which form at night as precipitation slows due to slightly increased nighttime humidity (accompanying decreased nighttime temperature). Alternating inclusion-rich and inclusion-poor growth bands documented in modern and ancient chevron halite crystals, in particular, have been interpreted as representing diurnal patterns (Dellwig 1955; Roedder 1982). Counting growth bands may allow for estimation of number of days of crystal growth. Seven to 14 days for growth of an individual chevron crystal is typical (Benison and Goldstein 1999). Cumulates tend to grow slightly faster than chevrons and represent a shorter growth period, perhaps less than one day. Cumulate crystals typically begin growth at the air–water interface, where evaporation is highest.

Halite is an excellent insulator. Studies of potential diffusion of hydrogen and helium have shown that those elements can diffuse through the solid crystalline structure of quartz, but not halite (e.g., Hall et al. 1991; Abuaisha et al. 2020). As long as bedded halite remains in conditions of moderately low temperature and pressure, without the presence of dilute water, it, and its fluid inclusions, can remain remarkably viable for tens of thousands of years (Schubert et al. 2009b; Mormile et al. 2003) and possibly for hundreds of millions of years (Schreder-Gomes et al. 2022; Vreeland et al. 2000, 2007). This explains why unaltered bedded halite is the best target for studies of ancient microbes; salt diapirs and deeply buried halite (more than approximately 3000 m depth) have undergone various stages of deformation; this compromises the fluid inclusions and any organic material in them (Benison et al. 2015). Petrographic observations that document growth bands defined by primary fluid inclusions and solid inclusions are a key first step to the study of organic material in halite (Goldstein and Reynolds 1994). Ultimately, any unaltered bedded halite has the potential to contain multiple self-contained ecosystems.

Traditionally, fossil preservation is enhanced by anaerobic environments. However, the formation of the mineral halite, NaCl, is not dependent on oxidizing or reducing conditions. Most bedded halite forms in oxygen-rich environments, where total organic matter is relatively low and waters are shallow and wind-blown. In less common cases, halite forms in stagnant, organic-rich conditions. Regardless of redox conditions of the precipitating environment, halite occludes air, oxygen, and other light-element gases. This means that fluid inclusions, once formed, and organic material they enclose, as well as solid inclusions, are no longer affected by oxidation.

Organic material at the Earth's surface is bombarded with cosmic radiation. However, minerals can block UV radiation. Thus, rapid encasement within salt minerals reduces exposure to radiation. Organic material trapped within halite may remain unaffected at the Earth's surface by the deleterious consequences of UV radiation, even at high elevations. In some evaporative environments, other minerals coat halite. For example, acid saline lakes in Western Australia precipitate halite and contain iron oxides that are both precipitated occasionally from the lake brines and blown into lakes as silt. Here, in the shallow (mm-cm) subsurface, groundwaters also precipitate iron oxides (Benison et al. 2007). Individual halite crystals, as well as beds of halite crystals, become coated with iron oxides. Experiments have shown that thin (mm-scale) coatings of hematite effectively block UV radiation, contributing to the excellent preservation of organic material in halite (Gomez et al. 2010). In addition, coatings of hematite and/or clay minerals may help to prevent dissolution of halite by dilute waters.

The combination of rapid growth, insulation from air and oxygen, and blockage of UV radiation all contribute to preservation of multiple sizes of organic material and their original shapes. Prokaryotic and algal cells ranging from 1 to 10 µm are amongst the smallest organic material, and are trapped within fluid inclusions and as solid inclusions (Fig. 4). Larger organic material, such as palynomorphs, plant cuticle, and insects, tends to be found as solid inclusions (Fig. 3F). Solid inclusions are in direct contact with halite, yet the halite has not changed the shape of the organic material. We have recovered three-dimensional pollen grains and plant cuticles from Permian bedded halite (Fig. 3A, C). Insects in modern halite retain their original shape and position (Fig. 2F). Most solid inclusions are typically encased within single halite crystals, whereas larger organic material, such as centipedes, leaves, and wood, are encrusted by multiple halite crystals that coat and/or fill internal spaces, resulting in macrofossils in bedded halite (Fig. 2D, G).

Organic Material in Other Salt Minerals

Other salt minerals besides halite are known to preserve organic material, but are less well studied than halite. A variety of organic material has been found in modern and ancient gypsum. Prokaryotes, algae, and pennate diatoms have been imaged in both fluid inclusions and as solid inclusions in gypsum from modern acid salars in Chile (Benison and Karmanocky 2014). In addition, long-chain hydrocarbons were detected with UV-vis fluorescence and laser Raman spectroscopy in primary fluid inclusions in this Chilean gypsum (Karmanocky and Benison 2016). The preservation of biosignatures in gypsum is enhanced by the co-precipitation of less soluble minerals such as hematite and clay minerals. *Dunaliella* algal cells, prokaryotes, and organic compounds such as beta-carotene have been found in fluid inclusions in various types of gypsum crystals from acid saline lakes and nearby dunes in Western Australia (Benison et al. 2016). In addition, microfossils have been documented in recent gypsum from lakes and salterns in South Australia, Mexico, and Peru (Schopf et al. 2012). Palynomorphs have been recovered from 35 ka gypsum from Mexico (Garofalo et al. 2010).

The majority of studies of organic material in ancient gypsum comes from the Miocene of Europe. Diatoms, algae, and bacteria have been found in Miocene gypsum crystals from northern Italy (Dela Pierre et al. 2015; Schopf et al. 2012; Pellegrino et al. 2021). Larger fossils, however, have also been found in Italian gypsum, including dragonfly larvae trapped as solid inclusions (Schlueter et al. 2003). Another example are pollen grains containing fossilized cytoplasm, recovered from Miocene gypsum

from Poland (Durska 2018). These pollen grains from Poland show that gypsum has the potential to preserve the highly biodegradable internal contents of pollen grains. Pollen grains have also been extracted from Paleocene gypsum from the Cedar Keys Formation (Florida, U.S.A.) (Klug 2023).

Rare examples of organic material in Mesozoic and Paleozoic gypsum have been briefly described. Unaltered gypsum from the Triassic Red Peak Formation (Wyoming, U.S.A.) hosts fluorescent prokaryotes and algae (Bradford et al. 2022). The Permian Seven Rivers Formation and Salado Formation (New Mexico, U.S.A.) host filamentous bacteria as solid inclusions in gypsum (Schopf et al. 2012). Permian gypsum from the Blaine and Easly Creek formations of the U.S.A. have yielded pollen grains (Klug 2023).

"Hairy blobs," clusters of microorganisms and sulfate crystals, have been found along with cocci (spherical) prokaryotes in reworked gypsum grains within hematite concretions in Western Australia (Farmer et al. 2009).

The presence of a variety of other sulfate minerals on Mars necessitates investigation of organics in previously understudied sulfate minerals. Mirabilite (Na_2SO_4–$10H_2O$) from spring deposits at Great Salt Lake (Utah, U.S.A.) contains primary fluid inclusions which host a variety of microorganisms and organic compounds (Gill et al. 2023a, 2023b). Prokaryotes, algae, fungi, diatoms, proterozoa, and suspect brine shrimp eggs have been described based on plane-transmitted light and UV-vis microscopy. Beta-carotene was documented by UV-vis spectroscopy and laser Raman spectroscopy (Gill et al. 2023a).

Close Relationship of Microfossils and Environmental Data from Fluid Inclusions

The location of microfossils and other organic material within primary fluid inclusions, and as solid inclusions in growth bands with primary inclusions, is notable. This close relationship of microfossils and fluid inclusions in halite, gypsum, mirabilite, and likely other salt minerals, allows for high-resolution interpretations of environmental conditions of the depositional environment in which the microfossils were living or deposited. Primary fluid inclusions in halite have been used to decipher surface water temperatures (and air temperatures), pHs, water compositions, and even air compositions (see Goldstein 2001 for overview). Growth bands of primary fluid inclusions record diurnal records of halite growth. Detailed measurements of environmental conditions from fluid inclusions, with careful stratigraphic control at the growth-band scale, can allow for interpretations of habitat conditions of microorganisms and microfossils. For example, studies of Permian bedded halite from the Opeche Shale (North Dakota, U.S.A.) and the Nippewalla Group (Kansas, U.S.A.) show that the halite was formed in ephemeral saline lakes with low pH (~ 2 and sometimes as low as –1) and Na-Cl-SO_4-Ca-Al-Si-Fe-rich composition (Benison et al. 1998). These lakes were adjacent to acid saline groundwaters. The lakes were impacted by winds, sometimes air and water temperatures as high as 74°C, and diurnal temperature ranges of up to 30°C (Benison and Goldstein 1999; Zambito and Benison 2013). Because all data was measured from individual primary fluid inclusions along growth bands, we can read them as snapshots of time at scales of minutes for individual fluid inclusions to days to weeks when stratigraphy of successive growth bands are considered. Observations of suspect prokaryotes, algae, palynomorphs, and organic compounds within primary fluid inclusions and as solid inclusions in individual growth bands allows us to interpret a more detailed depositional environment for these microfossils (Benison 2019). The microorganisms found in halite in the Opeche Shale and Nippewalla Group most likely were extremophiles living in warm, acid brines that fluctuated in salinity and occasionally desiccated in the dry climate of western equatorial Pangea. Ongoing study of pollen and fungi in this same Permian bedded halite refines understanding of local climate, as well as regional climate, and may even supply paleoelevation information about the interior of Pangea. Such co-location of

paleontological data with detailed environmental data from halite may be a powerful future tool for the reconstruction of ancient saline environments and climates, as well as life.

Habitability and Implications for Astrobiology

The search for extraterrestrial life relies on the best understanding we have of the range of habitable environments on Earth, which organisms live there, and how they are preserved. This has led to the study of extreme environments on Earth as analogs for Mars and other extraterrestrial bodies.

Some of the most extreme environments on Earth through geologic time may be settings with hypersaline waters. Salars Gorbea and Ignorado in northern Chile are low pH (down to pH 1.6) salars with pulses of HS-rich brines in an active volcanic setting (Karmanocky and Benison 2016). Microorganisms have been documented in the saline surface waters there (e.g., Demergasso et al. 2010; Escudero et al. 2018). Gypsum in these salars contains primary fluid inclusions that host microorganisms (Benison and Karmanocky 2014). Likewise, lakes in Western Australian with pH as low as 1.4 and salinity as high as 32% TDS (total dissolved solids; ~ 9× the salinity of seawater) precipitate halite and gypsum with entrapped microorganisms and organic compounds (Fig. 4; Mormile et al. 2009; Conner and Benison 2013; Zaikova et al. 2018; Benison 2019). Water-activity measurements of these acid lake brines in Western Australia were as low as 0.714 (Benison et al. 2021). In contrast, seawater has a water activity of 0.980.

The limits of life, that is, the lowest water activity in which organisms can survive, is considered to be ~ 0.600, as suggested by laboratory experiments. The most extreme haloarchaea known can grow at water activity as low as 0.635 (Stevenson et al. 2015). It is often assumed that haloarchaea are the most likely organism to live in extreme brines. For this reason, eukaryotes are overlooked in many biological studies of brines. However, the fungus *Aspergillus penicillioides* reproduces at water-activity values down to 0.585 in NaCl-saturated brines (Nazareth and Gonsalves 2014; Stevenson et al. 2017). This highlights the need for further studies of fungi in both modern brines and halite.

An improved understanding of microfossils and organic material in terrestrial halite, gypsum, and mirabilite, as well as other chemical sediments, is necessary for the search for biosignatures on Mars. Salt minerals, including chlorides and sulfates, have been discovered on Mars (e.g., Clark and Van Hart 1981; Clark et al. 2005; Osterloo et al. 2008). Scientific instruments on Mars rovers lack the ability to image or analyze for micron-scale organic material inside crystals. However, rocks and sediment brought to Earth as part of the Mars Sample Return mission will likely include salt minerals. By making observations of microorganisms, microfossils, and organic compounds in various salt minerals on Earth, the scientific community will be better prepared to search for biosignatures in evaporite samples from Mars.

Challenges to the Study of Organic Material in Salt Minerals

There are several reasons why there are limited studies of organic material in salt minerals. These include: 1) the assumption that brines are barren, as are their adjacent environments, 2) the cost and rarity of coring ancient salt minerals from the subsurface, 3) specialized methods, and 4) requirement of interdisciplinary knowledge.

Many introductory-level lessons on evaporites teach that they have no fossils. There is an assumption that brines cannot support life. The paucity of macroscopic life, such as fish and mollusks, in modern hypersaline surface waters have discouraged scientists from searching for signs of any life in recent and ancient chemical sediments. For these reasons, sedimentologists and paleontologists have traditionally not investigated halite and other salt minerals for fossils.

Documentation of organic material in ancient halite relies on well-preserved, high-recovery cores. Halite is particularly difficult to core because the dilute drilling muds used for most drilling would dissolve halite. Salt-saturated drilling muds and diesel drilling fluids can successfully yield halite cores, yet both have negative consequences: salt-saturated drilling fluids corrode drill rigs, and diesel drilling fluids are expensive and cause organic contamination of halite. Halite is cored mainly for specific industrial applications, including investigation of subsurface halite as a repository for CO_2 and other gases, liquid hydrocarbons, and radioactive waste. Subsurface salt mines accessible by people provide a place to sample ancient halite, but these are relatively rare and present contamination issues. Only rare cores, to date, have been drilled for strictly scientific purposes and include the cores at Death Valley and Saline Valley, part of scientific studies by Lowenstein and colleagues.

Both *in situ* study and extraction of organic material from salt minerals present challenges. Most of the fossils in salt minerals are small; a microscope is required to see them. Additionally, microscopic organic materials are typically trapped in the interiors of salt crystals, rather than on the outer surfaces. Long-working distance microscope objectives, high-magnification (400–2000×), and thicker-than-standard thin sections of halite chips are required to image most *in situ* organic material. Likewise, for organic material in salt minerals to be detected with fluorescence and laser Raman spectroscopy, analytical instruments must use high-magnification and high-resolution focus. Traditional scanning-electron-microscopy imaging does not capture fluid inclusions because any fluids breached during cleavage of the host salt minerals (in preparation for scanning-electron-microscopy work) are evaporated and result in a pit where the fluid used to be. Dissolution techniques may necessitate use of dangerous chemicals, such as concentrated HF and carcinogenic heavy liquids, requiring specialized laboratory facilities and training to safely handle and dispose of reagents. The specialized methods and instruments needed for study of organic materials in salt minerals are barriers to many scientists.

The various methods used to study organic material in salt minerals are not always compatible. For example, one cannot do petrographic analyses after dissolving a sample to recover organic material. Other techniques are designed to select for particular groups of organisms and not others. For example, microbiologists interested in halophilic bacteria and archaea may only use 16S rRNA, preventing them from recognizing any eukaryotes in the sample. Dissolution to recover palynomorphs will destroy any carbonates and silicates, thereby removing ostracods, diatoms, and some other fossils.

Scientists with different specialties have particular search images; that is, scientists may unconsciously, or consciously, overlook anything that is not their intended focus. Those undertaking petrographic analyses for microorganisms in fluid inclusions will be searching for organic material of a particular size and shape in particular locations. In contrast, palynologists making petrographic observations will be much more aware of larger pieces of organic material, such as palynomorphs and fragments of cuticle.

Studying organic materials in salt minerals is heavily reliant on interdisciplinary knowledge. Principles of chemical sedimentology are necessary to recognize depositional environments and state of preservation of salt minerals, providing a geologic context for any organic material discovered. Optical methods require training as a petrographer. Identifying the wide range of organic material in salt minerals needs an unusually broad knowledge of biology. Chemical methods used to help identify organic material and organic compounds, such as laser Raman spectroscopy, also require specialized training. All these skills are not standard training in any one discipline.

Recognition of organic material in salt minerals can be challenging, even when one is trained in relevant methods. For example, when looking for microfossils *in situ* in halite, hematite-coated silt and sand grains can be misleading, having shape, color, and size similar to that of some fossil pollen grains and spores (Fig. 5A). However, on closer inspection at higher magnification, it becomes apparent that these grains lack the identifying features of organic material. Other suspect pollen grains may be so hyaline

(clear and colorless; Fig. 5B) that identification is nearly impossible. Furthermore, fluid inclusions may contain amorphous structures which fluoresce blue under UV-vis light (Fig. 5C, D) and peculiar filamentous and tubular solid inclusions which also fluoresce blue (Fig. 5E, F).

Distinguishing origin of organic materials in salt minerals can also be challenging. We may know that some organic materials, including halophilic prokaryotes and algae, most likely lived in the parent brines that precipitated the host crystals. We can assume that pollen grains, plant spores, and insects were transported into the parent waters, and did not live in the parent brines. However, the origin of some organic materials trapped in salt minerals may prove difficult to ascertain. For example, in some brine systems, some fungal spores are carried by wind and some fungi live in the surface brines; distinguishing the origin between these may be challenging. Compounding this problem is the fact that few studies of fungi in brines have been conducted. Therefore, determination of habitability from organic material in salt minerals is not always straightforward.

Recommendations

We have several recommendations to the wider sedimentological and paleontological community about future work investigating fossils and other organic materials in salt minerals. When presented with cores or subsurface mine walls with bedded halite, consider making preliminary petrographic observations to investigate for microfossils and other organic material, as well as to confirm depositional origin and evaluate possible alteration by diagenesis and biological contamination before using any destructive techniques. Petrographic observations are non-destructive and will allow for precious rock samples to be conserved during preliminary assessments for organic material. Paleontologists, microbiologists, and evaporite sedimentologists interested in life in saline environments should collaborate with one another to ensure that such procedures are followed.

A particularly useful method is the targeting and extraction of individual fluid inclusions to test these micro-fluid samples for organic materials. This method was successfully used by Mormile et al. (2003) and Vreeland et al. (2000, 2007) with a custom-designed micro-syringe mounted to a microscope. This targeting of single inclusions may allow for confirmation of fluid origin. From a primary fluid inclusion in 97 ka bedded halite from Death Valley, culturing determined the presence of *Halobacterium salinarum* (Mormile et al. 2003). Extraction of individual fluid inclusions in Cretaceous halite yielded six strains of halophilic archaea (Vreeland et al. 2007). Vreeland et al. (2000) identified *Bacillus* 2-9-3, a species of spore-forming bacteria, in Permian halite. Continued and refined use of this method is needed in light of the recent discoveries of various types of organic material in modern and ancient halite.

More work is needed to understand the preservation potential of salt minerals. Although halite and gypsum are the most common chemical sediments, there is a diversity of chloride, sulfate, and carbonate minerals that form as chemical precipitates in brines. These minerals have a high potential to also trap organic material as they grow. The training of a new generation of scientists interested in chemical sediments, and the development of new preparation and analytical techniques, are necessary.

Bedded Halite as a Lagerstätte

Lagerstätten are sedimentary deposits that exhibit extraordinary fossils with exceptional preservation. Unaltered bedded halite meets this definition through the exceptional preservation of intact, large, and 3-D organic material, such as palynomorphs and plant cuticle, as well as the preservation of individual cells in an unaltered form. Furthermore, the occurrence of some of these organic materials within their host brine in fluid inclusions may make some biologically viable even over long geologic time periods. For these reasons we propose that unaltered bedded halite should be considered a Lagerstätte.
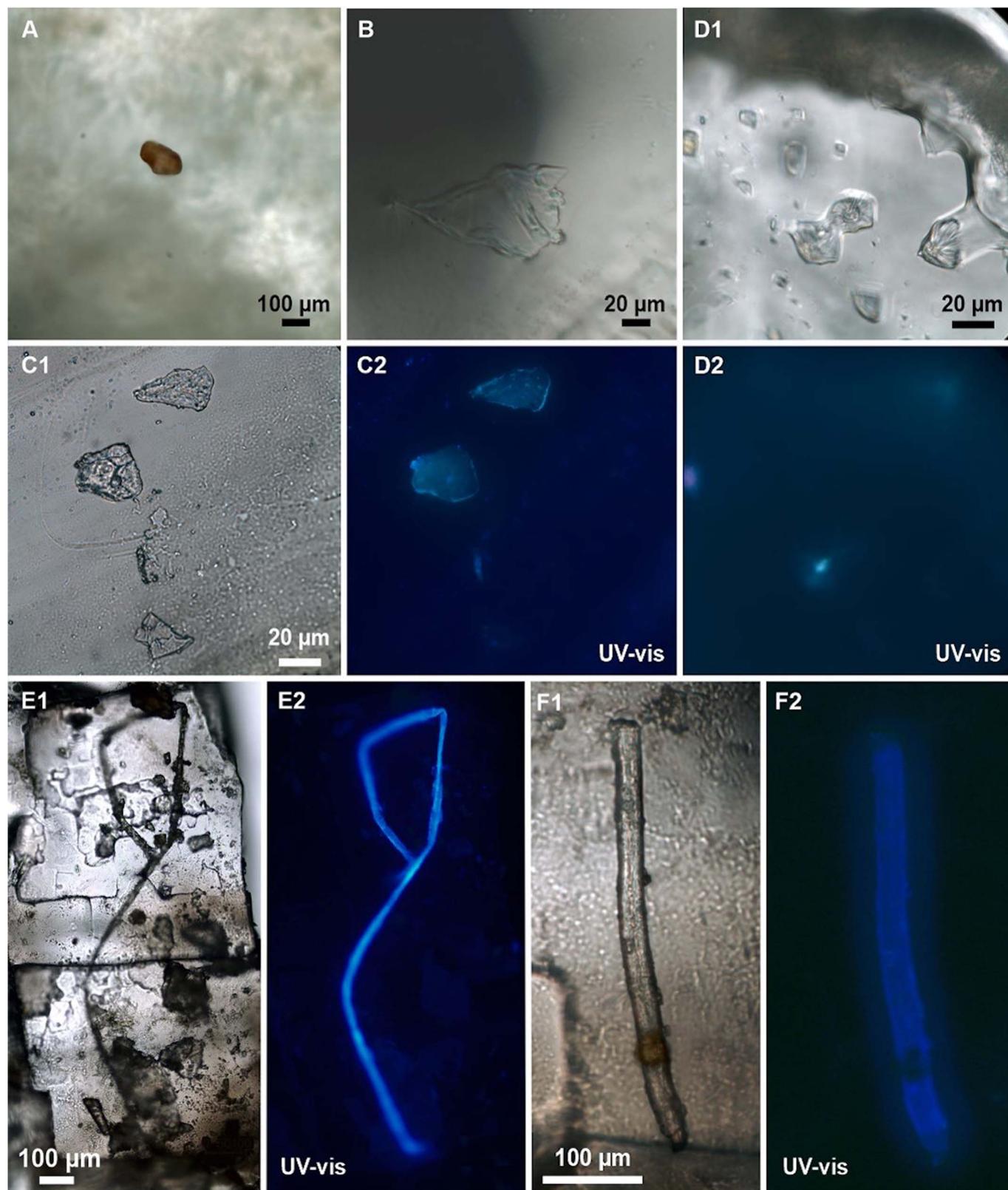
Fig. 5.—Problematic and suspect organic material in modern halite from Western Australia. **A)** Hematite coated grains may look like pollen grains in plane transmitted light in modern halite from Lake Magic. **B)** Translucent, clear amorphous organic material from Lake Gounter. **C1, C2)** Indistinct organic material inside fluid inclusions from Lake Gounter appear clear in plane transmitted light and fluoresce blue under UV light. **D1, D2)** Fluid inclusions in halite from Lake Gounter contain spiky sphere that appear clear under plane transmitted light and fluoresce blue in UV light. **E1, E2)** Looped filamentous suspect organic material in modern "dirty" halite from Lake Gounter fluoresces bright blue under UV light. **F1, F2)** Suspect tubular organic material and yellow sphere, possibly *Dunaliella*, from Lake Gounter, the tubular structure fluoresces blue under UV light.

CONCLUSIONS

In conclusion, there is a diversity of organic materials that have been discovered entrapped as solid inclusions and within fluid inclusions in bedded halite. Microorganisms and fossils in halite tend to be exceptionally well-preserved, as halite under certain conditions of pressure, temperature, and salinity acts as an excellent repository. The sedimentological and paleontological communities should not dismiss salt minerals as potential fossil hosts. Although some highly significant studies of microfossils have been made, too few scientists have turned their attention to salts. We propose that halite deposits might be considered Lagerstätten, hosting some of the best-preserved microfossils throughout geologic time.

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