

# Preservation of Biological Information in Thermal Spring Deposits: Developing a Strategy for the Search for Fossil Life on Mars

M. R. WALTER

*School of Earth Sciences, Macquarie University, North Ryde, New South Wales, Australia 2109*

AND

DAVID J. DES MARAIS

*Ames Research Center, Moffett Field, California 94035*

Received March 30, 1992; revised September 25, 1992

---

Current interpretations of the early history of Mars suggest many similarities with the early Earth and therefore raise the possibility that the Archean and Proterozoic history of life on Earth could have a counterpart on Mars. Terrestrial experience suggests that, with techniques that can be employed remotely, ancient springs, including thermal springs, could well yield important information. By delivering water and various dissolved species to the sunlit surface of Mars, springs very likely created an environment suitable for life, which could have been difficult, if not impossible, to attain elsewhere. The chemical and temperature gradients associated with thermal springs sort organisms into sharply delineated, distinctive and different communities, and so diverse organisms are concentrated into relatively small areas in a predictable and informative fashion. A wide range of metabolic strategies are concentrated into small areas, thus furnishing a useful and representative sampling of the existing biota. Mineral-charged springwaters frequently deposit chemical precipitates of silica and/or carbonate which incorporate microorganisms and preserve them as fossils.

The juxtaposition of stream valley headwaters with volcanoes and impact craters on Mars strongly implies that subsurface heating of groundwater created thermal springs. On Earth, thermal springs create distinctive geomorphic features and chemical signatures which can be detected by remote sensing. Spring deposits can be quite different chemically from adjacent rocks. Individual springs can be hundreds of meters wide, and complexes of springs occupy areas up to several kilometers wide. Benthic microbial mats and the resultant stromatolites occupy a large fraction of the available area. The relatively high densities of fossils and microbial mat fabrics within these deposits make them highly prospective in any search for morphological evidence of life, and there are examples of microbial fossils in spring deposits as old as 300 Myr. © 1993 Academic Press, Inc.

---

## INTRODUCTION

Current interpretations of the early history of Mars suggest many similarities with the early Earth and therefore raise the possibility that the Archean and Proterozoic history of life on Earth could have a counterpart on Mars (McKay 1986, McKay and Stoker 1989). Investigating that possibility is an intellectual and technical challenge of profound significance. The purpose of this paper is to draw from paleobiological experience on Earth to begin to develop a search strategy to be used on Mars. Here we advocate exploring for thermal spring deposits as a way to maximize the chance of finding fossil life on Mars.

The rationale for comparing Earth and Mars is expressed in Fig. 1 (from McKay and Stoker 1989). A significant element in the comparison is the view that the early atmosphere on Mars was comparable to that on Earth at the time, but was later lost. An aspect of this is that there was abundant liquid water which produced the fluvial channels that occur widely (Carr 1987). Although some current interpretations of the Martian valley systems raise some doubts about the view that the early atmosphere was substantially different from that now present, they nonetheless indicate that there was both surface flow and spring outflow (Gulick and Baker 1989).

There has been a good deal of discussion about search strategies for fossil life on Mars (reviewed in depth by McKay 1986 and McKay and Stoker 1989), and attention has focused on layered rocks (which might be lacustrine deposits), on the regolith, and on ground ice, among other sites. Lacustrine sediments are an obvious target, because lakes combine the environmental features required for life

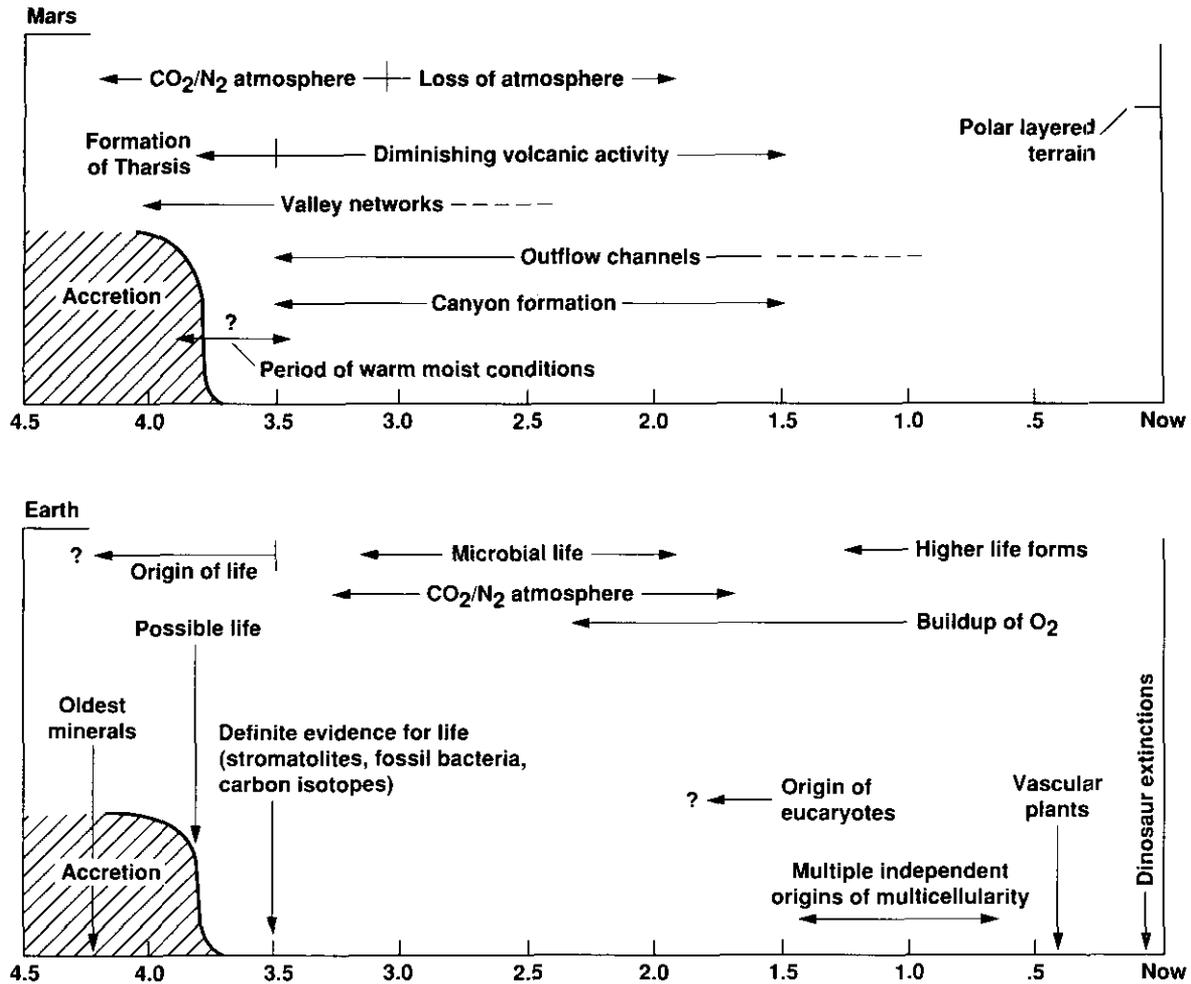


FIG. 1. Comparison of the history of Earth and Mars (after McKay and Stoker 1989).

on Earth, and fossils commonly are preserved and found in their sediments. The regolith is home for a substantial microbiota, even in the harshest environments on Earth, as in Antarctica. Terrestrial experience suggests that, with the techniques that can be employed remotely, ancient springs, including thermal springs, could well yield important information (Walter 1988).

A locality must satisfy several criteria in order to be a suitable fossil site. Thermal springs are remarkable in that they score highly in almost all of these criteria, which are as follows:

1. *Sustenance of life.* By delivering water and various dissolved chemical species to the sunlit surface of Mars, springs very likely created an early environment suitable for life, which could have been difficult, if not impossible, to attain elsewhere. Springwater at elevated temperatures could have supported a thermophilic lifestyle, which has been proposed for the common ancestor of life on Earth (Woese 1987, Stetter *et al.* 1990). They are sites of chemi-

cal disequilibrium that can be exploited as a source of energy for life. The chemical and thermal gradients associated with springs sort organisms into sharply delineated distinctive and different communities, and so diverse organisms are concentrated into relatively small areas in a predictable and informative fashion; an enormously wide range of metabolic strategies is concentrated into a small area, thus furnishing a usefully representative sampling of the existing biota. For some of the same reasons, submarine hydrothermal vents on Earth are a candidate site for the origin of life (Baross and Hoffman 1985), and certainly life is prolific at these vents now.

2. *Preservation.* Mineral-charged springwaters frequently deposit chemical precipitates of silica and/or carbonate which sequester microorganisms and preserve them as fossils. Such chemical sediments, in which organisms are often morphologically preserved, predominate in spring deposits. Allochthonous clastic sediments are relatively rare in spring settings, in contrast to the deposits

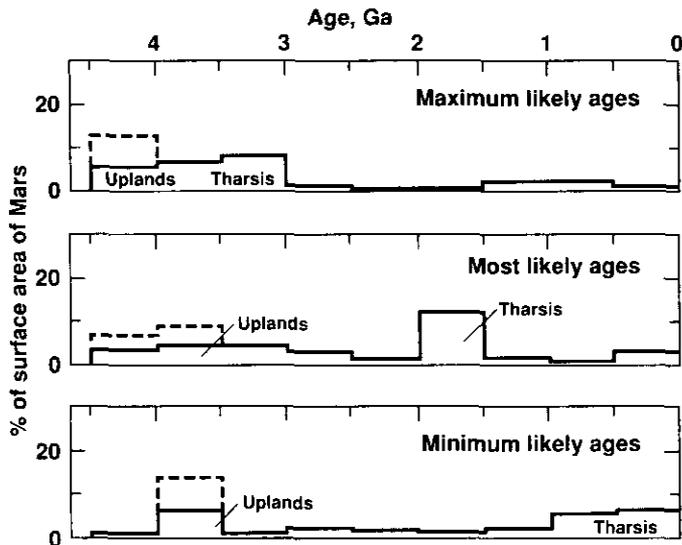


FIG. 2. Timing of volcanism on Mars as determined from cratering history (after Hartmann *et al.* 1981).

of rivers and lakes. The resultant preservation imitates successful examples of fossilization in Precambrian rocks on Earth. For instance, in the abundance of benthic microorganisms coupled with the deposition of primary silica, they can be compared with the stromatolite facies of iron formations (a comparison that is explored by Walter 1972).

**3. Thermal springs on Mars?** The juxtaposition of stream valley headwaters with volcanoes on Mars (e.g., Carr 1981) has been interpreted as indicating that subsurface heating of groundwater created thermal springs (Brakenridge 1990). The necessary groundwater (or ground ice) seems to have been available (Snyder 1979, Brakenridge *et al.* 1985, Carr 1987, McKay and Stoker 1989). Geomorphological analyses of many Martian valley networks suggest an origin through spring discharge (e.g., Baker and Partridge 1986, Squyres *et al.* 1987, Crown *et al.* 1992). The thermal spring environment could have persisted for much of Martian history, because the wide range of ages inferred for volcanic activity (Wise *et al.* 1979, Neukum and Hiller 1981, Hartmann *et al.* 1981, McSween 1985, Vickery and Melosh 1987; Fig. 2) indicates that near-surface heat sources were available. Because water or ground ice also was present throughout the planet's history, the generation of thermal springs was inevitable.

**4. Detection and sampling.** Thermal springs create distinctive geometric features and chemical signatures which can be detected by remote sensing. Spring deposits are most abundant near the source region and display a range of sediment types as a function of distance from the

source (Figs. 3 and 4). Individual springs can be hundreds of meters wide, and complexes of springs occupy areas up to several kilometers wide. Benthic microbial mats and the resultant stromatolites occupy a large fraction of the available area in thermal springs on Earth. The relatively high densities of fossils and microbial mat fabrics within these deposits make them highly prospective in any search for morphological evidence of life.

#### CHARACTERISTICS OF MODERN THERMAL SPRINGS

Many thousands of thermal springs have been documented on Earth (e.g., Waring 1965). They occur where deep artesian waters reach the surface of sedimentary basins, in tectonically active sites where deep faults provide conduits or shallow heat sources provide energy, and in areas of active or recently active volcanism. They are most abundant and best known from volcanic areas such as Yellowstone National Park (Wyoming), New Zealand, and Iceland (Waring 1965, White *et al.* 1988). Thermal spring deposits derive ultimately from the intense hydrothermal alteration of parent rock. Silica is typically deposited in springs because its solubility declines rapidly as the springwaters cool (Fournier 1973). Even though it is more soluble than quartz and chalcedony, amorphous silica is first to form because the kinetics of its precipitation are more rapid (Fournier 1973). The spherulitic texture of silica polymer is a very distinctive feature of this deposit. Deposits of silica are often accompanied by other minerals distinctively associated with hydrothermal activity (e.g., calcite, metal sulfides, and gold; Ellis and McMahon 1977). The following description of Yellowstone provides an overview of the thermal spring environment and addresses the first two issues raised above, the sustenance and preservation of life.

The present geothermal activity in Yellowstone is a result of extrusive volcanism which began about 2 Myr ago and continued until 70,000 years ago (Keefer 1971, Christiansen and Blank 1972). The rocks produced are largely rhyolites and rhyolitic welded tuffs, with some basalts; they form the "Yellowstone rhyolite plateau." Within the plateau is an enormous elliptical caldera, 70 by 45 km wide, partly filled with lava flows (Fig. 5). Pleistocene glacial sediments and Pleistocene and Holocene fluvial sediments are intercalated with and overlie the volcanics. Some of these sediments are described by Howard (1937) and White *et al.* (1988). Hydrothermal explosion breccias occur locally (Muffler *et al.* 1982). The springs are scattered over an area of several thousand square kilometers; the area of occurrence is irregular in shape but has a maximum dimension of about 90 km. There are approximately 3,000 springs in about 100 clusters (Allen and Day 1935). Many of the clusters are grouped into "geyser basins," which are areas of inten-

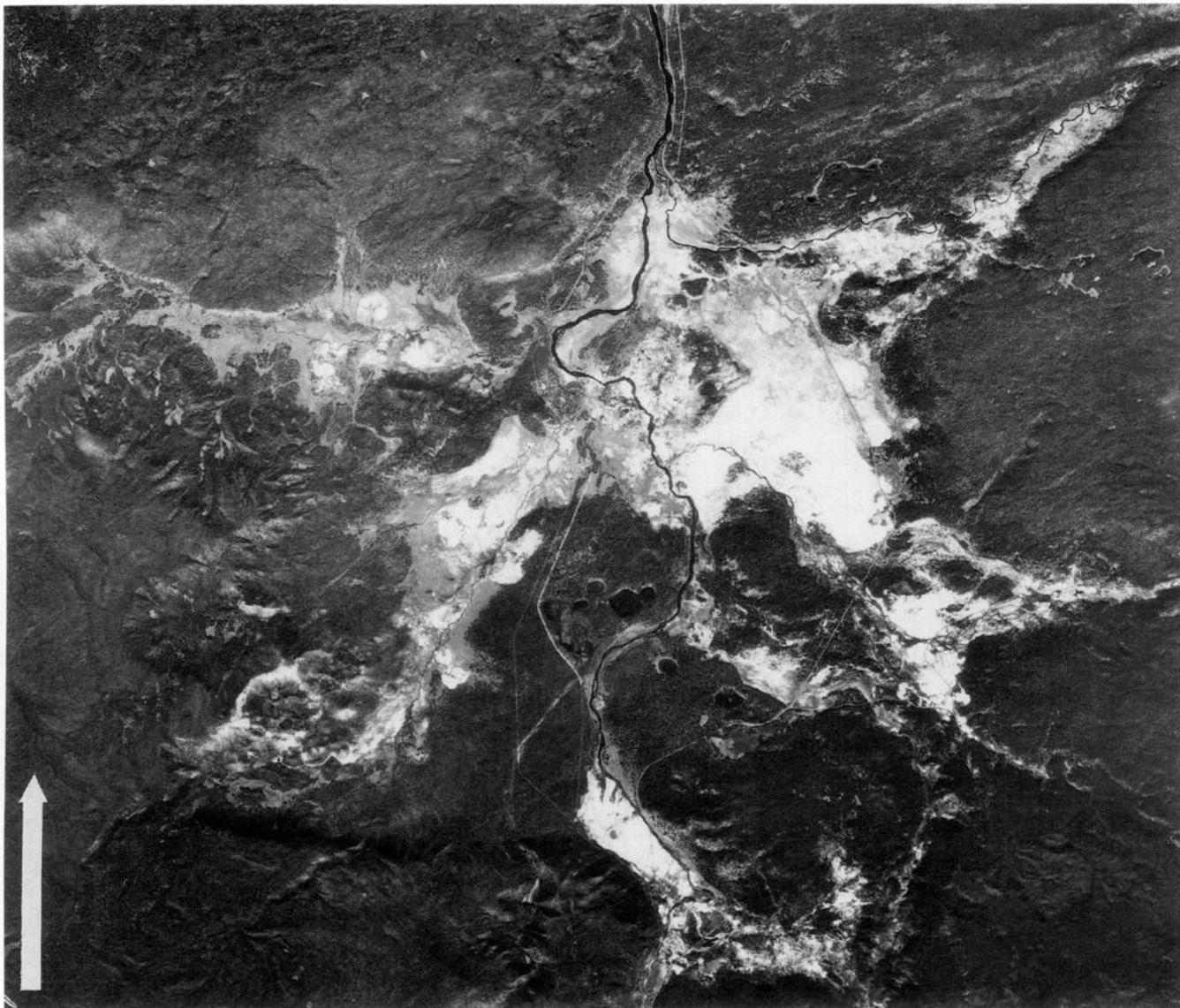


FIG. 3. High altitude image of Lower Geyser Basin, Yellowstone National Park. North arrow at lower left is also a scale bar which represents 2 km.

sive geothermal activity. These cover areas of several square kilometers. The major types are alkaline (carbonate or silica depositing) and acidic. The young thermal spring travertines of the Mammoth Geyser Basin (Weed 1889a, Allen and Day 1935) consist of aragonite. Very little deposition of silica occurs from acid waters such as those of the Norris Geyser Basin (rarely, acid springs do deposit geysersite; Walter 1976b, White *et al.* 1988). Extensive hydrothermal alteration of the rocks through which the spring waters pass is caused by both the alkaline and the acidic waters (Fenner 1936, Honda and Muffler 1970).

Only the silica-depositing neutral to alkaline thermal springs are considered further here, because the excellent

preservational characteristics of silica will maximize information retention during diagenesis and metamorphism. These are the most abundant of the springs in Yellowstone, and are also abundant in other hydrothermal fields. Their ubiquity suggests that stringent special conditions are not necessary for their occurrence. Passage of hot water through volcanic rocks seems to suffice. This is supported by their occurrence in basaltic terrains such as Iceland (Brock 1978, p. 245) as well as in the silicic volcanic terrain of Yellowstone National Park. Silica deposits are the most common precipitates from the hydrothermal alteration of volcanic rocks (Ellis and McMahon 1977). This emphasis on silica-depositing springs is not meant to imply that significant paleobiological information cannot



FIG. 4. Low level aerial photograph of Grand Prismatic Spring in the Midway Geyser Basin of Yellowstone National Park. The pool of near-boiling water is about 100 m wide. At the margin of the pool is light-colored nonbiogenic geysirite; this is surrounded by concentric zones of microbial sinter.

be preserved by other types of mineral deposits (especially calcium and magnesium carbonate, among many others), but reflects paleontological experience on Earth which demonstrates high fidelity of preservation in chert.

The broad features of thermal spring sediment distribution in Yellowstone National Park are shown in the U.S. Geological Survey Miscellaneous Geological Investigations Map I-710 (Richmond *et al.* 1972) and in detail on Map I-1373 (Muffler *et al.* 1982). The description that follows is based on these maps, the publications of Walter (1972, 1976a,b) and Walter *et al.* (1972, 1976), and the publications cited below. The geysirite and biogenic sinters have been described in detail, and many aspects of their formation are known, but the associated sediment types are very poorly known. The various forms of stromatolitic sinter and sinter breccia form accumulations up to 6-m thick with thin beds in which lateral facies changes occur frequently (Figs. 6–8). All consist of opaline silica with a spheroidal ultrastructure but each has its own char-

acteristic laminar microstructure (Walter 1976a, Walter *et al.* 1976).

A wide range of biological communities is observed along thermal gradients of spring-fed streams, with the major controls on their occurrence being temperature, pH, and  $H_2S$  and  $O_2$  concentrations (Ward *et al.* 1989). The most widespread microbial mats in thermal springs are those produced by cyanobacteria in neutral to alkaline springs. Above  $54^\circ C$  metazoans and metaphytes are absent, and no eucaryotes occur above  $58^\circ C$ . The diversity of organisms present is expressed in Table 1; there are cyanobacteria, photosynthetic bacteria, sulfate reducing bacteria, archaeobacteria, fungi, eucaryotic algae, and other organisms. Some of the microbial communities are entirely anaerobic. In Yellowstone in particular the biology of the springs has been studied in great detail (e.g., Brock 1978). Each of these communities is amenable to preservation in silica, and they are described briefly below.

*Temperatures above  $74^\circ C$ .* Geysirite is deposited as

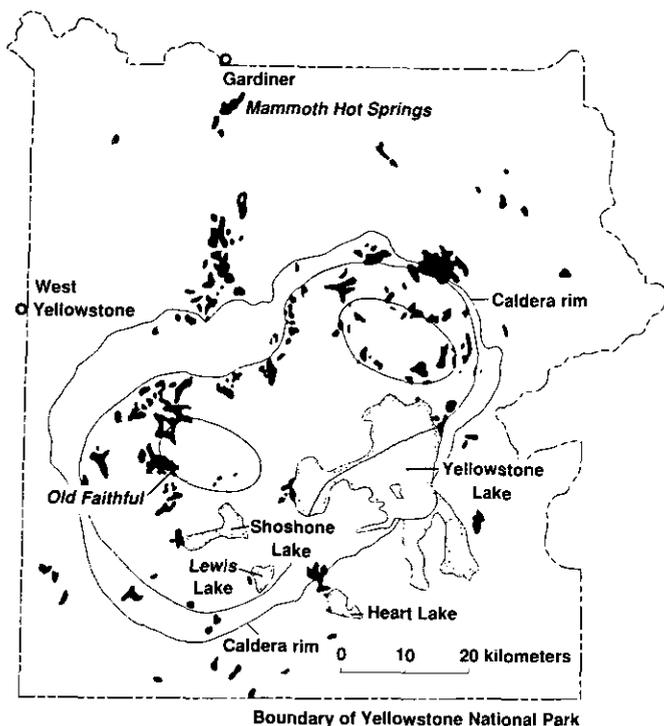


FIG. 5. Map of Yellowstone National Park showing the outline of the caldera and the distribution of active and fossil hydrothermal systems (in black). From White *et al.* (1988).

a result of the cooling and evaporation of waters hotter than about  $74^{\circ}\text{C}$  (White *et al.* 1964, Walter 1972, 1976). Consequently it forms only in and immediately adjacent to geysers, thermal springs, and outflow channels (Figs. 4, 6, 8). It consists largely of amorphous silica. Subaerial geysereite in splash zones has a nodular and columnar morphology (Fig. 6B) and characteristic extremely thin and regular laminae. Subaqueous geysereite is mostly flat-laminated with few features showing synoptic relief. Some pools contain a gravel of pisolitic geysereite. Bacteria of an unknown kind (Ward *et al.* 1991) rarely accumulate in these otherwise nearly sterile waters at temperatures of  $75\text{--}85^{\circ}\text{C}$  to form stringy masses which can be silicified (White *et al.* 1964, Fig. 11; possible fossil examples of such masses are described by White *et al.* 1989). Even at temperatures of  $92\text{--}100^{\circ}\text{C}$  there are eubacteria and archaeobacteria in the water (Ward *et al.* 1992) and, though they are not known to form any macroscopic accumula-

tions (e.g., biofilms, mats), their cells may well be able to be preserved in the geysereite.

*Temperatures between  $57$  and  $74^{\circ}\text{C}$ .* Filamentous bacteria, particularly the motile photosynthetic bacterium *Chloroflexus aurantiacus* Pierson and Castenholz, and also various species of the unicellular cyanobacterium *Synechococcus*, populate neutral to alkaline waters, mostly in the temperature range  $57\text{--}74^{\circ}\text{C}$  (Walter *et al.* 1976) but also as low as  $50^{\circ}\text{C}$  (Doemel and Brock 1974). These form laminated stratiform and, infrequently, nodular mats, which trap detrital particles. The nodules are about 0.5 to 1.0 cm wide and are ornamented with a distinctive stellate pattern of tiny ridges. The  $57^{\circ}\text{C}$  isotherm is usually within several meters of the spring and geyser vents so this mat type is areally very restricted.

*Temperatures between  $30$  and  $59^{\circ}\text{C}$ .* Filamentous cyanobacteria first appear in microbial mats in Yellowstone at about  $59\text{--}57^{\circ}\text{C}$ . Mats in the range  $59\text{--}30^{\circ}\text{C}$  are dominated by the finely filamentous cyanobacterium *Phormidium* (Copeland 1936) but also include a diverse range of eubacteria and archaeobacteria (Table 1). The mats assume a variety of macroscopic forms (Weed 1889a, plates 82–87, Fig 56; Walter *et al.* 1976; Figs 6C and 6D). In contrast to mats outside this temperature range, these frequently have distinctive structures with a growth relief of several centimeters or more (Walter *et al.* 1976). The mats form a locus for silica deposition (Fig. 7), forming sinter that is highly porous after decomposition of the organic matter, but which preserves much of the macro- and micro-structure of the original mats. The stromatolites have distinctive macro- and micro-morphologies, and the resultant sinter is easily distinguished from the other sinter types and from geysereite. Inspection of "subfossil" sinters at Queens Laundry Terrace (Fig. 7) and in the eroded walls of the Excelsior Geyser crater suggests that there is preservation of microscopic detail down to the level of the external morphology of bacterial cells, but this has yet to be carefully studied.

*Temperatures between ambient and  $30^{\circ}\text{C}$ .* Microbial mats in water cooler than about  $30^{\circ}\text{C}$  in Yellowstone are dominated by coarsely filamentous cyanobacteria such as *Calothrix*. They usually are stratiform, with less than 1 cm of surface relief, and are heavily silicified, forming firm, felt-like sheets. Laminae are thicker than in the high temperature sinters. The morphology and orientation of

FIG. 6. Spring and geyser vents and deposits in Yellowstone National Park. A. Geysereite cone, Lone Star Geyser. B. Columnar geysereite, Pearl Geyser, Norris Geyser Basin, scale-10 cm. C, D. High-temperature silica-encrusted microbial mats of different forms; C, *Conophyton* Pool; D, Column Spouter, Fairy Meadows, scale-10 cm applies to both. E, F. Scanning electron micrographs of spheroidal opaline silica in geysereite and sinter; the largest opal spheroids are about  $1\ \mu\text{m}$  wide, as are the bacterial filaments. E, from pisolites from Bead Geyser; F, silicified high temperature (*Conophyton*) microbial mats from Bronze Geyser: silica spheroids encrust the bacterial and cyanobacterial filaments and some of the unicellular cyanobacteria.

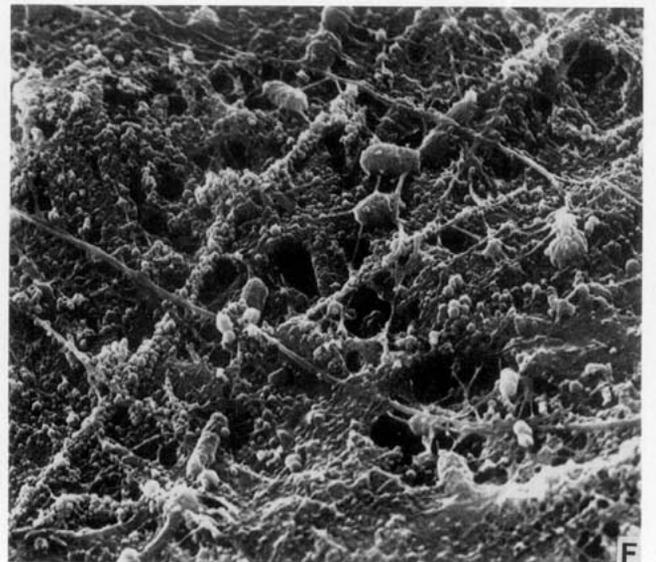
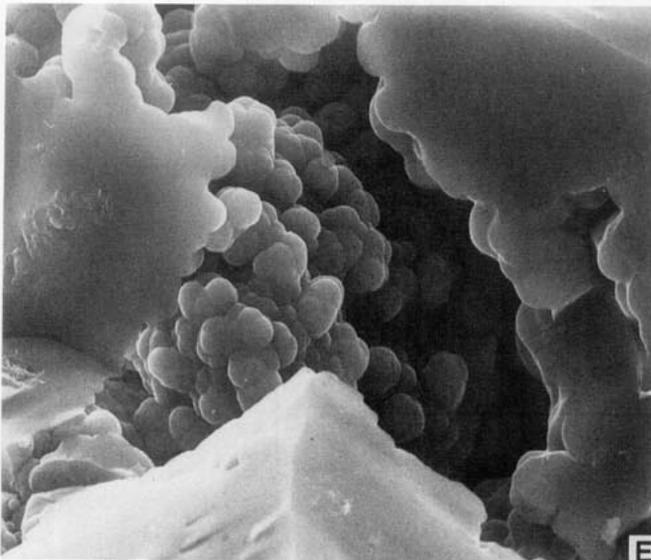
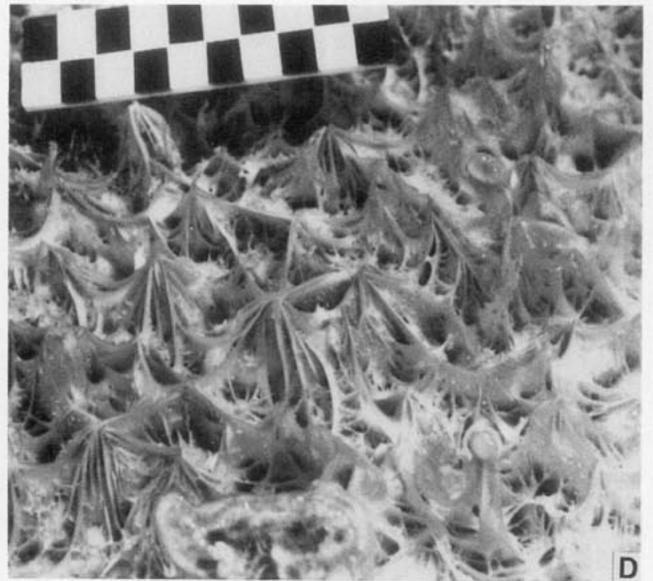
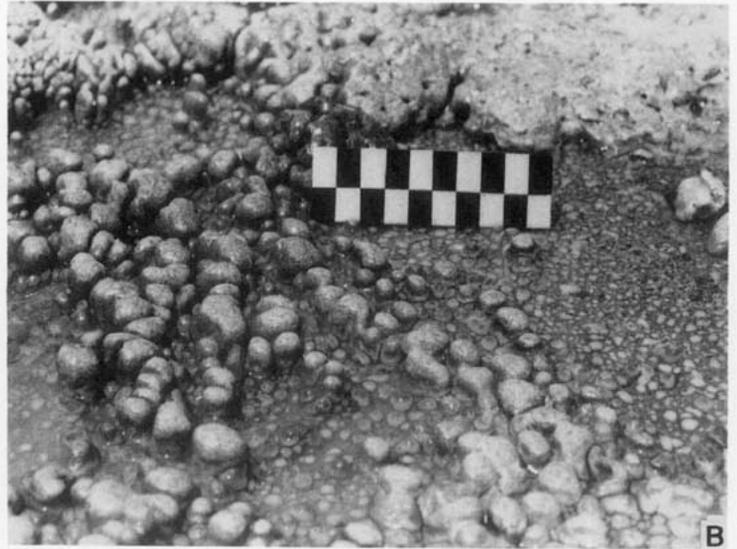


TABLE I  
An Example of the Metabolic Diversity of Thermal Spring Microbial Communities: Known or Suspected Members of the 50°C to 55°C Octopus Spring (Yellowstone National Park) Cyanobacterial Mat Community (from Ward *et al.* 1991)

Organism	Phylogenetic type	Physiologic type
1. Phototrophs		
<i>Synechococcus lividus</i>	eubacterium (cyanobacterium)	cyanobacterium
<i>Chloroflexus aurantiacus</i>	eubacterium (green nonsulfur group)	photosynthetic bacterium
2. Heterotrophic Consumers		
<i>Thermus aquaticus</i>	eubacterium (radioresistant cocci)	aerobic heterotroph
<i>Isosphaera pallida</i>	eubacterium (planctomycete group)	aerobic heterotroph
<i>Thermomicrobium roseum</i>	eubacterium (green nonsulfur group)	aerobic heterotroph
<i>Thermobacteriodes acetoethylicus</i>	eubacterium (Gram-positive group)	anaerobic fermenter
<i>Thermoanaerobium brockii</i>	eubacterium (Gram-positive group)	anaerobic fermenter
<i>Thermoanaerobacter ethanolicus</i>	eubacterium (Gram-positive group)	anaerobic fermenter
<i>Clostridium thermohydrosulphuricum</i>	eubacterium (Gram-positive group)	spore-forming anaerobic fermenter
<i>Clostridium thermosulfurogenes</i>	eubacterium (Gram-positive group)	spore-forming anaerobic fermenter
<i>Clostridium thermoautotrophicum</i>	eubacterium (Gram-positive group)	spore-forming anaerobic fermenter
3. Terminal Anaerobic Food Chain Consumers		
<i>Thermodesulfobacterium commune</i>	eubacterium (unique group)	sulfate-reducer
<i>Methanobacterium thermoautotrophicum</i>	archaeobacterium	methanogen

cyanobacterial filaments are clearly preserved by the silicification.

**Ambient temperatures.** Where marshes and meadows surround thermal spring systems they can support an abundant diatom flora, producing a sediment which, in some cases, is almost pure diatomite (Weed 1889c). In Yellowstone, diatomaceous silts cover many square kilo-

meters and are up to 4.5-m thick. Macroscopic plants are abundant in the marshes, and their roots are a significant component of the sediments. Prior to the evolution of eukaryotes such environments would presumably have been populated by benthic mat-building cyanobacteria, and the extraction of dissolved silica from the marsh waters would have been much less efficient. Yellowstone

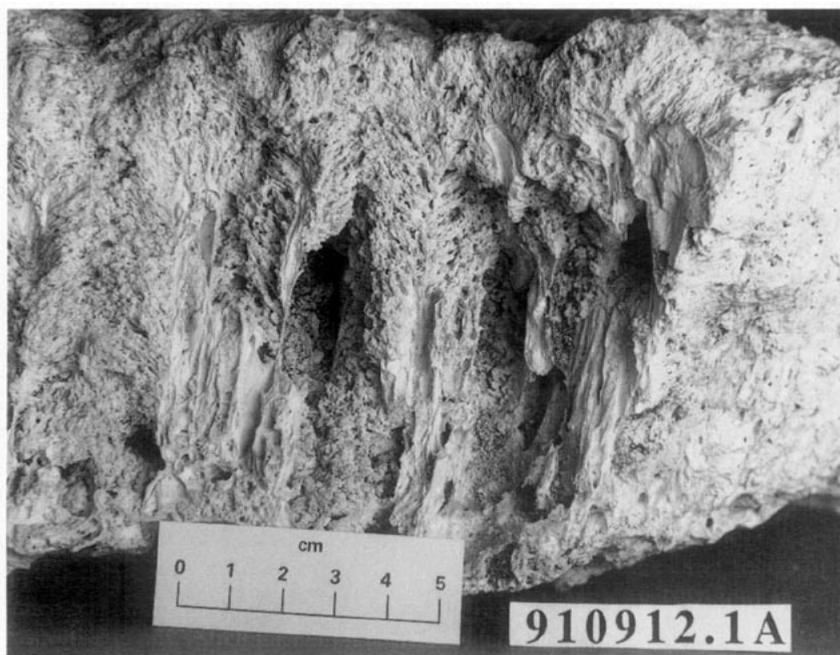


FIG. 7. Subfossil sinter from the Queens Laundry Terrace, Yellowstone National Park, showing preservation of the original microbial fabric in opaline silica.

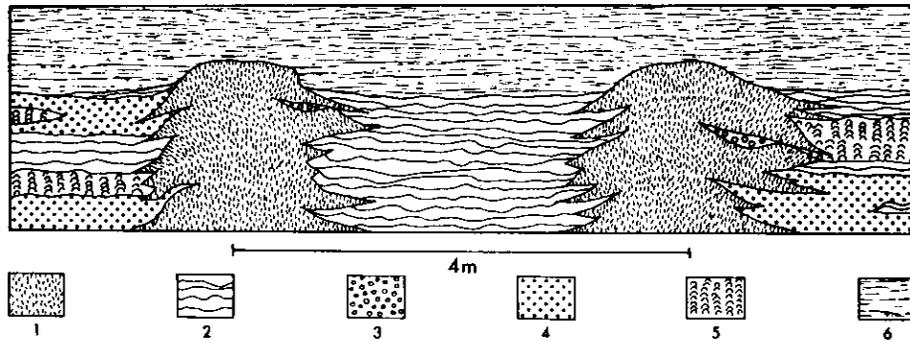


FIG. 8. Schematic diagram of facies relationships in thermal spring deposits (from Walter 1972). Facies are as follows: 1, columnar geyserite; 2, stratiform geyserite; 3, pisolitic geyserite; 4, intracrystalline sinter; 5, stromatolitic sinter; and 6, marsh deposits.

Lake, which is fed by thermal waters, deposits sediments that are unstratified, contain more than 80% (by weight) of diatom frustules, and are moderately rich in organic carbon (Goodwin and Schmit 1974). Siliceous pipes are constructed on the floor of the lake by hydrothermal springs (Remsen *et al.* 1990).

Additional information about the spring environment and its biota can be expected to be preserved in the chemical composition of the deposits. The thermal gradient associated with spring outflows should create a predictable trend in the  $\delta^{18}\text{O}$  value of the silica as it precipitates in near-equilibrium with the spring waters. The difference in  $\delta^{18}\text{O}$  between silica and water at equilibrium increases as the temperature declines (Friedman and O'Neil 1977). Also, as the flowing springwater evaporates, the remaining liquid should become progressively enriched in  $^{18}\text{O}$ . Both trends predict that, over the relatively short spatial scale of a spring outflow, the  $\delta^{18}\text{O}$  value of precipitating silica should increase with its distance from the spring orifice. This feature could be a useful signature for identifying ancient spring deposits.

The organic matter derived from biological communities also might create distinctive trends along the outflow. For example, the enzymatic uptake of dissolved inorganic carbon during photosynthesis is typically associated with a discrimination against  $^{13}\text{C}$ , relative to  $^{12}\text{C}$ . This discrimination can be as large as 3% (30 permil) but it is attenuated when the DIC supply becomes limiting (Smith and Walker 1980). Estep (1984) and Des Marais *et al.* (1992) observed an increase in  $\delta^{13}\text{C}$  (a measure of  $^{13}\text{C}/^{12}\text{C}$ ) of organic matter with lower concentrations of dissolved inorganic carbon (DIC) in the springwaters. Des Marais *et al.* (1992) observed that the trends of increasing  $\delta^{13}\text{C}$  and decreasing DIC occurred downstream along a spring outflow channel and coincided with the outgassing of springwater  $\text{CO}_2$  and lowering of DIC contents (Fig. 9). Within a suite of sediment samples from a spring outflow channel with its thermal gradient and associated  $\text{CO}_2$  outgassing, a parallel

$\delta^{13}\text{C}$  trend might be observed and could constitute a signature for biological carbon fixation. Such a trend might be observed within such a suite, despite outside sources of  $^{13}\text{C}/^{12}\text{C}$  variability in the atmosphere (Jakosky 1991). Any preserved organic matter could also contain complex hydrocarbons (biomarkers) derived from the decomposition of cellular material. These can be an important source of paleobiological information (Summons and Walter 1990). Some of the components of the microbial communities in

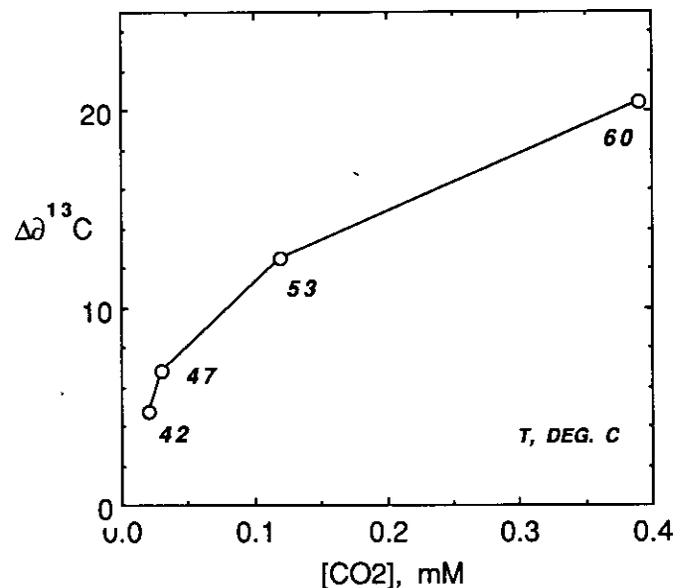


FIG. 9. Carbon isotope discrimination during mat growth versus the ambient concentration of dissolved carbon dioxide in a spring outflow at Orakei Korako thermal area, New Zealand (Des Marais *et al.* 1992). The term  $\Delta\delta^{13}\text{C}$  equals  $[\delta^{13}\text{C}_{\text{CO}_2} - \delta^{13}\text{C}_{\text{mat}}]$ . The mat was dominated by *Chlorogleopsis* cyanobacteria. Water temperatures ( $^{\circ}\text{C}$ ) at the sampling points are indicated by the numbers adjacent to the data points. The trend reflects changes in net isotopic discrimination during carbon fixation by the mats. This change is driven in part by the decline in  $\text{CO}_2$  concentration due to outgassing of the springwater.

the Yellowstone thermal springs are presently known only from their characteristic biomarker compounds (Ward *et al.* 1992).

#### ANCIENT THERMAL SPRINGS

We can have some confidence in our ability to find thermal spring deposits on Mars as a result of our experience on Earth. This section briefly summarizes that experience; a strategy for Mars is discussed later. There are many known examples of ancient submarine thermal springs on Earth, because they are targets for exploration for gold and base metals. However, subaerial thermal spring deposits are very poorly known. A small number of fossil subaerial hot springs have been described. Almost none have been studied for their paleobiology, although recent studies have concluded that the fossiliferous Devonian Rhynie Chert of Scotland is a thermal spring deposit (Rice and Trewin 1988, Trewin and Rice 1992). Late Paleozoic thermal spring sinters from Queensland, Australia, are among the oldest fairly well established examples (Cunneen and Sillitoe 1989, White *et al.* 1989). These were discovered in the course of mineral exploration in a subaerial felsic volcanic terrain, and have not yet been intensively studied. They contain anomalously high levels of gold, arsenic, and mercury. Those described by White *et al.* (1989) are especially relevant here. They were recognized as sinters because of their volcanic setting, siliceous mineralogy, and morphological similarity to the sinters of New Zealand and Yellowstone. They are well exposed at four sites, where they are interbedded with tuffs, lava, hydrothermal breccia, and lake sediments containing silicified plants. Although the silica is now all recrystallized to quartz, fine morphological detail is preserved. Features closely comparable with the stromatolitic sinters of Yellowstone are described. To judge from the descriptions, the deposits of at least two and possibly three different microbial communities are recognizable (stringy masses of bacteria, such as occur in the highest temperature parts of outflow channels, and two types of columnar stromatolites). These and other examples demonstrate the preservation potential of thermal spring deposits and indicate that long-term survival is feasible even in the tectonically active environments on Earth.

#### SOME LESSONS FROM THE SEARCH FOR EARLY LIFE ON EARTH

Paleontologists searching for morphological evidence of life on the early Earth face the following three major problems: 1, selecting a prospective site; 2, finding possibly biogenic structures; and 3, distinguishing biogenic from abiogenic structures. The search for fossil evidence of life on Earth during the Archean and Proterozoic

(3.9–0.54 Gyr) has been underway for about a century. Most seminal discoveries were made in the course of nonpaleontological investigations. For instance, the oldest known animal fossils, the Ediacara fauna of Australia, were discovered during regional geological mapping for a state government authority (Sprigg 1947). The discovery of microfossils preserved in chert of the Gunflint Iron Formation of Canada (Tyler and Barghoorn 1954), which led to all subsequent studies of Archean and Proterozoic chert microbiotas, resulted from observations made during a petrological study. Some of the oldest known stromatolites (now recognized as amongst the oldest evidence for life on Earth) were discovered in Western Australia by a graduate student engaged in field work for a study of barite deposits (Walter *et al.* 1980). Each of these discoveries led to later systematic and frequently successful searches by paleontologists. Many discoveries have resulted from regional mapping. There are two reasons why paleontologists have often followed other field geologists: they had to learn which rock types preserve remnants of unmineralized organisms and, even in those rock types, fossils usually are rare. It needs to be emphasized here that in this section we are referring to palaeobiological experience with marine and lacustrine sedimentary rocks of Archean and Proterozoic age, not to any experience with subaerial thermal spring deposits because as yet the oldest known convincing examples of these are Paleozoic.

The lesson that cherts are the best commonly occurring rock type for the preservation of unmineralized microorganisms is applied here by suggesting silica-depositing springs as sites for exploration. The problem of rarity is addressed also, as a high proportion of the sediments of springs preserve morphological evidence of life. Fossil preservation in silica is vastly superior to preservation in any other commonly occurring media, and indeed this form of preservation is common and provides an informative record of the early history of bacteria, cyanobacteria, and microalgae (e.g., Schopf 1970, Knoll 1985). Such preservation is known in the oldest well preserved rocks on Earth (3.5 Gyr, Awramik *et al.* 1983, Walsh and Lowe 1985, Schopf and Packer 1987). In exceptional examples, cell contents can be preserved (Oehler 1976a), although this is frequently disputed. Nonetheless, diagenesis and thermal alteration of silicified materials can and do alter original biological features. Artifacts can arise due to differential preservation of cells and mucilage, mineral recrystallization, and the addition of extraneous material by migrating fluids. The processes of silicification have been studied under laboratory conditions (e.g., Leo and Barghoorn 1976, Oehler 1976b, Francis *et al.* 1978a,b) but are still not well understood. Detailed studies of several well-known deposits have documented the morphological consequences in fossil cells of microbial degradation and the diagenetic growth of new mineral phases (e.g., Hofmann

1976, Knoll and Simonson 1981, Knoll *et al.* 1988, Lanier 1989).

As has been shown by Knoll *et al.* (1988), amongst others, many Proterozoic fossil assemblages have been exposed to burial diagenesis and low-temperature regional metamorphism to the prehnite–pumpellyite facies (approximately 200°C). This metamorphic overprint is responsible for some destruction of fabric and loss of biogenic information. However, despite the lack of submicroscopic preservation in regionally metamorphosed sediments, a biogenic signature still persists in the isotopic composition of organic matter (kerogen) derived from cells. The possible preservation of surface deposits on Mars with limited burial should result in a very low degree of thermal alteration.

By far the most abundant morphological fossils in Precambrian rocks are stromatolites (Walter 1972, 1983, Grotzinger 1989). It is conceivable that stromatolites formed on Mars. If part of the strategy were to search for them on Mars, as is sometimes suggested (McKay and Stoker 1989), the following observations of stromatolites on Earth should be considered:

1. The only abundant rock types in which these occur frequently are limestone and dolostone. They also occur in some siliciclastic rocks (sandstones) but are exceedingly rare. Limestones and dolostones are rare in Archean sedimentary rock sequences.

2. It is rare to find a well-preserved limestone or dolostone with no stromatolites, but it is normal to search extensively within any such rock body (and in cherts) before finding convincing stromatolites.

3. Stromatolites are restricted to only a small fraction of the available area in most environments where they occur now (lakes, rivers, marine embayments, and open ocean). The reasons for this restriction are very poorly understood.

4. There are many abiogenic structures that resemble stromatolites. Many abiogenic structures closely resemble biogenic fossils, and where the fossils are of simple organisms, these two classes of objects can be very difficult to distinguish with confidence (see, e.g., Hofmann 1971, Walter 1976a, 1983, Cloud and Morrison 1979, Glaessner 1984, Buick 1990). It is important in such cases to know the full geological context (sedimentary facies relationships) of the objects to determine whether an interpretation of a structure as biogenic is reasonable. Furthermore, any one set of observations is unlikely to be conclusive; it is frequently necessary to combine field scale (macroscopic) observations of geometry with observations on a microscopic scale before confident interpretation is possible, and even then substantial differences of opinion occur (e.g., Awramik *et al.* 1983, 1988, Buick 1984, 1988, 1990). Confidence can be raised substantially

by the use of several independent techniques to recognize biogenicity, for instance by adding stable isotope (e.g., Schidlowski *et al.* 1983) and organic biomarker analyses (Summons and Walter 1990). Stromatolites are the most abundant morphological evidence of life on the early Earth, but interpretations can be confused and confidence lowered by the possibility of mistaking partly or entirely abiogenic structures such as pedogenic deposits (calcrete, silcrete, etc.) and geyserite for biogenic stromatolites. The isotopic composition of carbon and sulfur-containing minerals provides important evidence for early life on Earth (e.g., Schidlowski *et al.* 1983), but this evidence in isolation may not be sufficient to be convincing evidence of life. For instance, the 3.8 Myr old sedimentary rocks at Isua in Greenland are so altered by thermal metamorphism that all possible morphological evidence of life has been destroyed. It is often argued that the carbon isotopic composition of the contained carbonate and graphite is evidence for the same type of biological carbon fixation as is found in the later geological record. But this interpretation is frequently disputed, to a large extent because it cannot be corroborated by any independent evidence. Experience with the discovery and interpretation of fossil microbial life on Earth clearly demonstrates the importance of using multiple criteria to demonstrate biogenicity (e.g., Schopf 1983).

#### A SEARCH STRATEGY

Any strategy employed must first of all address the need for multiple criteria for convincingly demonstrating biogenicity. Second, it must be possible to find whatever type of site is advocated, with a high degree of confidence. And third, it must be technically feasible to collect the data and samples required. Fossil thermal spring deposits meet all of these requirements.

We suggest that the search for fossil life on Mars focus on areas of long-lived volcanism where there is evidence of groundwater discharge. There is a great deal of experience in the search for ancient hydrothermal systems on Earth as these are prime sites for the exploration for gold, silver, and other rare metals. The use of remote sensing to locate the rock alteration haloes typical of hydrothermal systems is central to many such exploration programs, and the characteristic mineral suites can be detected remotely (Goetz *et al.* 1983, Kahle 1986, Huntington and Green 1988, Kruse and Taranik 1989, Watson *et al.* 1990, Kruse *et al.* 1990). Such sites are typified by an abundance of clays and oxides or hydroxides, and abundance of secondary precipitates such as silica and calcite. The experience gained through these programs should be of value in locating similar systems on Mars.

Geomorphological analysis of many Martian valley systems suggests that they originated through spring sapping

(e.g., Baker and Partridge 1986). More specifically, the former presence of thermal springs has been inferred from the juxtaposition of volcanic features and apparently spring-fed valleys (Brakenridge 1990). Interpretation of the morphology of the valley systems recognized on several of the volcanoes of Mars suggests formation by headward sapping as a result of groundwater flow from springs (Gulick and Baker 1989). Already it is possible to suggest, tentatively, several sites where fossil hydrothermal systems might occur on Mars. Springs and outflow streams might have existed on the volcano Hecates Tholus, as is mentioned above (Gulick and Baker 1989). Dao Valles on the margin of Hadriaca Patera is also considered to have originated through spring discharge (Squyres *et al.* 1987, Crown *et al.* 1992). Spring sites in general have the advantage of preserving evidence of life at the ground surface rather than in buried sediments.

The forthcoming Mars Observer mission will provide a great deal of information which should assist with the selection of prospective sites. In particular, data from the thermal emission spectrometer (Christensen *et al.* 1992) should enable searches for mineral suites associated with hydrothermal alteration. Individual spring mounds are generally ten to several hundred meters wide, and they frequently occur in clusters which occupy areas of the order of 10 km<sup>2</sup> (Fig. 5). Consequently, high resolution imagery is needed for confident identification of spring sites; the Mars Observer camera has a resolution of 1.5 m, though most of its coverage will be at a much lower resolution. The planned Russian Mars 94 mission will carry a high resolution stereo camera with a resolution of 10 m.

Thermal spring deposits may not be good sites for the preservation of organic material, because of their high initial porosity (although if the early environment of Mars were not markedly oxidizing this might not be a problem). However, these springs are excellent sites for the preservation of morphological fossils due to the mineral precipitation that is characteristic of thermal systems. Furthermore, preservable microbial communities occupy a high proportion of the available area in hydrothermal spring systems, enhancing the chance of discovery.

Lacustrine sediments are prime sites for the discovery of chemical evidence for life on Mars, because that evidence (organic matter, isotopic patterns in minerals) would be widely dispersed and therefore readily found. However, it is likely to be much more difficult to find morphological evidence for life at such sites, because suitable sediments could well be areally very restricted (e.g., stromatolites frequently occupy only a small proportion of the available area of a benthic subaqueous deposit, and fossils of unmineralized microorganisms are characterized by patchy and infrequent distribution). Furthermore, the vertical exposures needed to allow

searches of numerous sedimentary layers might be inaccessible.

If a site selection strategy for Mars were to include spring as well as lake deposits, the chances of finding convincing evidence of life would be significantly enhanced. The deposits of these different environments often occur in close proximity. On Mars, some spring-fed channels flow into central basins which contain sediments cited as examples of lacustrine deposition (Goldspiel and Squyres 1991). Both spring and lake deposits could provide samples for sensitive chemical life-detection analyses, including isotopic and biomarker approaches.

In preparation for the application of this strategy it will be necessary to develop detailed geometric and facies models of thermal springs to allow their recognition on Mars with as much confidence as possible. At the same time well-exposed examples of fossil hot springs should be studied, reconstructing their sedimentology, biology, and ecology using every technique available, with the purpose of testing, developing, and refining techniques for acquiring paleobiological information. This requires that the transformation of the various thermal spring communities to their fossil equivalents be understood. Information will be lost during diagenesis and mineral transformation, so it will be important to document the effects of this loss. The transition from opaline silica to chalcedony and then to quartz can be studied in progressively older springs. A combination of sedimentology, morphological paleontology, petrology, and stable isotope geochemistry is likely to be most effective. Such an approach should be an excellent way to test the techniques for evaluating biogenicity on Mars (not only in relation to thermal springs) and for exploring ways to draw maximal biological information from the sediments.

If visual and spectroscopic observations ranging from the macroscopic to the microscopic were combined with chemical and isotopic analyses, it should be possible to select probably biogenic and fossiliferous deposits from among a larger sample set on the surface of Mars.

#### ACKNOWLEDGMENTS

This research is supported by NASA's Exobiology Program. Our colleagues on this and related projects, Jack Farmer, Nancy Hinman, and Don Lowe, made many helpful comments which contributed to the development of this paper, as did the journal's two reviewers, Bruce Jakosky and another who is anonymous.

#### REFERENCES

- ALLEN, E. T., AND A. L. DAY 1935. *Hot Springs of Yellowstone National Park*. Carnegie Inst. Washington Spec. Publ. 466.
- AWRAMIK, S. M., J. W. SCHOPF, AND M. R. WALTER 1983. Filamentous fossil bacteria from the Archean of Western Australia. *Precambrian Res.* **20**, 357-374.
- AWRAMIK, S. M., J. W. SCHOPF, AND M. R. WALTER 1988. Carbona-

- ceous filaments from North Pole, Western Australia: Are they fossil bacteria in Archean stromatolites? A discussion. *Precambrian Res.* **39**, 303–309.
- BAKER, V. R., AND J. B. PARTRIDGE 1986. Small Martian valleys: Pristine and degraded morphology. *J. Geophys. Res.* **91**, 3561–3572.
- BAROSS, J. A., AND S. E. HOFFMAN 1985. Submarine hydrothermal vents and associated gradient environments as sites for the origin and evolution of life. *Origins Life* **15**, 327–345.
- BRAKENRIDGE, G. R. 1990. The origin of fluvial valleys and early geologic history, Aeolis Quadrangle, Mars. *J. Geophys. Res.* **95**, 17,289–17,308.
- BRAKENRIDGE, G. R., H. E. NEWSOM, AND V. R. BAKER 1985. Ancient hot springs on Mars: Origin and paleoenvironmental significance of small Martian valleys. *Geology* **13**, 859–862.
- BROCK, T. D. 1978. *Thermophilic Microorganisms and Life at High Temperatures*. Springer-Verlag, New York.
- BUICK, R. 1984. Carbonaceous filaments from North Pole, Western Australia: Are they fossil bacteria in Archean stromatolites? *Precambrian Res.* **24**, 157–172.
- BUICK, R. 1988. Carbonaceous filaments from North Pole, Western Australia: Are they fossil bacteria in Archean stromatolites? A reply. *Precambrian Res.* **39**, 311–317.
- BUICK, R. 1990. Microfossil recognition in Archean rocks: An appraisal of spheroids and filaments from a 3500 M.Y. old chert-barite unit at North Pole, Western Australia. *Palaios* **5**, 441–459.
- CARR, M. H. 1981. *The Surface of Mars*. Yale Univ. Press, New Haven.
- CARR, M. H. 1987. Water on Mars. *Nature* **326**, 30–35.
- CHRISTENSEN, P. R., D. L. ANDERSON, S. C. CHASE, R. N. CLARK, H. H. KIEFFER, M. C. MALIN, J. C. PEARL, J. CARPENTER, N. BANDIERA, F. G. BROWN, AND S. SILVERMAN 1992. Thermal emission spectrometer experiment: Mars Observer Mission. *J. Geophys. Res.* **97**, 7719–7734.
- CHRISTIANSEN, R. L., AND H. R. BLANK, JR. 1972. *Volcanic Stratigraphy of the Quaternary Rhyolite Plateau in Yellowstone National Park*. U.S. Geol. Survey Prof. Paper 729-B, pp. 1–18.
- CLOUD, P., AND K. MORRISON 1979. On microbial contaminants, micro-pseudofossils, and the oldest records of life. *Precambrian Res.* **9**, 81–91.
- COPELAND, J. J. 1936. Yellowstone thermal Myxophyceae. *Ann. N.Y. Acad. Sci.* **36**.
- CROWN, D. A., K. H. PRICE, AND R. GREELEY 1992. Geologic evolution of the east rim of the Hellas Basin, Mars. *Icarus* **100**, 1–25.
- CUNNEEN, R., AND R. H. SILITOE 1989. Paleozoic hot spring sinter in the Drummond Basin, Queensland, Australia. *Econ. Geol.* **84**, 135–142.
- DES MARAIS, D. J., J. BAULD, A. C. PALMISANO, R. SUMMONS, AND D. M. WARD 1992. The biogeochemistry of carbon in modern microbial mats. In *The Proterozoic Biosphere* (J. W. Schopf and C. Klein, Eds.), Section 6.8, pp. 299–308. Cambridge Univ. Press, New York.
- DOEMEL, W. N., AND T. D. BROCK 1974. Bacterial stromatolites: Origin of laminations. *Science* **184**, 1083–1085.
- ELLIS, A. J., AND W. A. J. MCMAHON 1977. *Chemistry and Geothermal Systems*. Academic Press, New York.
- ESTEP, M. L. F. 1984. Carbon and hydrogen isotopic compositions of algae and bacteria from hydrothermal environments, Yellowstone National Park. *Geochim. Cosmochim. Acta* **48**, 591–599.
- FENNER, C. N. 1936. Borehole investigations in Yellowstone Park. *J. Geol.* **44**, 225–315.
- FOURNIER, R. O. 1973. In *Proc., Symp. Hydrogeochem, Biogeochem.* **1**, 122–139.
- FRANCIS, S., L. MARGULIS, AND E. S. BARGHOORN 1978a. On the experimental silicification of microorganisms. II. On the time of appearance of eukaryotic organisms in the fossil record. *Precambrian Res.* **6**, 65–100.
- FRANCIS, S., E. S. BARGHOORN, AND L. MARGULIS 1978b. On the experimental silicification of microorganisms. III. Implications of the preservation of the green prokaryotic alga *Prochloron* and other coccoids for interpretation of the fossil record. *Precambrian Res.* **7**, 377–383.
- FRIEDMAN, I., AND J. R. O'NEIL 1977. *Compilation of Stable Isotope Fractionation Factors of Geochemical Interest*. Geol. Surv. Prof. Paper 440-K.
- GLAESSNER, M. F. 1984. *The Dawn of Animal Life: A Biohistorical Study*. Cambridge Univ. Press, Cambridge.
- GOETZ, A. F. H., B. N. ROCK, AND L. C. ROWAN 1983. Remote sensing for exploration: An overview. *Econ. Geol.* **78**, 573–590.
- GOLDSPIEL, J. M., AND S. W. SQUYRES 1991. Ancient aqueous sedimentation on Mars. *Icarus* **89**, 392–410.
- GOODWIN, J. H. AND C. R. SCHMIT 1974. Sedimentology and geochemistry of piston cores from Yellowstone and Jackson Lakes, Wyoming. *Geol. Soc. Am., Abstr. Progr.* **6** (7), 760.
- GREELEY, R. 1990. *Mars Landing Site Catalog*. NASA Reference Publication 1238.
- GROTZINGER, J. P. 1989. Facies and evolution of the Precambrian carbonate depositional systems: Emergence of the modern platform archetype. *SEPM Special Publication* **44**, 79–106.
- GULICK, V. C., AND V. R. BAKER 1989. Fluvial valleys and Martian palaeoclimates. *Nature* **341**, 514–516.
- HARTMANN, W. K., *et al.* 1981. Chronology of planetary volcanism by comparative studies of planetary cratering. In *Basaltic Volcanism Study Project, Basaltic Volcanism on the Terrestrial Planets*. Pergamon, New York.
- HOFMANN, H. J. 1971. *Precambrian Fossils, Pseudofossils and Problematica in Canada*. Geol. Survey Canada Bull. 189.
- HOFMANN, H. J. 1976. Precambrian microflora, Belcher Islands, Canada: Significance and systematics. *J. Paleont.* **50**, 1040–1073.
- HONDA, S., AND L. J. P. MUFFLER 1970. Hydrothermal alteration in core from research drill hole Y-1, Upper Geyser Basin, Yellowstone National Park. *Am. Mineral.* **55**, 1714–1737.
- HOWARD, A. D. 1937. *History of the Grand Canyon of the Yellowstone*. Geol. Soc. Amer. Spec. Pap. 6.
- HUNTINGTON, J. F., AND A. A. GREEN 1988. Recent advances and practical considerations in remote sensing applied to gold exploration. *Geol. Soc. Aust. Abstract Ser.* **22**, 246–258.
- JAKOSKY, B. M. 1991. Mars volatile evolution: evidence from stable isotopes. *Icarus* **94**, 14–31.
- KAHLE, A. B. 1986. Surface emittance, temperature, and thermal inertia derived from thermal infrared multispectral scanner (TIMS) data for Death Valley, California. *Geophysics* **52**, 858–874.
- KEEFER, W. R. 1971. *The Geologic History of Yellowstone National Park*. U.S. Geol. Survey Bulletin 1347.
- KNOLL, A. H., AND B. M. SIMONSON 1981. Early Proterozoic microfossils and penecontemporaneous quartz sedimentation in the Sokoman Iron Formation, Canada. *Science* **211**, 278–280.
- KNOLL, A. H. 1985. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Phil. Trans. R. Soc. London B* **311**, 111–122.
- KNOLL, A. H., P. K. STROTHER, AND S. ROSSI 1988. Distribution and diagenesis of microfossils from the Lower Proterozoic Duck Creek Dolomite, Western Australia. *Precambrian Res.* **38**, 257–279.

- KRUSE, F. A., AND D. L. TARANIK 1989. Mapping hydrothermally altered rocks with the airborne imaging spectrometer (AIS) and the airborne visible/infrared imaging spectrometer (AVIRIS). In *Proc. 12th Canadian Symposium on Remote Sensing 1989* pp. 952–955.
- KRUSE, F. A., K. S. KIERSIN-YOUNG, AND J. W. BOARDMAN 1990. Mineral mapping at Cuprite, Nevada, with a 63-channel imaging spectrometer. *Photogramm. Eng. Remote Sens.* **56**, 83–92.
- LANIER, W. P. 1989. Interstitial and peloid microfossils from the 2.0 Ga Gunflint Formation: Implications for the paleoecology of Gunflint stromatolites. *Precambrian Res.* **45**, 291–318.
- LEO, R. F., AND E. S. BARGHOORN 1976. Silicification of wood. *Botanical Museum Leaflets, Harvard Univ.* **25**, 1–46.
- MCKAY, C. P., AND C. R. STOKER 1989. The early environment and its evolution on Mars: Implications for life. *Rev. Geophys.* **27**, 189–214.
- MC SWEEN, H. Y., JR. 1985. SNC meteorites: Clues to Martian petrologic evolution. *Rev. Geophys.* **23**, 391–416.
- MUFFLER, L. J. P., D. E. WHITE, A. H. TRUESDELL, AND R. O. FOURNIER 1982. *Geologic Map of Lower Geyser Basin, Yellowstone National Park, Wyoming*. U.S. Geol. Survey Miscellaneous Investigations Series Map I-1373.
- NEUKUM, G., AND K. HILLER 1981. Martian ages. *J. Geophys. Res.* **86**, 3097–3121.
- OEHLER, D. Z. 1976a. Transmission electron microscopy of organic microfossils from the Late Precambrian Bitter Springs Formation of Australia: Techniques and survey of preserved ultrastructure. *J. Paleont.* **50**, 90–106.
- OEHLER, J. H. 1976b. Experimental studies in Precambrian paleontology: Structural and chemical changes in blue-green algae during simulated fossilization in synthetic chert. *Geol. Soc. Am. Bull.* **87**, 117–129.
- PACKER, B. M., AND M. R. WALTER 1986. Late Archean hot spring deposits, Pilbara Block, Western Australia. *12th International Sediment. Congress, Canberra*, p. 232.
- REMSEN, C. C., J. V. KLUMP, J. KASTER, R. PADDOCK, P. ANDERSON, AND J. S. MAKI 1990. Hydrothermal springs and gas fumaroles in Yellowstone Lake, Yellowstone National Park, Wyoming. *National Geograph. Res.* **6**, 509–515.
- RICE, C. M., AND N. H. TREWIN 1988. A lower Devonian gold-bearing hot-spring system, Rhynie, Scotland. *Inst. Min. Metall. Trans. Sect. B* **97**, 141–144.
- RICHMOND, G. M., K. L. PIERCE, AND H. A. WARDROP 1972. *Surficial Geologic Map of Yellowstone National Park*. U.S. Geol. Survey Miscellaneous Investigations Series Map I-710.
- RIMSTIDT, J. D., AND D. R. COLE 1983. Geothermal mineralization. I. The mechanism of formation of the Beowawe, Nevada, siliceous sinter deposit. *Am. J. Sci.* **283**, 861–875.
- SCHIDLowski, M., J. M. HAYES, AND I. R. KAPLAN 1983. Isotopic inferences of ancient biochemistries. In *The Earth's Earliest Biosphere: Its Origin and Evolution* (J. W. Schopf, Ed.), Chap. 7, pp. 149–186. Princeton Univ. Press, Princeton, NJ.
- SCHOPF, J. W. 1970. Precambrian micro-organisms and evolutionary events prior to the origin of vascular plants. *Biol. Rev.* **45**, 319–352.
- SCHOPF, J. W. (Ed.) 1983. *The Earth's Earliest Biosphere: Its Origin and Evolution*. Princeton University Press, Princeton, NJ.
- SCHOPF, J. W., AND B. PACKER 1987. Early Archean (3.3 billion to 3.5 billion-year-old) microfossils from Warrawoona Group, Australia. *Science* **237**, 70–73.
- SILBERMAN, M. L., D. E. WHITE, T. E. C. KEITH, AND R. D. DOCKTER 1979. *Duration of Hydrothermal Activity at Steamboat Springs, Nevada, from Ages of Spatially Associated Volcanic Rocks*. U.S. Geol. Survey Prof. Paper 458-D.
- SMITH, F. A., AND N. A. WALKER 1980. Photosynthesis by aquatic plants: Effects of unstirred layers in relation to assimilation of CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> and to carbon isotopic discrimination. *New Phytol.* **86**, 245–259.
- SNYDER, C. W. 1979. The planet Mars as seen at the end of the Viking mission. *J. Geophys. Res.* **84**, 8487–8519.
- SPRIGG, R. C. 1947. Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Trans R. Soc. South Aust.* **71**, 212–224.
- SQUYRES, S. W., D. E. WILHELMS, AND A. C. MOOSMAN 1987. Large-scale volcano-ground ice interactions on Mars. *Icarus* **70**, 385–408.
- STETER, K. O., G. FIALA, R. HUBER, AND A. SEGERER 1990. Hyperthermophilic microorganisms. *FEMS Microbiol. Rev.* **75**, 117–124.
- SUMMONS, R. E., AND M. R. WALTER 1990. Molecular fossils and microfossils of prokaryotes and protists from Proterozoic sediments. *Am. J. Sci.* **290-A**, 212–244.
- TREWIN, N. H., AND C. M. RICE 1992. Stratigraphy and sedimentology of the Devonian Rhynie chert locality. *Scott. J. Geol.* **28**, 37–47.
- TYLER, S. A., AND E. S. BARGHOORN 1954. Occurrence of structurally preserved plants in pre-Cambrian rocks of the Canadian shield. *Science* **119**, 606–608.
- VICKERY, A. M., AND H. J. MELOSH 1987. The large crater origin of SNC meteorites. *Science* **237**, 738–743.
- WALSH, M. M., AND D. R. LOWE 1985. Filamentous microfossils from the 3500 Myr-old Onverwacht Group, Barberton Mountain Land, South Africa. *Nature* **314**, 530–532.
- WALTER, M. R. 1972. A hot spring analog for the depositional environment of Precambrian iron formations of the Lake Superior region. *Econ. Geol.* **67**, 965–980.
- WALTER, M. R. 1976a. Geysers of Yellowstone National Park: An example of abiogenic "stromatolites." In *Stromatolites* (M. R. Walter, Ed.), pp. 87–112. Elsevier, Amsterdam.
- WALTER, M. R. 1976b. Hot spring sediments in Yellowstone National Park. In *Stromatolites* (M. R. Walter, Ed.), pp. 489–498. Elsevier, Amsterdam.
- WALTER, M. R. 1983. Archean stromatolites: Evidence of the Earth's earliest benthos. In *The Earth's Earliest Biosphere: Its Origin and Evolution* (J. W. Schopf, Ed.), (Chap. 8) pp. 187–213. Princeton Univ. Press, Princeton.
- WALTER, M. R. 1988. Fossil life on Mars. In *Exobiology and Future Mars Missions*, NASA Conf. Pub. 10027, p. 60. National Technical Information Service, Springfield, VA.
- WALTER, M. R., J. BAULD, AND T. D. BROCK 1972. Siliceous algal and bacterial stromatolites in hot spring and geyser effluents of Yellowstone National Park. *Science* **178**, 402–405.
- WALTER, M. R., J. BAULD, AND T. D. BROCK 1976. Microbiology and morphogenesis of columnar stromatolites (*Conophyton*, *Vacerrilla*) from hot springs in Yellowstone National Park. In *Stromatolites* (M. R. Walter, Ed.), pp. 273–310. Elsevier, Amsterdam.
- WALTER, M. R., R. BUICK, AND J. S. R. DUNLOP 1980. Stromatolites 3400–3500 Myr old from the North Pole area, Western Australia. *Nature* **284**, 443–445.
- WARD, D. M., R. WELLER, J. SHIEA, R. W. CASTENHOLZ, AND Y. COHEN 1989. Hot spring microbial mats: Anoxygenic and oxygenic mats of possible evolutionary significance. In *Physiological Ecology of Benthic Microbial Communities* (Y. Cohen and E. Rosenberg, Eds.), pp. 3–15. American Society for Microbiology, Washington.
- WARD, D. M., J. BAULD, R. W. CASTENHOLZ, AND B. K. PIERSON 1992. Modern phototrophic microbial mats: Anoxygenic, intermittently oxygenic/anoxygenic, thermal, eukaryotic and terrestrial. In *The Proter-*

- ozoic Biosphere* (J. W. Schopf and C. Klein, Eds.), pp. 309-324. Cambridge Univ. Press, New York.
- WARING, G. A. 1965. *Thermal Springs of the United States and Other Countries of the World—A Summary*. U.S. Geol. Surv. Prof. Paper 492.
- WATSON, K., F. A. KRUSE, AND S. HUMMER-MILLER 1990. Thermal infrared exploration in the Carlin trend, northern Nevada. *Geophysics* **55**, 70-79.
- WEED, W. H. 1889a. Formation of travertine and siliceous sinter by vegetation of hot springs. *U.S. Geol. Survey 9th Annu. Rep. 1887-1888*, 613-676.
- WEED, W. H. 1889b. On the formation of siliceous sinter by the vegetation of thermal springs. *Am. J. Sci.* **37**, 351-359.
- WEED, W. H. 1889c. The diatom marshes and diatom beds of the Yellowstone National Park. *Bot. Gaz.* (May 1889), 117-120.
- WHITE, D. E. 1968. *Hydrology, Activity, and Heat Flow of the Steamboat Springs Thermal System, Washoe County, Nevada*. U.S. Geol. Survey Prof. Paper 458-C.
- WHITE, D. E., R. A. HUTCHINSON, AND T. E. C. KEITH 1988. *The Geology and Remarkable Thermal Activity of Norris Geyser Basin, Yellowstone National Park, Wyoming*. U.S. Geol. Survey Prof. Paper 1456.
- WHITE, D. E., G. A. THOMPSON, AND C. H. SANDBERG 1964. *Rocks, Structure, and Geologic History of Steamboat Springs Thermal Area, Washoe County, Nevada*. U.S. Geol. Survey Prof. Paper 458-B.
- WHITE, D. E., W. W. BRANNOCK, AND K. J. MURATA 1965. Silica in hot spring waters. *Geochim. Cosmochim. Acta* **10**, 27-59.
- WHITE, N. C., D. G. WOOD, AND M. C. LEE 1989. Epithermal sinters of Paleozoic age in north Queensland, Australia. *Geology* **17**, 718-722.
- WISE, D. U., M. P. GOLOMBEK, AND G. E. MCGILL 1979. Tectonic evolution of Mars. *J. Geophys. Res.* **84**, 7934-7939.
- WOESE, C. R. 1987. Bacterial evolution. *Microbiol. Rev.* **51**, 221-271.