

# 830-million-year-old microorganisms in primary fluid inclusions in halite

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## ABSTRACT

**Primary fluid inclusions in bedded halite from the 830-m.y.-old Browne Formation of central Australia contain organic solids and liquids, as documented with transmitted light and ultraviolet–visible (UV-vis) petrography. These objects are consistent in size, shape, and fluorescent response with cells of prokaryotes and eukaryotes and with organic compounds. This discovery shows that microorganisms from saline depositional environments can remain well preserved in halite for hundreds of millions of years and can be detected *in situ* with optical methods alone. This study has implications for the search for life in both terrestrial and extraterrestrial chemical sedimentary rocks.**

## INTRODUCTION

As halite (NaCl) grows from saline surface waters, primary fluid inclusions entrap parent waters, becoming microenvironments within the host crystal. Microorganisms have been identified in modern and recent halite-precipitating waters (e.g., Oren, 2005; Zaikova et al., 2018). Optical, chemical, and biological methods have documented microorganisms and organic compounds in fluid inclusions in halite and gypsum, most of which is modern or recent (e.g., Mormile et al., 2003; Schubert et al., 2009a, 2009b, 2010; Lowenstein et al., 2011; Conner and Benison, 2013; Winters et al., 2013; Benison, 2019). Genus- and species-level identifications of prokaryotes have been made from ancient halite (as old as Permian; e.g., Norton et al., 1993; Fish et al., 2002; Stan-Lotter et al., 2002; Vreeland et al., 2000; Thompson et al., 2021). However, limitations of these studies are that they (1) have focused on prokaryotes; (2) have sampled either by bulk crushing or bulk dissolution or by extraction by syringe from individual large fluid inclusions of undetermined origin; and/or (3) have analyzed secondary features such as cements on mine walls. Because petrographic context has been overlooked in the documentation of prokaryotes in ancient halite, most of these studies have not proven that the identified

prokaryotes are the same age as the host halite. Additionally, eukaryotes in ancient halite have not been fully considered. Therefore, a question has persisted amongst geomicrobiologists: What are the oldest chemical sedimentary rocks that contain prokaryotic and eukaryotic microorganisms from the depositional environment?

The Neoproterozoic (Tonian) Browne Formation of the Buldya Group is a well-dated stratigraphic unit of well-preserved chemical and siliciclastic sedimentary rocks found in the subsurface of the Officer Basin in central Australia (Stevens and Apak, 1999; Hill et al., 2000; Pisarevsky et al., 2001; Haines et al., 2004; Grey et al., 2005; Fig. 1). The Empress 1A core was drilled in 1997 by the Geological Survey of Western Australia and contains the ~274 m vertical extent of the Browne Formation, located at 1531.8 to 1247.1 m depth (Stevens and Apak, 1999). The age of the Browne Formation has been estimated as ca. 830 Ma by radiometric dating of associated basalt (Pisarevsky et al., 2001; Zi et al., 2019; Fig. 1B). Lithologies include red siliciclastic mudstones and sandstones, displacive halite in red mudstone or sandstone, bedded gypsum and/or anhydrite, bedded halite, and dolomite and/or chert (Haines et al., 2004). Previous analyses of primary fluid inclusions in the Browne Formation halite estimated Neoproterozoic atmospheric oxygen levels of ~10.9% and Mg-Cl-Na-Ca-SO<sub>4</sub>-rich brines of low to neutral pH (Spear et al., 2014; Blamey et al., 2016; Bernau, 2017). We investigated primary fluid inclusions in unaltered bedded halite of

the Browne Formation for any microorganisms that can be detected with *in situ*, nondestructive optical techniques.

## MATERIALS AND METHODS

Core samples of the Neoproterozoic Browne Formation from the Empress 1A core were used for this study. Our work included observations of 10 halite beds from core depths between 1480.7 m and 1520.1 m. We used a razor blade to cleave halite to a thickness of ~1–2 mm. We then optically examined halite interiors *in situ* and nondestructively so there was no contamination of the fluid inclusions.

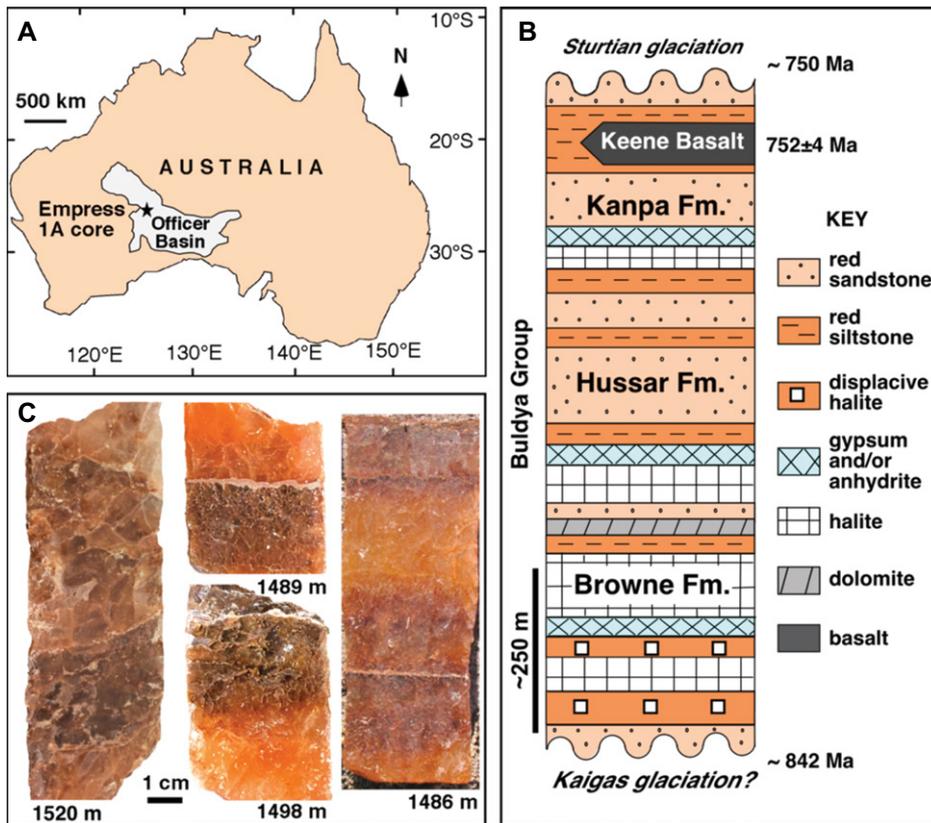
Halite chips were examined with Olympus microscopes with long-working-distance Olympus objectives with 6.3×–2000× magnification range, allowing centimeter- to micron-scale resolution of features below the crystal surfaces. First, we viewed chips at low magnification to identify halite crystal types and distinguish between assemblages of primary and secondary fluid inclusions. Then, at as much as 2000× magnification, we examined individual primary fluid inclusions for their components. We utilized transmitted light to describe size, shape, and color of liquids, gases, minerals, and suspect organic matter. We used cross-polarized light to distinguish minerals and ultraviolet–visible (UV-vis) light (combined 330 nm and 385 nm wavelengths) to test for fluorescent response of any suspect microorganisms and/or organic compounds that would confirm the presence organic matter. We employed digital cameras and SPOT 5 Flex software to document any microorganisms and organic compounds.

## RESULTS

Browne Formation halite in the Empress 1A core consists of (1) millimeter-scale cumulate crystals that formed at the air-water interface and/or in the water column, and (2) centimeter-scale bottom-growth chevron crystals that formed at the sediment-water interface (Roedder, 1984:

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**Figure 1.** The Neoproterozoic Browne Formation in central Australia. (A) Map of Australia with approximate Empress 1A core location (black star) in Officer Basin. (B) Idealized stratigraphic column of the Buldya Group, showing lithologies and ages; modified after Haines et al. (2004), Gray et al. (2005), and Zi et al. (2019). (C) Images of representative core slabs of bedded halite used in this study from the Empress 1A core.

Figs. 2A and 2B). The presence of both chevrons and cumulates in the same beds suggest halite precipitation in shallow saline surface waters. Beds of cumulate and chevron crystals are interbedded with laminations of microcrystalline halite, interpreted as efflorescent crusts that

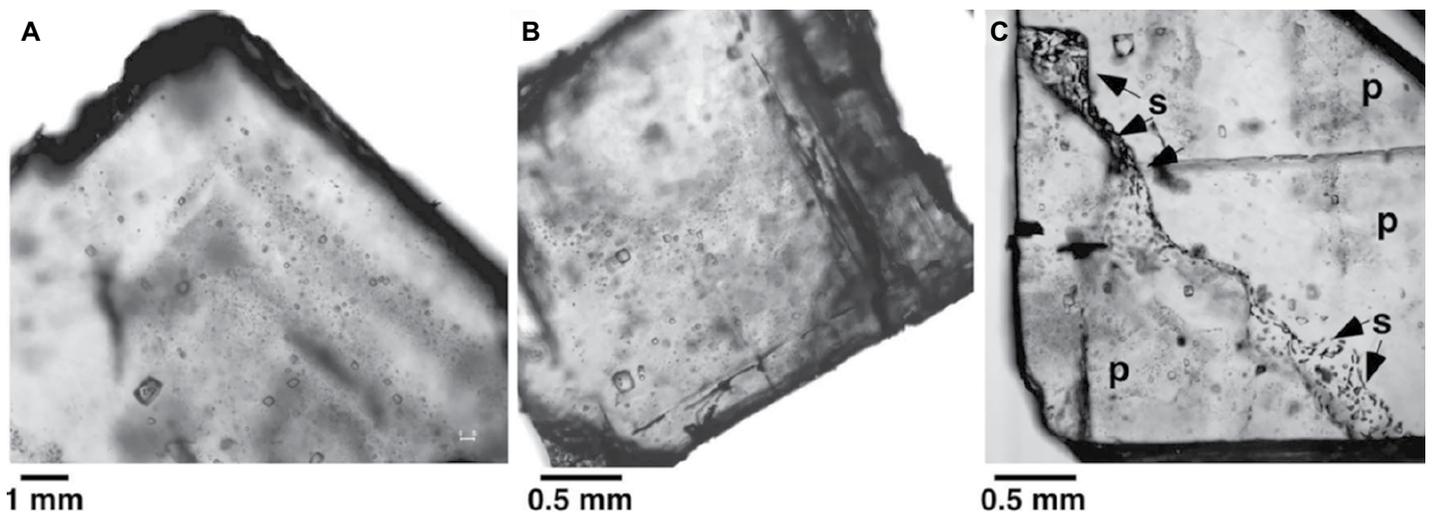
formed during desiccation. These observations of cumulates, chevrons, and efflorescent crusts indicate that halite-precipitating surface brines were likely ephemeral (Lowenstein and Hardie, 1985).

Primary fluid inclusions form as halite crystals precipitate from parent surface waters. Sec-

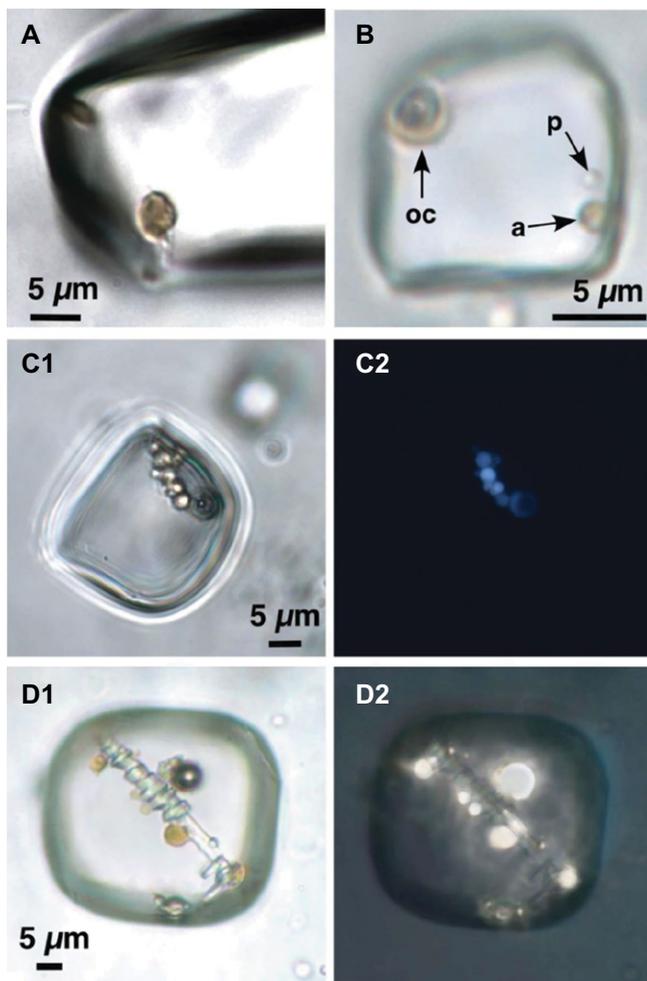
ondary fluid inclusions develop at some time after crystal growth as any fractures in the crystal heal. Primary and secondary inclusions in halite crystals were distinguished based on their size, shape, and distribution (Roedder, 1984; Goldstein and Reynolds, 1994; Fig. 2). Most primary fluid inclusions in Browne Formation halite are ~5–30 μm long, cubic to subcubic, and oriented parallel to one another along growth bands. In contrast, secondary fluid inclusions are larger, irregularly shaped, all-liquid fluid inclusions that are situated along wavy planes, many of which cross-cut growth bands of primary fluid inclusions (Fig. 2C). This study focused on observations of primary fluid inclusions in chevron and cumulate crystals to assure the depositional origin and Neoproterozoic age of microorganisms.

Primary fluid inclusions in the Browne Formation contain water, and many also include a solid and/or gas phase. The solids include “accidental” daughter crystals (minerals that already exist in the depositional environment and get trapped “accidentally” in primary fluid inclusions as the host halite crystal grows) and/or microorganisms and organic compounds (see Figure 3D1 for a view of water, gas bubble, crystal, and microorganisms in a single inclusion; Figs. S1 and S2 in the Supplemental Material<sup>1</sup>). When present in primary fluid inclusions, gas appeared as dark spherical bubbles of various sizes. Their paucity, inconsistent gas:liquid ratio,

<sup>1</sup>Supplemental Material. Primary fluid inclusions in Browne Formation (central Australia) bedded halite that contain individual microorganisms (Figure S1) and daughter crystals (Figure S2). Please visit <https://doi.org/10.1130/GEOLOGY.S.19601863> to access the supplemental material, and contact [editing@geosociety.org](mailto:editing@geosociety.org) with any questions.



**Figure 2.** Fluid inclusions in Browne Formation (central Australia) bedded halite, from the Empress 1A core, in plane-transmitted light. (A) Chevron halite crystal with abundant primary fluid inclusions along growth bands, at 1502.2 m core depth. (B) Cumulate crystal with abundant primary fluid inclusions on growth bands, 1502.6 m core depth. (C) Curved train of secondary fluid inclusions (marked with “s” and arrows) cross-cutting cloudy patches of primary fluid inclusions (marked with “p”), 1498.0 m core depth.



**Figure 3. Microorganisms in individual primary fluid inclusions in Browne Formation (central Australia) halite from the Empress 1A core, at 1520.1 m core depth. (A) Brown algal cell, viewed in plane-transmitted light. (B) Clear prokaryotic cocci (p), orange algal cell (a), and organic compound halo (oc) around air bubble; plane transmitted light. (C) Plane transmitted light (C1) and UV-vis light (C2) images of a chain of yellow algal cells, clear cocci, and an air bubble with a halo of clear organic compound that fluoresce blue. (D) Plane transmitted light (D1) and UV-vis light (D2) images of clear prokaryotes, yellow algae, suspect organic compound halo, air bubble, and clear accidental daughter crystals; organics fluoresce white and gold.**

and geologic context in ephemeral saline lake halite suggests that the gas is likely trapped air.

We observed possible prokaryotic and eukaryotic cells, as well as suspect organic compounds, in primary fluid inclusions in the Browne Formation bedded halite (Fig. 3). We use the term “suspect” for the organic compounds because we cannot fully identify their composition by their optical appearance and fluorescent response to UV-vis light. The organic compounds are morphologically ambiguous, unlike the microorganisms, which have characteristic sizes and shapes.

Tiny ( $\sim 0.5 \mu\text{m}$  to  $\sim 1 \mu\text{m}$ ) cocci-like spheres are abundant both within fluid inclusions and as solid inclusions in host halite. Some primary fluid inclusions contain cocci as the sole organic component. They appear bright with high relief and are white, pale orange, or pale blue when viewed under plane-transmitted light. When illuminated with UV-vis light, some cocci exhibit either pale gold to white or blue fluorescence (Fig. 3C2; Fig. S1A). However, fluorescent response was not observed for all cocci. These cocci are consistent in size, shape, and optical appearance with some prokaryotes (bacteria and/or archaea). However, we cannot rule out that they are spores of bacteria or fungi.

Eukaryotic cells, likely algae and/or fungi, are 2–5- $\mu\text{m}$ -diameter spheres observed in primary fluid inclusions (Figs. 3A and 3D1; Fig. S1A). They are pale orange, pale yellow, pale brown, or clear when viewed under plane-transmitted light. They commonly have a dark rim. Some have a dark spot inside the sphere, some have a dimpled surface texture, and some have a thin,  $\sim 1\text{-}\mu\text{m}$ -thick isopachous halo surrounding the cell. Like for the prokaryotic cocci, fluorescent response to UV-vis light is not ubiquitous. When eukaryotes do exhibit fluorescence, it is pale gold to white or blue (Figs. 3C2 and 3D2). Some cells have features consistent with the halophilic algal genus *Dunaliella*, including a yellow color, a dimpled surface texture, and a dark rim (Schubert et al., 2010).

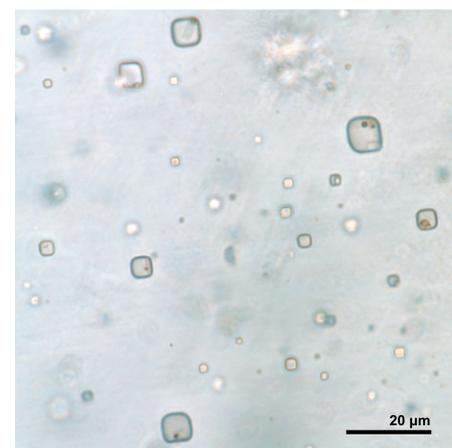
Suspect organic compounds in fluid inclusions consist of liquids or amorphous solids. We observed organic compounds most commonly as liquid halos around some air bubbles and eukaryotic cells and less commonly as solids. Some suspect organic compounds around air bubbles are largely indistinguishable in plane-transmitted light. However, fluorescent response to UV-vis light distinguishes the organic halos from the nonfluorescent air bubbles (Fig. 3C2). These liquid organic com-

pounds enveloping air bubbles exhibit white, blue to blue-green, or pale orange to red fluorescent response to UV-vis light. Some may be insoluble organic compounds such as beta-carotene. Other, rare organic compounds around air bubbles were organic crystalline solids. Solid organic compounds have an amorphous shape, are clear to pale yellow in plane-transmitted light, and exhibit a faint fluorescence under UV-vis light.

There is a great range of abundance of microorganisms and organic compounds within and among individual growth bands in single crystals as well as among halite crystals from different depths in the core. Several of the crystals used in this study have an exceptionally high concentration of microorganisms and suspect organic compounds within primary fluid inclusions. For these crystals, we estimated that  $\sim 40\%$  of inclusions contained suspect microorganisms. (Fig. 4). But some crystals had abundant primary inclusions yet did not contain any obvious microorganisms.

Some fluid inclusions contain several (10 or more) microorganisms. These fluid inclusions typically contain both prokaryotes and eukaryotes as well as accidental daughter crystals and suspect organic compounds. Primary fluid inclusions with several microorganisms were generally larger than neighboring inclusions.

Accidental daughter crystals are common in the Browne Formation halite. The presence of accidental daughter crystals may indicate that other minerals were co-precipitating in the parent surface brine. We observed gypsum and/or anhydrite and other hydrated sulfate minerals (Fig. S2) and iron oxides as accidental daughter crystals. The Browne Formation halite precipitated from complex surface brines. The microorganisms, therefore, were either extremophiles and/or microbes blown into the surface waters by wind.



**Figure 4. Distribution of microorganisms in primary fluid inclusions in Browne Formation halite (central Australia) from the Empress 1A core, at 1520.1 m depth.**

## DISCUSSION

The discovery of microorganisms in primary fluid inclusions in 830 Ma Browne Formation halite is evidence for entrapment of microorganisms in Tonian waters and their preservation within depositional crystals over a long geological time span on Earth. The range of fluorescent response to UV-vis light may indicate some alteration due to organic decay. The blue fluorescence is consistent with that of modern microorganisms, suggesting unaltered organic material (e.g., Mormile and Storrie-Lombardi, 2005; Conner and Benison, 2013). In contrast, the white and gold fluorescence in some cells and lack of fluorescence in other cells may be the result of organic decay.

Are microorganisms in Browne Formation halite alive? Some halophilic microorganisms, such as *Dunaliella* algae, shrink and greatly reduce biological activity when host waters become too saline; these algal cells may be revived during later flooding events (Oren, 2005). Survival of bacteria and archaea in primary fluid inclusions in 97 and 150 ka halite have been described (Mormile et al., 2003; Lowenstein et al., 2011). The oldest known halite from which living prokaryotes have been extracted and cultured is Permian (ca. 250 Ma; Vreeland et al., 2000). Therefore, it is plausible that microorganisms from the Neoproterozoic Browne Formation are extant.

Possible survival of microorganisms over geologic time scales is not fully understood. It has been suggested that radiation would destroy organic matter over long time periods, yet Nicastro et al. (2002) found that buried 250 Ma halite was exposed to only negligible amounts of radiation. Additionally, microorganisms may survive in fluid inclusions by metabolic changes, including starvation survival and cyst stages, and coexistence with organic compounds or dead cells that could serve as nutrient sources (e.g., McGenity et al., 2000; Schubert et al., 2009a, 2010; Stan-Lotter and Fendrihan, 2015). One such organic compound, glycerol, produced by the cellular breakdown of some algae, may provide energy for longevity of coexisting prokaryotes (Schubert et al., 2010; Lowenstein et al., 2011). Furthermore, both non-spore-forming and spore-forming prokaryotes may have advantages for long-term survival in fluid inclusions. Non-spore-forming prokaryotes are continually, but minimally, metabolically active, so they are able to repair DNA should it be necessary (Johnson et al., 2007). Alternately, spores formed by prokaryotes may provide another way of long-term survival in a dormant state (Vreeland et al., 2000; Lowenstein et al., 2011).

The results of our study suggest the possibility of similar long-term preservation of biosignatures on Mars. The Browne Formation is a possible analog for some martian rocks because both contain a similar suite of minerals, sedi-

mentary structures, and diagenetic features (e.g., Squyres et al., 2004; Benison and Bowen, 2006). Mars once contained saline lakes that precipitated chemical sediments, including halite (e.g., Osterloo et al., 2008). Microorganisms that may have existed in surface brines on Mars in the ancient past may be trapped as microfossils in chemical sedimentary rocks (Benison, 2019).

Optical examination should be considered a fundamental step in any study of biosignatures in ancient rocks. It allows geologic context of microorganisms to be known prior to further chemical or biological analyses, such as laser Raman spectroscopy, microbial culturing, and metagenomic studies, and it provides a target for such analyses.

## CONCLUSIONS

The well-preserved primary fluid inclusions in Neoproterozoic Browne Formation halite are remnants of original surface waters that hosted prokaryotes, eukaryotes, and organic compounds. These microorganisms have been trapped since the halite precipitated at ca. 830 Ma. In that time, they have not experienced significant decomposition and are able to be optically recognized *in situ*. Fluids inside primary inclusions serve as microhabitats for trapped microorganisms, allowing exceptional preservation of organic matter over long periods of geological time. Ancient chemical sediments, both of terrestrial and extraterrestrial origin, should be considered potential hosts for ancient microorganisms and organic compounds.

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## REFERENCES CITED

- Benison, K.C., 2019, How to search for life in Martian chemical sediments and their fluid and solid inclusions using petrographic and spectroscopic methods: *Frontiers in Environmental Science*, v. 7, 108, <https://doi.org/10.3389/fenvs.2019.00108>.
- Benison, K.C., and Bowen, B.B., 2006, Acid saline lake systems give clues about past environments and the search for life on Mars: *Icarus*, v. 183, p. 225–229, <https://doi.org/10.1016/j.icarus.2006.02.018>.
- Bernau, J.A., 2017, Fluid inclusion analyses of bedded halite from the Neoproterozoic Browne Formation of central Australia to determine parent water origin and pH [M.S. thesis]: Morgantown, West Virginia University, 225 p., <https://doi.org/10.33915/etd.5192>.

- Blamey, N.J.F., Brand, U., Parnell, J., Spear, N., Lécuyer, C., Benison, K.C., Meng, F.W., and Ni, P., 2016, Paradigm shift in determining Neoproterozoic atmospheric oxygen: *Geology*, v. 44, p. 651–654, <https://doi.org/10.1130/G37937.1>.
- Conner, A.J., and Benison, K.C., 2013, Acidophilic halophilic microorganisms in fluid inclusions in halite from Lake Magic, Western Australia: *Astrobiology*, v. 13, p. 850–860, <https://doi.org/10.1089/ast.2012.0956>.
- Fish, S.A., Shepherd, T.J., McGenity, T.J., and Grant, W.D., 2002, Recovery of 16S ribosomal RNA gene fragments from ancient halite: *Nature*, v. 417, p. 432–436, <https://doi.org/10.1038/417432a>.
- Goldstein, R.H., and Reynolds, T.J., 1994, Systematics of fluid inclusions in diagenetic minerals: SEPM (Society for Sedimentary Geology) Short Course 31, 199 p., <https://doi.org/10.2110/scn.94.31>.
- Grey, K., Hocking, R.M., Stevens, M.K., Bagas, L., Carlsen, G.M., Irimies, F., Prianjo, F., Haines, P.W., and Apak, S.N., 2005, Lithostratigraphic nomenclature of the Officer Basin and correlative parts of the Paterson Orogen, Western Australia: Geological Survey of Western Australia Report 93, 89 p.
- Haines, P.W., Mory, A.J., Stevens, M.K., and Ghori, K.A.R., 2004, GSWA Lancer 1 well completion report (basic data), Officer and Gunbarrel Basins, Western Australia: Geological Survey of Western Australia Record 2004/10, 39 p.
- Hill, A.C., Cotter, K.L., and Grey, K., 2000, Mid-Neoproterozoic biostratigraphy and isotope stratigraphy in Australia: *Precambrian Research*, v. 100, p. 281–298, [https://doi.org/10.1016/S0301-9268\(99\)00077-7](https://doi.org/10.1016/S0301-9268(99)00077-7).
- Johnson, S.S., et al., 2007, Ancient bacteria show evidence of DNA repair: *Proceedings of the National Academy of Sciences of the United States of America*, v. 104, p. 14,401–14,405, <https://doi.org/10.1073/pnas.0706787104>, corrections available at <https://doi.org/10.1073/pnas.0710637104> and <https://doi.org/10.1073/pnas.0804198105>.
- Lowenstein, T.K., and Hardie, L.A., 1985, Criteria for the recognition of salt-pan evaporites: *Sedimentology*, v. 32, p. 627–644, <https://doi.org/10.1111/j.1365-3091.1985.tb00478.x>.
- Lowenstein, T.K., Schubert, B.A., and Timofeeff, M.N., 2011, Microbial communities in fluid inclusions and long-term survival in halite: *GSA Today*, v. 21, no. 1, p. 4–9, <https://doi.org/10.1130/GSATG81A.1>.
- McGenity, T.J., Gemmel, R.T., Grant, W.D., and Stan-Lotter, H., 2000, Origins of halophilic microorganisms in ancient salt deposits: *Environmental Microbiology*, v. 2, p. 243–250, <https://doi.org/10.1046/j.1462-2920.2000.00105.x>.
- Mormile, M.R., and Storrie-Lombardi, M., 2005, The use of ultraviolet excitation of native fluorescence for identifying biomarkers in halite crystals, *in* Hoover, R.B., et al., eds., *Astrobiology and Planetary Missions: SPIE (The International Society of Optics and Photonics) Proceedings 5906*, 8 p., <https://doi.org/10.1117/12.616906>.
- Mormile, M.R., Biesen, M.A., Carmen Gutierrez, M., Ventosa, A., Pavlovich, J.B., Onstott, T.C., and Fredrickson, J.K., 2003, Isolation of *Halobacterium salinarum* retrieved directly from halite brine inclusions: *Environmental Microbiology*, v. 5, p. 1094–1102, <https://doi.org/10.1046/j.1462-2920.2003.00509.x>.
- Nicastro, A.J., Vreeland, R.H., and Rosenzweig, W.D., 2002, Limits imposed by ionizing radiation on the long-term survival of trapped bacterial spores: Beta radiation: *International Journal of Radiation Biology*, v. 78, p. 891–901, <https://doi.org/10.1080/09553000210155905>.

- Norton, C.F., McGenity, T.J., and Grant, W.D., 1993, Archaeal halophiles (halobacteria) from two British salt mines: *Microbiology*, v. 139, p. 1077–1081, <https://doi.org/10.1099/00221287-139-5-1077>.
- Oren, A., 2005, A hundred years of *Dunaliella* research: 1905–2005: *Aquatic Biosystems*, v. 1, 2, <https://doi.org/10.1186/1746-1448-1-2>.
- Osterloo, M.M., Hamilton, V.E., Bandfield, J.L., Glotch, T.D., Baldrige, A.M., Christensen, P.R., Tornabene, L.L., and Anderson, F.S., 2008, Chloride-bearing materials in the southern highlands of Mars: *Science*, v. 319, p. 1651–1654, <https://doi.org/10.1126/science.1150690>.
- Pisarevsky, S.A., Li, Z.X., Grey, K., and Stevens, M.K., 2001, A paleomagnetic study of Empress 1A, a stratigraphic drillhole in the Officer Basin: Evidence for a low-latitude position of Australia in the Neoproterozoic: *Precambrian Research*, v. 110, p. 93–108, [https://doi.org/10.1016/S0301-9268\(01\)00182-6](https://doi.org/10.1016/S0301-9268(01)00182-6).
- Roedder, E., 1984, The fluids in salt: *American Mineralogist*, v. 69, p. 413–439.
- Schubert, B.A., Lowenstein, T.K., Timofeeff, M.N., and Parker, M.A., 2009a, How can prokaryotes survive in fluid inclusions in halite for 30,000 years?: *Geology*, v. 37, p. 1059–1062, <https://doi.org/10.1130/G30448A.1>.
- Schubert, B.A., Lowenstein, T.K., and Timofeeff, M.N., 2009b, Microscopic identification of prokaryotes in modern and ancient halite, Saline Valley and Death Valley, California: *Astrobiology*, v. 9, p. 467–482, <https://doi.org/10.1089/ast.2008.0282>.
- Schubert, B.A., Timofeeff, M.N., Polle, J.E.W., and Lowenstein, T.K., 2010, *Dunaliella* cells in fluid inclusions in halite: Significance for long-term survival of prokaryotes: *Geomicrobiology Journal*, v. 27, p. 61–75, <https://doi.org/10.1080/01490450903232207>.
- Spear, N., Holland, H.D., Garcia-Veigas, J., Lowenstein, T.K., Giegengack, R., and Peters, H., 2014, Analysis of fluid inclusions in Neoproterozoic marine halite provide oldest measurement of seawater chemistry: *Geology*, v. 42, p. 103–106, <https://doi.org/10.1130/G34913.1>.
- Squires, S.W., et al., 2004, In situ evidence for an ancient aqueous environment at Meridiani Planum, Mars: *Science*, v. 306, p. 1709–1714, <https://doi.org/10.1126/science.1104559>.
- Stan-Lotter, H., and Fendrihan, S., 2015, Halophilic Archaea: Life with desiccation, radiation and oligotrophy over geological times: *Life (Chicago)*, v. 5, p. 1487–1496, <https://doi.org/10.3390/life5031487>.
- Stan-Lotter, H., Pfaffenhuemer, M., Legat, A., Busse, H.-J., Radax, C., and Gruber, C., 2002, *Halococcus dombrowskii* sp. nov., an archaeal isolate from a Permian alpine salt deposit: *International Journal of Systematic and Evolutionary Microbiology*, v. 52, p. 1807–1814, <https://doi.org/10.1099/00207713-52-5-1807>.
- Stevens, M.K., and Apak, S.N., 1999, GSWA Empress 1 and 1A well completion report, Yowalga Sub-basin, Officer Basin, Western Australia: Geological Survey of Western Australia Record 1999/4, 110 p.
- Thompson, T.P., Kelly, S.A., Skvortsov, T., Plunkett, G., Ruffell, A., Hallsworth, J.E., Hopps, J., and Gilmore, B.F., 2021, Microbiology of a NaCl stactite “salticle” in Triassic halite: *Environmental Microbiology*, v. 23, p. 3881–3895, <https://doi.org/10.1111/1462-2920.15524>.
- Vreeland, R.H., Rosenzweig, W.D., and Powers, D.W., 2000, Isolation of a 250 million-year-old halotolerant bacterium from a primary salt crystal: *Nature*, v. 407, p. 897–900, <https://doi.org/10.1038/35038060>.
- Winters, Y.D., Lowenstein, T.K., and Timofeeff, M.N., 2013, Identification of carotenoids in ancient salt from Death Valley, Saline Valley, and Searles Lake, California, using laser Raman spectroscopy: *Astrobiology*, v. 13, p. 1065–1080, <https://doi.org/10.1089/ast.2012.0952>.
- Zaikova, E., Benison, K.C., Mormile, M.R., and Johnson, S.S., 2018, Microbial communities and their predicted metabolic functions in a desiccating acid salt lake: *Extremophiles*, v. 22, p. 367–379, <https://doi.org/10.1007/s00792-018-1000-4>.
- Zi, J.W., Haines, P.W., Wang, Z.C., Jourdan, F., Rasmussen, B., Halverson, G.P., Sheppard, S., and Li, C.F., 2019, Pyroxene <sup>40</sup>Ar/<sup>39</sup>Ar dating of basalt and applications to large igneous provinces and Precambrian stratigraphic correlations: *Journal of Geophysical Research: Solid Earth*, v. 124, p. 8313–8330, <https://doi.org/10.1029/2019JB017713>.

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