YELLOWSTONE SCIENCE

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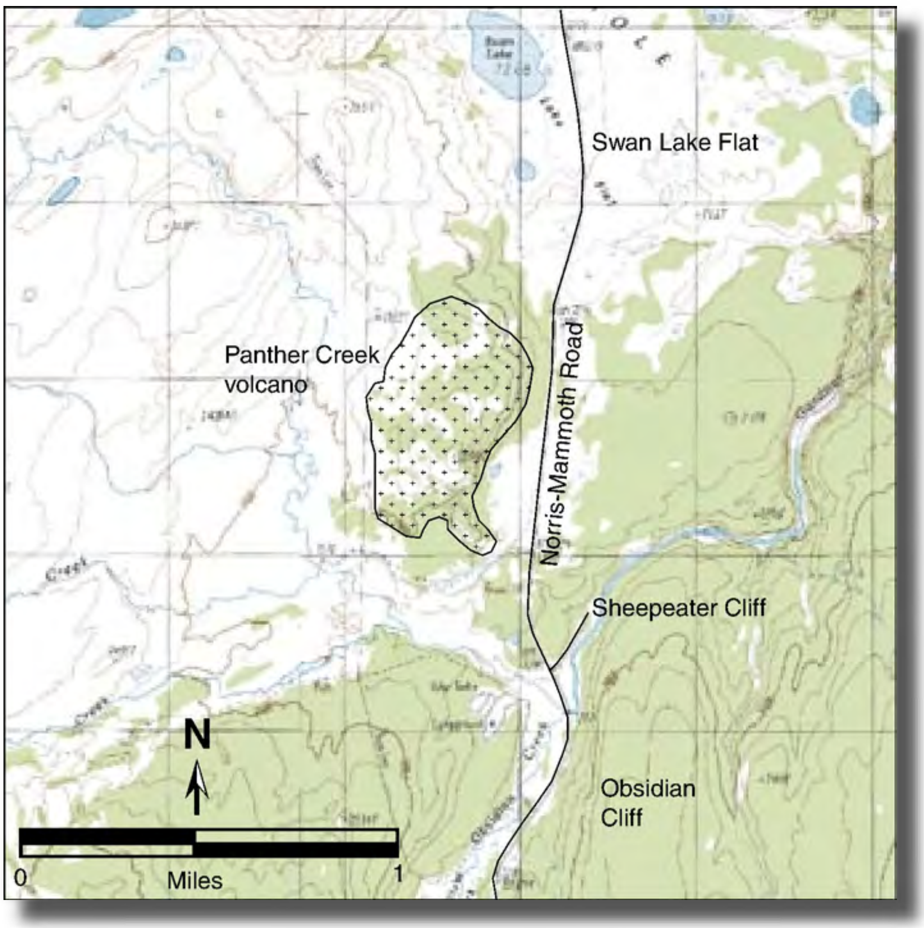

Panther Creek Volcano

The Lowly Lodgepole

Microbial Ecology

John Varley Retires

THIS IS THE FIRST ISSUE of *Yellowstone Science* published after the February 3, 2006, retirement of its co-founder, John D. Varley. John's career in Yellowstone spanned more than 30 years, the last 13 of which he spent as Director of the Yellowstone Center for Resources (YCR), the park division combining natural and cultural resource staff that he worked to create in 1993. A proven innovator and servicewide leader of resource stewardship within the National Park Service, John firmly established science and research as a foundation for resource management in Yellowstone. He not only unified the park's previously disparate functions of natural and cultural resource management, he also created the Biennial Scientific Conferences on the Greater Yellowstone Ecosystem, which began in 1991; established a research permit coordinator to serve the park; and developed a professional resource publication program that has produced many large milestone reports and books, as well as *Yellowstone Science*—without John, you wouldn't be reading this magazine. In the past 13 years, *Yellowstone Science* has featured articles written by dozens of researchers from many disciplines. It is distributed to more than 2,500 readers in the scientific community, regional libraries, interest groups, political leaders, journalists, and the public. A future issue of *Yellowstone Science* will, in turn, feature an interview with John.

In the debut issue of *Yellowstone Science* in 1992 (above), co-founder and then-editor Paul Schullery wrote: "Our primary goal is to explore the full breadth of the work being done in the park—to celebrate, through the eyes and ears and voices of the researchers themselves, the knowledge and wonder they so often find in this amazing place." In this issue, Eugene Smith and Kristeen Bennett report on the Panther Creek volcano, which may represent the beginning of a new caldera cycle and perhaps the formation of a new supervolcano. John Spear et al. are back with more explorations into the search for and study of microbial life in Yellowstone's unusual geothermal environments. And Bill Romme and Dan Tinker share their appreciation for the underappreciated lodgepole pine.

As the YCR transitions into new leadership, *Yellowstone Science* will continue to provide investigators with an opportunity to share their work, and their wonder. We also thank John for his long commitment to science and research in the park and to us, and wish him the best in his new endeavors.

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a quarterly devoted to
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Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address: Editor, *Yellowstone Science*, P.O. Box 168, Yellowstone National Park, WY 82190. You may also email: Tami_Blackford@nps.gov.

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on the cover:
Map showing location of Panther Creek volcano in Yellowstone.
Eugene Smith and Kristeen Bennett.

JOHN SPEAR

A view down into Obsidian Pool in the Hayden Valley region. This hot spring has one of the highest concentrations of dissolved hydrogen, H_2, in Yellowstone. The spring has revealed a wealth of knowledge on the diversity of bacteria in the environment. Several newly described phyla of *Bacteria* were first found here and have since been found in a number of other environments. The source hot spring (80°C) is at the lower left; it rapidly transitions to cooler, 50°C zones as evidenced by the brown and green microbial mats to the lower right.

FEATURES

DEPARTMENTS

NEWS & NOTES

NPS

Yellowstone Wolf Research Gets Funding Infusion

An anonymous donor in Colorado has pledged to give $140,000 each year for the next 10 years ($1.4 million total) to support wolf research in Yellowstone National Park. Approximately $100,000 per year will go to the National Park Service's Yellowstone Wolf Project; the remaining $40,000 per year will go to wolf researchers from the University of Minnesota.

In recent years, private donations have made up a majority of the funding for the Yellowstone Wolf Project, which provides short- and long-term research and monitoring of Yellowstone's wolves and studies their effects on the park's ecosystem. The Yellowstone Park Foundation (YPF) has typically provided about $150,000 in private donations for the Yellowstone Wolf Project each year to add to funding from the National Park Service.

The new donations will pay for radio tracking equipment, flight time, data analysis, and other research costs. Specific projects will include research on how wolves interact with scavengers and other predators, and the creation of population pedigrees to determine patterns of wolf reproduction as well as movements in and out of Yellowstone.

At the University of Minnesota, the donation will fund research for graduate students working with David Mech, a longtime wolf researcher and a senior scientist with the U.S. Geological Survey.

The $1.4 million donation is the largest ever received by the Yellowstone Park Foundation for the Yellowstone Wolf Project. YPF will continue to seek support for future wolf research.

Absaroka–Beartooth Wolverine Project

Staff for the newly initiated wolverine project completed training in early January and began setting live traps to capture wolverines on January 16, 2006. From July to November, 2005, 28 live traps (log huts) were constructed by study personnel and employees of the Gardiner Ranger District. The traps were built along Yellowstone's Northeast and East Entrance roads, and on national forest land in the general vicinity of Yellowstone's north and east boundaries. The goal for this winter is to capture and radio-mark (with GPS collars) five or more wolverines. The traps are located in four geographic areas and will be tended by four capture teams until mid- to late March 2006, depending on bear activity in the vicinity of the trap lines. The traps are baited with beaver carcasses (purchased from beaver trappers in northern Montana), or ungulate carrion (roadkill). The objectives of the project are to collect basic information on wolverines in the eastern portion of the Yellowstone ecosystem and to assess the effects of human activity (e.g., winter recreation) on the species. Another goal is to improve public awareness of wolverines and support for their conservation. The project is designed to last until early 2010.

The project is led by Yellowstone National Park and the U.S. Forest Service–Rocky Mountain Research Station (Missoula, Montana). Other cooperators include the Gallatin and Shoshone national forests; Wyoming Game and Fish; Montana Fish, Wildlife and Parks; the University of Montana; the Rocky Mountain Cooperative Ecosystem Studies Unit; and the Yellowstone Park Foundation.

Diseases Investigated as Possible Cause of Wolf Decline

Tests are underway to determine whether canine parvovirus was responsible for killing 84% of the 2005 wolf pups-of-the-year on Yellowstone's northern range. In January 2006, it was found that only 8 of 49 total pups on the northern range had survived; parkwide, just 22 of 69 pups (32%, down from a typical 75%), survived. This represents the lowest pup survival since wolves were restored to Yellowstone in 1995–1996. The total number of wolves in the park dropped by 32% last year, from 171 to 118. The largest single-year drop before that (11 wolves) occurred in 1998–1999, when pup survival was only 40%, again, likely due to an incidence of parvovirus. Wolf density on the northern range has lowered by half in the past two years; in 2004, there were 105 wolves on the northern range; in 2005, 85; in 2006, 54.

Although most of the field data collected point to parvovirus as the primary cause of the mortality figures, this year's unusually high adult mortality—more than in any previous year—may indicate that there was more than one disease affecting the park's wolf population. The discovery of malformed, discolored, loose teeth in one wolf is more consistent with distemper than with parvovirus.

Parvovirus and distemper can both be determined by blood tests. Samples

NPS/YELLOWSTONE WOLF PROJECT

will be sent away for analysis after this winter's capture operations are completed. Results will take several months to receive; the exact causes of the deaths may not be known conclusively until this coming spring or midsummer, if ever. Park visitors can help minimize the transmission of diseases by having their dogs immunized prior to entering the park, and by collecting and properly disposing of their dogs' feces while in the park, as per existing park regulations.

Bison in Arch Park, near Yellowstone's North Entrance.

USFWS Announces Intent to Remove the Rocky Mountain Population of Gray Wolves from Endangered Species List

On February 2, the U.S. Fish and Wildlife Service (USFWS) announced an advance notice of proposed rulemaking that outlines the agency's intent to remove gray wolves in the northern Rocky Mountains from the federal list of threatened and endangered species. The notice is being issued in order to give the public time to review and comment on the USFWS's proposed strategy of designating and proposing to delist the distinct population segment (DPS) of wolves in the northern Rocky Mountains that have exceeded biological recovery goals and no longer require protection under the Endangered Species Act—the DPS encompassing the geographic boundary of all of Montana, Idaho, and Wyoming, the eastern third of Washington and Oregon, and a small part of north-central Utah.

However, any future rulemaking on a delisting decision for Rocky Mountain wolves is still contingent on USFWS-approved state laws and wolf management plans, as required under the Endangered Species Act.

Consistent with regulatory requirements, the U.S. Department of Interior and USFWS have previously transferred much of the federal management responsibilities for gray wolves to the states of Montana and Idaho. These two states now implement control actions for problem wolves, monitor wolf packs, coordinate research, conduct public information programs and take wolves for scientific and other purposes in accordance with federal regulations. Important elements of the Idaho and Montana management frameworks are adequate regulatory mechanisms to manage the human take of wolves, consistent definitions of a "pack," and agreement to manage for 15 packs in each state.

Wyoming's state law and wolf management plan have not been approved by the USFWS in part because Wyoming's law defines wolves as a "predatory animal," which means that wolves could be killed at any time, by anyone, without limit, and by any means except poisoning. Concerns regarding Wyoming state law and its plan must be resolved before the northern Rocky Mountain DPS proposed delisting regulation can progress.

Comments from the public on the Service's intent to propose to establish a distinct population segment and to delist the wolves in the northern Rocky Mountains should be mailed to U.S. Fish and Wildlife Service, Western Gray Wolf Recovery Coordinator, 585 Shepard Way, Helena, MT 59601. Comments are required to be submitted by close of business 60 days after the Federal Register publication date.

Stephens Creek Bison Capture Facility

Yellowstone's bison capture facility at Stephens Creek closed for the second time this winter on February 17. During the 25 days that the facility was in operation, 939 bison were captured, 849 animals were transported to slaughter (with the meat distributed to food assistance programs), and 87 sero-negative calves were provided for a quarantine feasibility research project at Corwin Springs, Montana. Three bison died while being held in the facility.

Yellowstone Christmas Bird Count Results

On December 18, 2005, the Yellowstone Christmas Bird Count (YCBC) was conducted in the Gardiner, Montana, and Mammoth, Wyoming, areas for the 33rd year. The 2005 Yellowstone Christmas Bird Count tallied a total of 40 bird species and 1,749 individual birds, resulting in a slightly above-average number of bird species and an above-average number of total individual birds counted. Weather conditions were some of the coldest on record for this count, with temperatures ranging from –10°F to 15°F, with strong winds. Snow depths varied from 0–6" depending on the elevation, and the edges of rivers were frozen, especially at shoreline.

NPS/MCENEANEY

American dippers were seen during the Christmas Bird Count.

No new species of wintering birds were detected during the 2005 YCBC. However, a lesser scaup (a new species) was detected during count week. Notable finds for the YCBC included: 1 red-tailed hawk, 3 rough-legged hawks, 1 Cooper's hawk, 1 sharp-shinned hawk, and 2 Virginia rails.

Few bird records were tied or broken during the 2005 YCBC. Ten pine grosbeaks were counted, tying the previous record set in 1997. Only one abundance record was broken: 34 black-capped chickadees were counted, breaking the previous record of 32 set in 2002. During count week, a record 13 gray partridges were observed; the previous record was 1 gray partridge observed during count week in 1997.

A grand total of 97 species have been recorded on the YCBC (103 species with the YCBC and count week combined) over the course of the count's 33 years. Colder temperatures and above-average snow depths are the optimum conditions for finding the greatest bird richness and abundance during the YCBC.

USFWS Denies ESA Protection for Yellowstone Cutthroat Trout

On February 21, the U.S. Fish and Wildlife Service (USFWS) announced that results of a recent status review indicate that Endangered Species Act (ESA) listing of the Yellowstone cutthroat trout is not warranted. The status review found that stable, viable, and self-sustaining populations of the fish are widely distributed throughout its historic range.

In making this finding, the USFWS considered information and comments received from several state fish and wildlife agencies, the U.S. Forest Service, Yellowstone National Park, environmental organizations, Native American tribes, and the public. Numerous ongoing conservation efforts on behalf of the Yellowstone cutthroat trout demonstrate broad interest in protecting the species by state, federal, tribal, local, and non-governmental organizations and the public at large. However, the decision was based primarily on the present-day status and trend of Yellowstone cutthroat trout populations and the mitigation of many of the existing factors that can affect the species.

The Biodiversity Legal Foundation, the Alliance for the Wild Rockies, and the Montana Ecosystems Defense Council petitioned the USFWS in 1998 to list the Yellowstone cutthroat trout as threatened throughout its historic range. In 2001, the USFWS found that the petition failed to present substantial information indicating that listing was warranted. A complaint was filed in court, and the USFWS was ordered to produce a finding regarding the status of Yellowstone cutthroat trout by February 14, 2006.

In the status review findings, published in the February 21 Federal Register, the USFWS stated that many factors that have historically affected Yellowstone cutthroat populations, such as harvest by anglers or stocking of non-native fishes, can be effectively countered by the ongoing current management actions of state and federal agencies. Also, hybridization with non-native rainbow trout continues to affect Yellowstone cutthroat populations, but the eventual extent of future hybridization in Yellowstone cutthroat trout habitat may be stream-specific and difficult to predict. The criteria used for this finding were consistent with the genetic standards adopted by state fishery managers and allow for the limited presence of genetic material from other fish species in Yellowstone cutthroat trout conservation populations.

There are serious concerns about the future of the Yellowstone cutthroat trout population in Yellowstone Lake. The USFWS shares those concerns and will monitor the situation closely, but expects that the large scope of the Yellowstone Lake ecosystem should ensure the trout will persist in this ecosystem, at least for the foreseeable future. The USFWS did not find justification for applying the Distinct Population Segment (DPS) designation to this or any other subpopulation within the range of Yellowstone cutthroat trout.

The historic range of Yellowstone cutthroat trout generally consists of the waters of the Snake River drainage (Columbia River basin) upstream from Shoshone Falls, Idaho, and those of the Yellowstone River drainage (Missouri River basin) upstream from and including the headwaters of the Tongue River, in eastern Montana. Historic range in the Yellowstone River drainage thus includes large regions of Wyoming and Montana; that of the Snake River drainage includes large regions of Wyoming and Idaho, and small parts of Utah and Nevada. Today, various Yellowstone cutthroat trout stocks remain in at least 35 of the 40 major river drainages they historically occupied in Montana, Wyoming, Idaho, Utah, and Nevada.

Most of the habitat for Yellowstone cutthroat trout lies on lands administered by federal agencies, especially the U.S. Forest Service and National Park Service. Many of the strongholds for Yellowstone cutthroat trout occur within roadless or wilderness areas or Yellowstone National Park. For more information, please visit <http://mountain-prairie.fws.gov/species/fish/yct/index.htm>.

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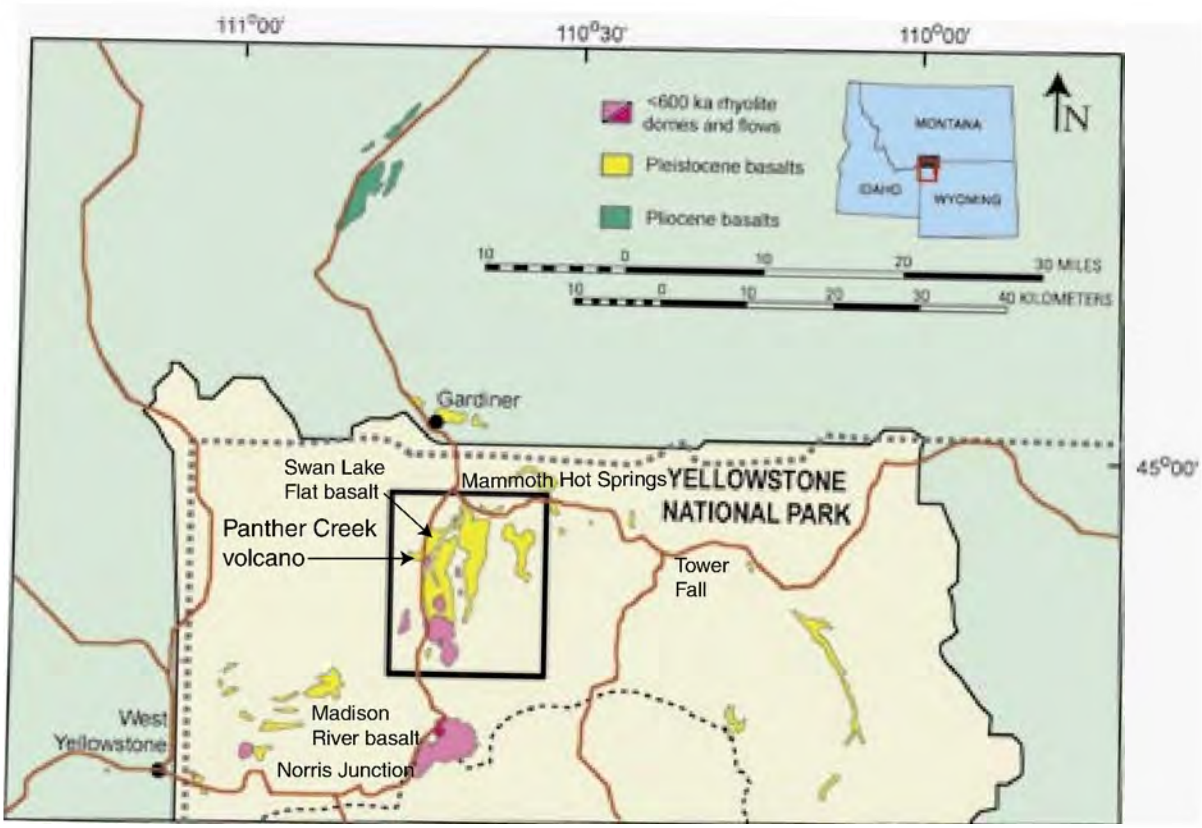


Figure 1. Location of the Panther Creek volcano and Swan Lake Flat basalt between Mammoth and Norris Junction. (Box indicates the area covered in Figure 6.)

Panther Creek Volcano

Eugene Smith and Kristeen Bennett

MANY PEOPLE MAY NOT REALIZE that the volcanoes we see on the Earth's surface have a variety of sizes and shapes. Volcanoes are some of the world's most spectacular phenomena. During an eruption, molten rock (magma) accumulates in the form of lava flows and pyroclastic material to form a volcano. The nature of an eruption is controlled by many factors, including the temperature, gas content, and composition of the magma. Higher-temperature basaltic magma may erupt quietly to form broad shield volcanoes similar to those on the island of Hawaii, or may erupt explosively to produce cinder cones like those at Craters of the Moon National Monument, Idaho. Lower-temperature rhyolitic magma may produce lava domes and flows or generate explosive eruptions that in extreme cases may result in ash-flow tuffs and caldera formation (a supervolcano). Volcanoes are complex features that develop over time by means of different types of eruptions. If conditions change during an eruption, the nature of the volcano may change. Even smaller volcanoes can be quite complex and be formed in a series of phases. One of the main goals of volcanology is to unravel this complexity and determine the geologic history of volcanoes.

Yellowstone National Park is a natural laboratory for the study of volcanoes. In the park, the most famous volcano is the Yellowstone Caldera, or supervolcano. Additionally, but less well-known, are numerous rhyolite domes and flows, and basaltic shields and cinder cones. This paper focuses on the geologic history of the Panther Creek basalt volcano, which we discovered during our mapping just west of the Norris-to-Mammoth road. This volcano is the source of the basalt at Sheepeater Cliff. Also discussed are other basalt volcanoes located north of the Yellowstone Caldera between Norris Junction and Mammoth Hot Springs, and especially on basalt exposures near Swan Lake Flat (Figure 1).

Background

The area between Norris Junction and Mammoth Hot Springs is well known for geyser basins and hot springs. This corridor also contains numerous rhyolite and basalt flows and volcanoes. The best place to see a rhyolite flow in this area is at Obsidian Cliff. The glassy rhyolite obsidian observed here covers an area of about five square kilometers and erupted 106,000 years ago. Rhyolite usually rises from magma chambers deep in the crust (1 km or more) to the surface through narrow linear fissures or semi-circular conduits. It is likely that most of the Obsidian Cliff rhyolite erupted to the surface and little remains underground.

The majority of the basalt in the corridor predates eruption of the Obsidian Cliff rhyolite (Spell et al. 2004). Basalt mainly occurs as flows and broad lava shields of the Swan Lake Flat basalt (Christiansen 2001). Swan Lake Flat basalt can be easily seen at the Sheepeater Cliff roadside exhibit, where lava flows display spectacular columnar jointing. The volcanoes, lava flows, and thermal areas of the Norris-to-Mammoth corridor lie to the north of the Yellowstone supervolcano, a caldera that erupted the widespread Lava Creek tuff about 640,000 years ago (Christiansen 2001).

Basaltic volcanism is relatively rare in Yellowstone National Park (YNP), but very common to the west, in the Snake River Plain. The reason for this is unclear, but the Snake River Plain follows an ancient boundary between blocks of crust of different ages. Perhaps basalt was able to rise more easily to the surface through this boundary zone. In YNP and adjacent areas, basaltic volcanism younger than the Lava Creek tuff began about 588,000 years ago, with the eruption of the Undine Falls basalt. This was followed by basalt eruptions in the western part of the park along the Madison River 355,000 years ago. Finally, Swan Lake Flat and Osprey basalt erupted in the Norris-to-Mammoth corridor between 350,000 and 209,000 years ago (Bennett and Smith 2004; Smith and Bennett 2004; Spell et al. 2004).

Basalt and rhyolite volcanism are closely related. In the early 1980s, Wes Hildreth of the U.S. Geological Survey suggested that basalt magma was "fundamental" in the production of rhyolitic magma, the type that might result in explosive volcanic eruptions and caldera formation (Hildreth 1981). In his model, basalt is the fuel that runs the magma engine: as it rises from its place of origin in the mantle, basalt magma carries heat from the mantle into the crust. This heat causes melting of crustal rock, producing rhyolitic magmas. If enough rhyolite magma is created, it may coalesce into a large magma chamber.

Magma and rock density control how close to the surface magma can rise. Magma rises because it is less dense than the confining rock. Because rhyolite magma is less dense than basaltic magma, rising basalt magma stalls beneath low density barriers produced by pooled rhyolitic magma. The stalled

Glossary

Two of the best places to find definitions of volcanology terms are the U.S. Geological Survey Photo Glossary of volcanology terms, <http://volcanoes.usgs.gov/Products/Pglossary/pglossary.html>, and the Volcano World web page produced by the University of North Dakota, <http://volcano.und.nodak.edu/vwdocs/glossary.html>.

Common terms used in the paper, modified from the Volcano World web page:

Agglutinated scoria: A pyroclastic deposit consisting of an accumulation of originally plastic and partially molten ejecta and formed by the sticking together of the fragments upon solidification.

Ash-flow tuff: A turbulent mixture of gas and rock fragments, most of which are ash-sized particles, ejected violently during a caldera-forming eruption. The mass of pyroclastic material is normally of very high temperature and moves rapidly down the slopes or even along a level surface.

Basalt: Dark-colored volcanic rock (or lava) that contains 45–54% silica, and generally is rich in iron and magnesium.

Block: Angular chunk of solid rock ejected during an eruption.

Bomb: Fragment of molten or semi-molten rock, 2½ inches-to-many feet in diameter, which is blown out during an eruption. Because of their plastic condition, bombs take on aerodynamic shapes during their flight or upon impact.

Caldera: The Spanish word for cauldron, a basin-shaped volcanic depression; by definition, at least a mile in diameter. Such large depressions are typically formed by the evacuation of a magma chamber. Ash-flow tuffs are commonly related to the formation of calderas.

Cinder cone: A volcanic cone built of loose, fragmented pyroclastic material, scoria, and agglutinated scoria. Cinder cones may have a summit lava lake. Lava flows commonly erupt from the base of cinder cones.

Crust: Solid, outer layers of the Earth, including the rocks of the continents.

Crater: A steep-sided, usually circular depression formed by either explosion or collapse at a volcanic vent.

Dike: A sheet-like body of igneous rock that cuts across layering or contacts in the rock into which it intrudes.

Dome: A steep-sided mass of viscous (doughy) lava extruded from a volcanic vent (often circular in aerial view) and spiny, rounded, or flat on top. Its surface is often rough and blocky as a result of fragmentation of the cooler, outer crust during growth of the dome. Rhyolite magma commonly forms domes. Rhyolite along the margins of domes is glassy and forms obsidian. Banding in the rhyolite (called flow banding) reflects the flow patterns of lava in the dome.

Fault: A fracture in the Earth's surface along which movement occurs. Movement along the fault can cause earthquakes.

Fault scarp: A steep slope or cliff formed directly by movement along a fault and representing the exposed surface of the fault before modification by erosion and weathering.

Fissures: Elongated fractures or cracks on the slopes of a volcano. Fissure eruptions typically produce liquid flows, but pyroclastics may also be ejected.

Lava: Magma that has reached the surface through a volcanic eruption. The term is most commonly applied to streams of liquid rock that flow from a crater or fissure. It also refers to cooled and solidified rock.

Lava flow: An outpouring of lava onto the land surface from a vent or fissure. Also, a solidified, tongue-like or sheet-like body formed by outpouring lava.

Magma: Molten rock beneath the surface of the earth.

Magma chamber: The subterranean cavity containing the gas-rich liquid magma that feeds a volcano.

Mantle: The zone of the Earth below the crust and above the core.

Obsidian: A black or dark-colored rhyolitic volcanic glass.

Pyroclastic: Pertaining to fragmented (clastic) rock material formed by a volcanic explosion or ejection from a volcanic vent.

Rhyolite: Volcanic rock (or lava) that characteristically is light in color, contains 69% silica or more, and is rich in potassium and sodium.

Scoria: A bomb-sized (> 64 mm) pyroclast that is irregular in form and generally vesicular. It is usually heavier, darker, and more crystalline than pumice (light-colored, frothy volcanic rock, usually of dacite or rhyolite composition, formed by the expansion of gas in erupting lava).

Shield volcano: A gently sloping volcano in the shape of a flattened dome and built almost exclusively of lava flows.

Vesicle: A small air pocket or cavity formed in volcanic rock during solidification.

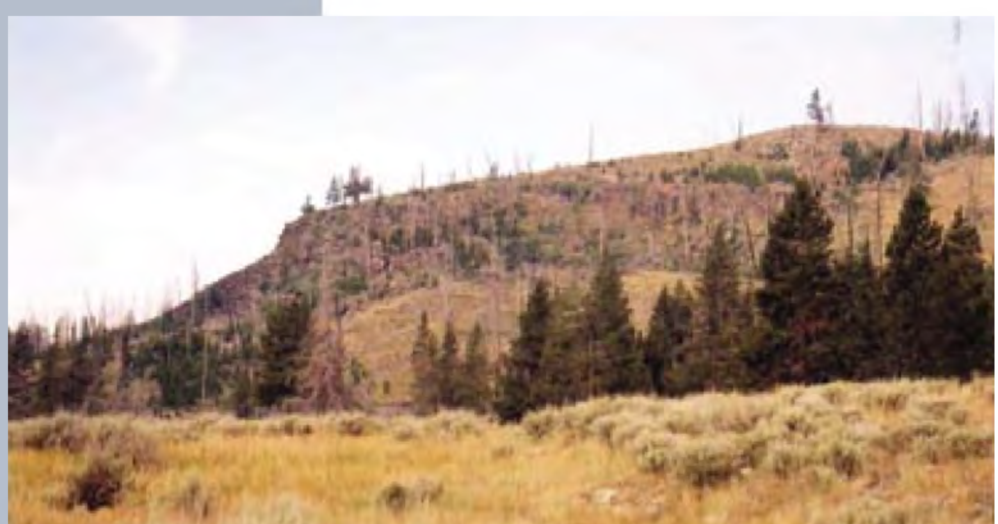
Volcano: A vent in the surface of the Earth through which magma and associated gases and ash erupt; also, the form or structure (usually conical) that is produced by the ejected material.

basaltic magma acts like a burner on a stove and continuously heats the overlying pool of rhyolitic magma. In this way, rhyolitic magma bodies can grow in size and may survive in the upper part of the crust for long periods of time (20,000 years for small volumes of rhyolitic magma and up to one million years for large volumes). Eruptions from this magma chamber produce domes of rhyolite and ash-flow tuffs, and may result in caldera formation.

Volcanism in the Yellowstone area occurs at two scales. On one level are the huge eruptions that formed the Yellowstone supervolcanoes. Over the past 2.3 million years, three major eruptions produced three large calderas. The last of these produced the Yellowstone Caldera 640,000 years ago. On the other end of the scale are smaller eruptions that produce rhyolite domes and flows and basalt cinder cones and shield volcanoes. The two types of eruptions may be related. The smaller eruptions may either represent the last phase of a supervolcano eruption or, more ominously, the initial phase of a new supervolcano. Our study suggests that the basalt and rhyolite eruptions in the Norris-to-Mammoth corridor may represent the beginning of a new caldera cycle and perhaps the formation of a new supervolcano. This large event will probably not occur in the near future, but it is likely that smaller eruptions like those that have taken place over the past 500,000 years may become more likely.

Panther Creek Volcano

Mapping the Panther Creek volcano was difficult because of extensive vegetation cover and beveling of the volcano by glaciation. Erosion, however, has exposed the interior of the cone on its east side, allowing for a comprehensive study of its eruptive history. We know that the volcano was glaciated because boulders (erratics) of Precambrian metamorphic rock



The Panther Creek volcano, looking to the northwest. The prominent cliff on the south (left) side of the volcano is a lava flow formed during phase 2. The peak is formed by the phase-3 scoria cone.

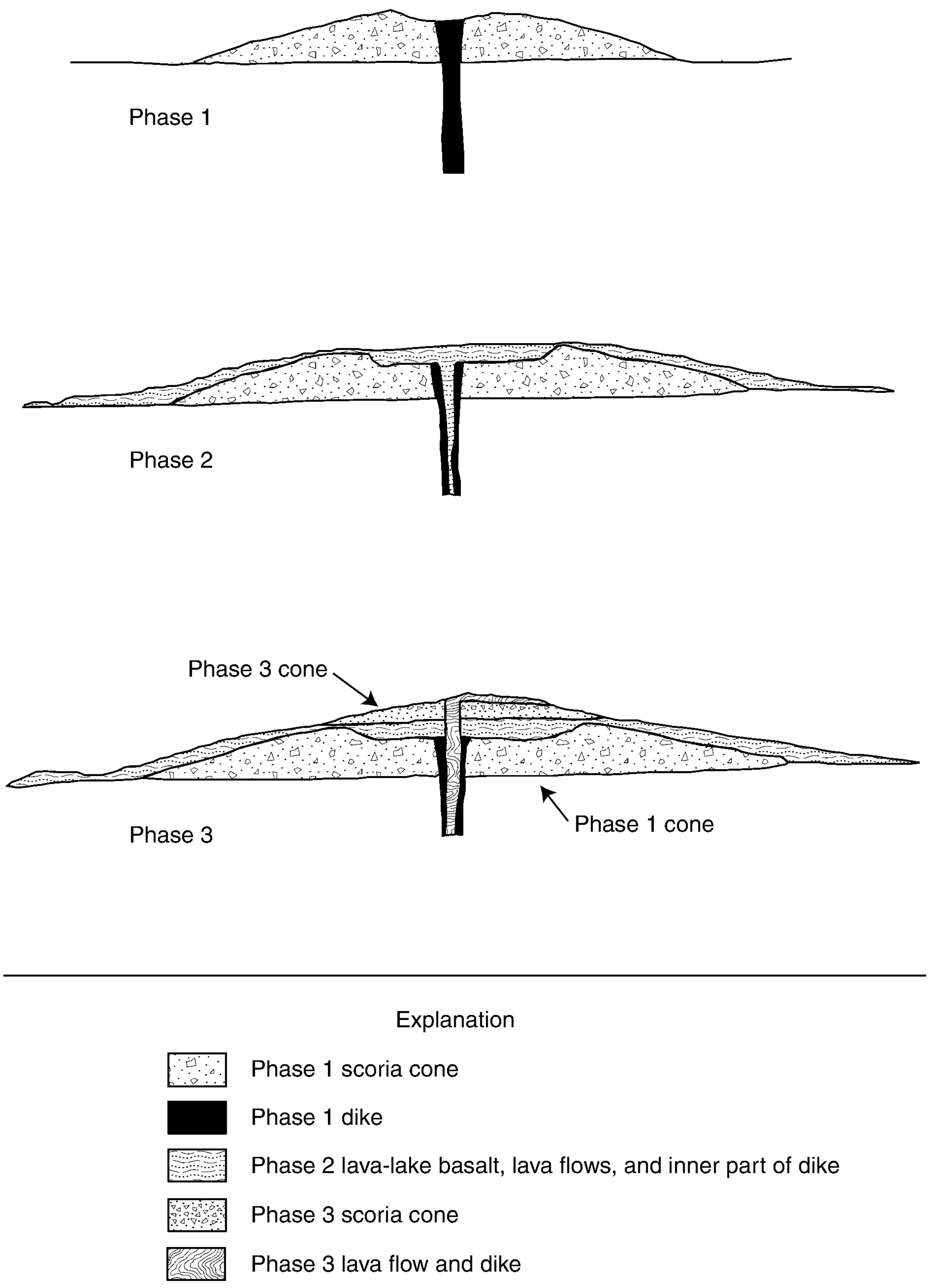


Figure 2. Generalized eruptive history of the Panther Creek volcano. (Sketches are not to scale.)

sit directly on top of it. These erratics were probably carried from the nearby Gallatin Range and left on the volcano by retreating glaciers.

The Panther Creek volcano is perched on the edge of an east-facing cliff that may be an eroded fault scarp. This geologic structure is part of a broad, north-trending fault zone that extends the length of the Norris-to-Mammoth corridor. The fault zone probably provided a pathway for magma to reach the surface and controlled the location of the volcano. The Panther Creek volcano is about 0.75 km in diameter, and erupted lava flows that cover an area of approximately 6 km^2. Because Pleistocene glaciation has eroded the cone, it is impossible to determine its original height, but at present it is about 50 meters high.

The Panther Creek volcano formed in at least three stages, or phases (Figure 2). During the first phase, partially molten, reddish-brown scoria and bombs produced a broad cinder cone with a summit crater. At this point in its history, the volcano may have resembled one of the cinder cones at Craters of the Moon National Monument. Because fragments ejected during the eruption were hot, they welded together, forming agglutinated scoria. This type of eruption is commonly referred to as Strombolian (named for the volcanic activity on the island of Stromboli, Italy), and is characterized by episodic eruptions of cinder and scoria, commonly producing a cinder cone and associated lava flows. Incorporated in the scoria deposits are volcanic bombs, some of which are cored with partially melted "granitic" blocks (Figure 3). These blocks probably represent Precambrian crystalline rock that was incorporated in the rising magma and carried to the surface. Because the temperature of the basaltic magma is so much higher than the melting temperature of the granitic blocks (1,200°C vs. 700°C), the granitic blocks partially melted, producing a dark volcanic glass (obsidian).

The second eruptive phase produced a lava lake within the summit crater. Remnants of the lava lake are exposed near the summit of the cone as a one-meter-thick, massive basalt exposure that overlies the deposits of agglutinated scoria. The lava-lake basalt has subtle banding identified by alternating light and dark gray streaks (Figure 4). Besides differing in color, these light and dark streaks differ in mineral abundance and composition. The light gray bands contain rectangular plagioclase crystals about 0.5 mm in size, and rare magnetite grains. The dark gray bands contain fewer, and smaller (<0.2 mm) plagioclase crystals, and larger and more abundant magnetite grains. This streaking and mineral zonation may reflect the mode of eruption of the lava-lake basalt. The summit crater may have filled with many thin surges of lava. Each flow (related to a single surge) stagnated in the crater for a period of time, allowing the denser magnetite to settle and the lighter plagioclase to rise. This process was repeated many times, producing the banded nature of the lava-lake basalt. An alternative way to produce the banding is by lava flow. Flow velocity is different in different parts of a lava flow, resulting in shear as faster parts of the flow move against slower areas. Flow shear can result in banding and mineral zonation. Flow banding, common in obsidian domes and flows, is produced in this manner.

Figure 3. Volcanic bomb in phase-2 scoria cored by a granite block.

Figure 4. Photograph of the subtle banding in the lava-lake basalt. The quarter coin on the ledge in the upper part of the photo is for scale.

Near the end of the second phase the lava lake overflowed, producing lava flows that traveled to the east toward Sheepeater Cliff, and toward the south to the present site of the Indian Creek campground. The flow near the Indian Creek campground is approximately 3.5 meters thick, while the flow exposed at Sheepeater Cliff is 8 meters thick. The total volume of the flows produced during this phase of activity is approximately 0.03 km^3. Near the lava lake many of these lava flows have a swirly appearance. The visible swirls appear to be the same light and dark gray bands visible in lava-lake basalt. The swirly texture was formed by the folding of the bands as the lava flows spilled over the rim of the summit crater and down the slopes of the broad cone. Lava flows with this swirly texture are found as far south as Indian Creek, and as far north as 0.5 km southwest of Swan Lake.

Figure 5. Contact of the dike (left) with phase-2 scoria (right). The contact is just to the right of the hammer. The hammer sits on the outer part of the dike; the more massive basalt (behind the tree and to the left of the hammer) is the central part of the dike.

During the third phase, the eruption produced a cone of welded scoria that sits on the lava lake deposits. The reddish-brown agglutinated scoria produced during this phase lacks the partially melted granitic blocks characteristic of the first eruptive phase. Much of these deposits has been eroded, so their original extent cannot be determined.

The conduit, or feeder dike for the Panther Creek volcano is exposed on the northeast side of the cone (Figure 5). Identifying the feeder dike is important because it represents the pathway to the surface of magma produced by partial melting of the mantle. Furthermore, it is strong support of the hypothesis that the Panther Creek feature is a volcano. Feeder dikes are often complex, because multiple batches of magma commonly use the same conduit to reach the surface. This is the case for the Panther Creek dike. Its outer part (about 25 cm wide) is massive basalt that contains a few crystals of plagioclase feldspar, and partially-melted granitic blocks 4–25 cm in diameter that are similar to those in the phase-1 scoria. We suggest that the outer part of the dike represents the conduit for the phase-1 scoria. The inner part of the dike is two meters wide and is also composed of massive basalt with small plagioclase crystals; however, it does not contain melted granitic blocks. This part of the conduit is probably responsible for the eruption of the lava-lake basalt, Sheepeater Cliff and Indian Creek lava flows, and the phase-3 scoria. Near the top of the inner dike, the dike appears to "turn over" and travel to the north as a thin, short flow that overlies the phase-3 scoria. This thin flow may be the last eruption from the Panther Creek volcano.

Tower Road shield volcano.

Swan Lake Flat Basalt

Christiansen and others (2001) identified three volcanoes related to Swan Lake Flat basalt. Our work showed that each of these volcanoes erupted at least one basalt flow (Figure 6). To the east of basalt flows erupted from the Panther Creek volcano is the Tower Road volcano, a broad, 120-m-high, shield-type volcano. This volcano is very difficult to study because it is covered by thick vegetation; however, it can be recognized as a volcano by its shield shape and by the occurrence of agglutinated scoria at its summit. Basalt flows radiated from this cone and traveled to the Mammoth-to-Tower Fall road to the north and as far as eight km to the south. Two additional volcanoes are located just east of Obsidian Cliff. These features, called the Horseshoe Hill volcanoes, were the source of two flows. The western volcano erupted a flow that traveled nearly 30 km to the north, to just south of Sheepeater Cliff. The eastern cone erupted flows that abutted against basalt from the Tower Road cone. Another area of Swan Lake Flat basalt to the east of the Tower Road volcano appears to have erupted from another volcano, but its location has not yet been determined.

Radiometric dating is a precise way of determining the age of basalt flows. The technique is based on the principle of radioactive decay. Isotopes of potassium (potassium with a mass number of 40, or ^{40}K) present in feldspar crystals in lava flows decay to an isotope of argon (argon with a mass number of 40, or ^{40}Ar). The decay takes place at a predictable pace, so that the amount of ^{40}Ar in feldspar is directly related to the age of the rock. Using a high-precision $^{40}Ar/^{39}Ar$ dating technique, we determined that Swan Lake Flat basalt erupted over a 150,000-year period. The youngest eruptions were from the Panther Creek volcano 209,000 years ago, and the oldest occurred at the Tower Road volcano 350,000 years ago.

Importance of the Panther Creek Volcano and Swan Lake Flat Basalt

An obvious question is why the discovery of the Panther Creek volcano and the study of Swan Lake Flat basalt are

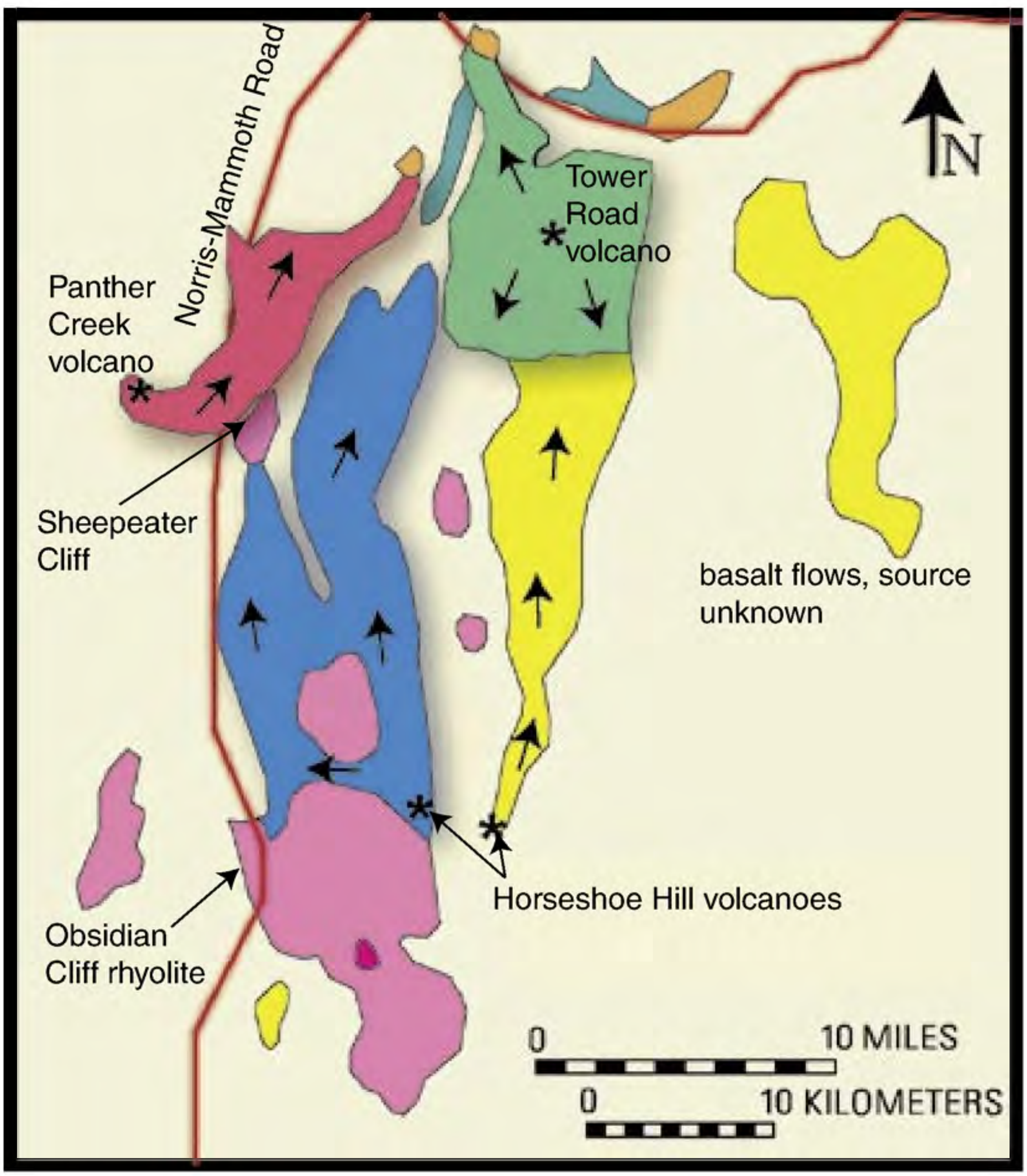


Figure 6. Generalized map showing the four volcanoes forming the Swan Lake Flat basalt (Panther Creek, Tower Road, and the two Horseshoe Hill volcanoes). Lava flows and approximate direction of flow (shown by arrows) are also indicated on the map.

important. In addition to satisfying scientific curiosity about the volcanic history of Yellowstone National Park and identifying a style of eruption that may be a future volcanic hazard, the study of the Panther Creek volcano and Swan Lake Flat basalt has important implications for understanding future volcanic activity. In the Norris-to-Mammoth corridor, eruptions of basalt occurred at roughly the same time as eruptions of rhyolite domes. The specific timing of eruptions, however, provides important clues to unraveling the area's volcanic history. The first eruptions of Swan Lake Flat basalt (350,000 years ago) immediately preceded the eruption of the first rhyolite dome (Willow Creek dome, 326,000 years ago). Contemporaneous production of basalt and rhyolite is demonstrated by the banded lavas found below Swan Lake Flat basalt at Sheepeater Cliff. Mixing of basalt and rhyolite magma occurred between 316,000 and 263,000 years ago. In the corridor, basalt eruptions ended 209,000 years ago with the formation of the Panther Creek volcano, but rhyolite activity continued until 80,000 years ago. (This detailed chronology was determined by University of Nevada–Las Vegas graduate student Nicole Nastanski and her advisor, Dr. Terry Spell, using the $^{40}Ar/^{39}Ar$ dating technique.)

What are the implications of these events? We suggest that they support the model proposed by Hildreth (1981), and that they may represent the initial stage of a new caldera (supervolcano) event. Basalt magma acted as a heat source to produce rhyolite volcanism. At first, areas of rhyolite were small, and basalt found its way to the surface. After about 209,000 years ago, though, the area of rhyolite in the crust became large enough to block the rise of basaltic magma. If basalt is required to sustain rhyolitic eruptions, then basalt magma is still present in the crust but is trapped beneath a lid of rhyolite. If these observations and assumptions are correct, then they imply that a rhyolitic magma chamber may exist beneath the Norris-to-Mammoth corridor, and that the corridor may be the site of future volcanic activity. Future studies of the Panther Creek volcano, Swan Lake Flat basalt, and rhyolite in the Norris-to-Mammoth corridor are critical to an understanding of future volcanism in Yellowstone National Park.

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Eugene Smith (left) is a professor of geology at the University of Nevada, Las Vegas (UNLV). He has been at UNLV for 25 years and teaches courses in volcanology and igneous petrology. Gene is the author of over 200 publications dealing with topics ranging from planetary geology to volcanology. In addition to studies in Yellowstone, Gene is also doing research in volcanic fields in Nevada, Arizona, and California, and is the principal investigator on projects to determine the hazard of volcanism near the proposed nuclear waste repository at Yucca Mountain, Nevada, and to characterize the geology of the new Sloan Canyon National Conservation Area just south of Las Vegas. He lives in Henderson, Nevada, with his wife, Diane Pyper Smith, an astronomy professor at UNLV. **Kristeen Bennett** (middle) is currently a geologist with GeoTrans, Inc., a subsidiary of Tetra Tech, Inc., in Irvine, California. Kristeen completed her thesis research for a Master of Science degree at UNLV on basalt primarily within the Norris–Mammoth corridor, north of the Yellowstone Caldera. She obtained her Bachelor of Science in Geology from California State University–Chico in northern California. She lives in Orange Park Acres, California. Right: field assistant Sara Girard.

In Praise of the Lowly Lodgepole

Bill Romme and Dan Tinker

Earlier Yellowstone visitors warned Hayden to leave the party's wagons at Bottler's. There were miles and miles, he was told, around Yellowstone Lake and among the mountains bordering it, where pines grew so closely together that it was nearly impossible for pack animals to pass through. Many areas were heavily strewn with once-towering pine trees, felled by autumnal fires and later blowdowns. Networks of these fallen pines could cover thirty or more miles at a height of three to six feet. Hayden wisely decided that his exploring team would rely on mules and horses to transport its supplies, equipment, and specimens.

—*Marlene Deahl Merrill,* Yellowstone and the Great West: Journals, Letters, and Images from the 1871 Hayden Expedition, *Lincoln: University of Nebraska Press, 1999*

While driving the Grand Loop Road in Yellowstone National Park, many visitors become bored by the seemingly endless expanses of lodgepole pine forest that squeeze the roadsides and cover some 80% of the park. Lodgepoles rarely grow to majestic size like ponderosa and other western pines; on the contrary, lodgepoles often crowd together in dense, "doghair" thickets of tiny trees. Lodgepole pine is typically the only tree species encountered over much of the Yellowstone Plateau: no aspen with soft green leaves and white bark to add color to the drab green of lodgepole pine needles, no downsweeping branches of spruce or fir to add visual variety to the erect, pruned shapes of the lodgepoles. We usually find far fewer numbers and kinds of wildflowers beneath a dense lodgepole pine forest than in a forest of aspen or spruce or fir. Similarly, the numbers and variety of birds and other animals are generally less in lodgepole than in other common forest types of the Rocky Mountains. Indeed, wildlife biologists sometimes refer to lodgepole pine forests as "biological deserts." Thus, where the Grand Loop Road runs for long stretches through lodgepole pine forest, passengers are apt to use this time to read the map, play license-plate games, or doze. It is in the meadows, stream-sides, and thermal basins where the wildlife and other Yellowstone specialties are to be seen; the lodgepole pine forests are mostly filler between the interesting stuff. One Yellowstone trail guide actually discourages travel on a particular trail because it runs mostly through "boring" lodgepole pine forest.

But what if Yellowstone had no lodgepole pine? What if this particular tree species had never evolved, or had been wiped out by some pathogen or other disaster long ago, and thus had never been here to colonize the naked rock of the Yellowstone Plateau that was exposed when the Pleistocene glaciers melted some 12,000–14,000 years ago? Yellowstone would be a very different place today—a place, perhaps, not nearly as appealing. Let us consider some of the ways that Yellowstone would be different without its lodgepole pine.

The first important point is that most of the Yellowstone Plateau—the broad expanse of ancient lava flows that cover most of the central portion of Yellowstone Park—is composed of various types of volcanic rocks that generally do not produce very good soil. The widespread rhyolitic flows and tuffs, in particular, are deficient in calcium, phosphorus, and other nutrients that all plants need for growth. In fact, most western tree species simply cannot thrive in the shallow, nutrient-poor soils that have weathered out of the common rocks of the Yellowstone Plateau. This includes aspen, spruce, and fir. The sharp-eyed traveler will spot occasional individuals of these species growing alongside the more numerous lodgepole, but these rare individuals are mostly restricted to localized pockets of slightly better soil and moisture conditions. Yellowstone's long, cold winters and short, cool summers also exclude most of the tree species common to lower and warmer elevations. Truth be told, only one western tree species is capable of tolerating this combination of poor soils and short growing seasons—and that tree is the lodgepole pine. Notably, lodgepole pine does not merely tolerate the harsh conditions of the Yellowstone Plateau; it actually thrives in this environment. Elsewhere in the Rockies, where soils and climate are more conducive to tree growth, the lodgepole is usually a minor component of the forest, abundant only during the early stages of forest recovery after major disturbances like forest fires, while the other trees are becoming re-established—or lodgepole pine may be absent altogether. Apparently, lodgepole pine cannot compete with the other tree species in places where growing conditions are more favorable; rather, it seems to specialize in growing where nothing else can prosper.

Recently burned lodgepole near Cub Creek in fall 2003.

Twisted, fallen lodgepole snag among young lodgepole saplings near the Heart Lake trailhead.

So, if Yellowstone had no lodgepole pine, there would likely be no trees of any kind over much of the park area. If this were true, what kind of non-arboreal vegetation might cover the Yellowstone Plateau in its place? To answer this question, we can look at the other plants that grow today in natural openings within the lodgepole pine forest. Outside of some scattered wet areas that support meadows and bogs, we generally see sagebrush, a few grasses and wildflowers, and a lot of rock and bare ground. Thus, without lodgepole pine, most of the Yellowstone Plateau probably would be covered by a sparse sagebrush-bitterbrush steppe, perhaps resembling the vegetation in the semi-arid basins surrounding Yellowstone.

Without its forest cover, the Yellowstone Plateau would attract and support a very different complement of wildlife species. The bison, elk, and other species of open habitats could still live here, but true forest species—the pine marten, the red squirrel, the porcupine, the goshawk—would never have been here in any numbers. Grizzlies would have been present in the early days, because they can forage quite nicely in meadows and sagebrush. However, without the extensive lodgepole pine forests for escape, grizzlies probably would have been hunted to extinction soon after trigger-happy settlers and prospectors arrived in the area in the late 1800s, long before effective protection was afforded by national park status.

And what of the national park itself? In 1872, when park proponents were working to convince the U.S. Congress that the unusual natural features of this area should be protected for all Americans for all time, they had only incomplete surveys of the geysers and other "curiosities" as they were called at the time. When it came time to draw a boundary line around the new park, they wisely included a lot of extra territory, just in case there were additional special features out there that nobody had yet documented. Thus, Yellowstone became not only the first national park in America (and the world), but also one of the largest in the world today. But what if the Yellowstone Plateau had not been covered by that extensive, almost impenetrable, lodgepole pine forest that had convinced Hayden to leave his wagons behind? The Washburn and Hayden expeditions of 1870 and 1871 might have more easily surveyed a larger area and accurately mapped greater numbers of the individual thermal features and other curiosities. We must remember that the concept of *ecosystem* was unknown at that time; the word itself had not yet even been coined. Given the prevailing utilitarian philosophy of the day, the new national park likely would have consisted of several postage-stamp parcels centered on the major geyser basins, the Upper and Lower Falls and Grand Canyon of the Yellowstone River, and a few other scenic locations, while the intervening lands (supposedly containing nothing of special interest or importance) would have been excluded from the park.

Dense lodgepole seedlings that naturally regenerated following the 1988 fires in Yellowstone.

Let us further consider the implications of a Yellowstone National Park comprised of a fragmented collection of individual geysers and other scenic features, rather than the expansive and mostly intact natural ecosystem that we have today. The sagebrush steppe surrounding the geyser basins and other curiosities probably would have passed into private ownership for grazing and other economic activities, as occurred with most non-forested lands in the West. The motels and curio shops of West Yellowstone might have extended clear to the Lower Geyser Basin, as industrious entrepreneurs scrambled to secure the premier locations along the lazy windings of the Madison River. The bison, elk, and large carnivores probably would have been extirpated by over-hunting and competition with domestic livestock, just as they were elsewhere in the Rockies during the late 1800s and early 1900s. And the geysers themselves, isolated from the watersheds that feed their subterranean plumbing networks, would likely have dried up or been irrevocably altered, as wells were drilled and streams were dammed and diverted for utilitarian purposes. All of these things would have resulted in major geological and ecological changes, and would have precluded any possibility of establishing such a grand national park as we have today. Yet all of this did *not* happen—in large part, and perhaps primarily, because the lowly lodgepole pine tree can grow on those poor soils of the Yellowstone Plateau.

Fireweed and heartleaf arnica flowering near the south arm of Yellowstone Lake in 1991.

But we should not celebrate lodgepole pine only because it prevented an even worse outcome for the Yellowstone country than an endless expanse of boring forests. Upon deeper acquaintance, one learns that this is a truly remarkable form of life. The name, "lodgepole," apparently derives from its typically small size and straight, clean growth form, which makes it an ideal structural timber for skin-covered lodges or tepees.

The small size of the trees results from the usually dense stands in which these pines tend to grow, such that no individual can obtain more than the bare minimum of water and nutrients from the poor soils on which they are found. The straight, clean trunk is a consequence of the leaves' inability to tolerate low light levels; lower branches are shed as soon as they begin to be shaded by higher foliage and are unable to carry their metabolic weight. In fact, most lodgepoles typically contain just a small crown of green needles at the tip of a slender trunk.

Curiously, the scientific name for this organism is *Pinus contorta,* which translated literally from the Latin means the "twisted" or "contorted" pine. How did such an amazingly straight-growing tree receive such an unfitting scientific name?

The answer lies in the vagaries of nineteenth-century botanical exploration and the rules of scientific nomenclature. The first individuals of this species to be described and named by a scientist, back in the early 1800s, just happened to be growing along the Pacific coast of North America, where the trees do indeed have a dwarfed and twisted growth form, with very short needles, all because of the area's constant wind and sea-spray. We now know that these coastal populations are atypical of the great majority of lodgepole pine trees growing in the interior of the continent. However, the earliest name applied to a species of organisms always has priority over any subsequent name that might be suggested. Appropriately, taxonomists have acknowledged the difference between coastal and interior populations by designating the interior trees as a separate variety: the broad-leaf lodgepole pine, or *Pinus contorta* var. *latifolia.*

The hardiness of lodgepole pine in the face of inhospitable soil and climate has already been emphasized, but we should add that it also is the most fire-adapted of all Rocky Mountain trees. This is important, because forest fires are as much a natural part of the Yellowstone ecosystem as bison and bears. Hundreds of lightning strikes occur every year, though in most summers the weather is too wet for fires to result. However, in two or three summers out of every decade, the weather becomes dry enough to permit some of those lightning strikes to ignite wide-spreading forest fires, and once every century or so the Yellowstone country experiences an unusually dry summer in which fires can burn over tens of thousands of hectares—as occurred in 1988. To be precise, we should point out that adult lodgepole pine trees, while quite fire-adapted, are actually not very *fire-tolerant;* their thin bark means that they usually die even in relatively low-intensity fires. However, in places where fires have occurred fairly regularly during the past several thousand years, such as the lower-elevation landscapes near the west entrance of Yellowstone Park, most of the lodgepole pine trees produce serotinous cones. These are cones that remain closed even after they are mature. They retain viable seeds for up to several decades—until high temperatures (as in a forest fire) melt the sealing resins and allow the seeds to fall from the cones. Interestingly, in those places where fires have never been very frequent, such as in the high country of the Central Plateau and Two Ocean Plateau, most lodgepole pine cones are not serotinous, and the trees release their seeds at maturity just like other pines. Nevertheless, wherever lodgepole pine forests contain even a small number of individuals with serotinous cones, there will be copious quantities of seeds in the forest canopy, ready to fall to the ground and germinate after even the most intense fire, and, phoenix-like, to create a vibrant new forest in the ashes of the forest that burned. This capacity to regenerate prolifically after fire is very evident today in the places that burned in 1988. Thus, the lodgepole pine can survive, can even thrive, on the poorest soils, in the coldest climates, and, as John Muir described, on "the most dangerous flame-swept slopes and ridges of the Rocky Mountains," a tree that is "brave, indomitable, and altogether admirable."

Spend some time in a lodgepole pine forest, and you will notice little things that evade the eye and ear of the casual or hurried traveler—the gentle murmur of the wind in the aromatic branches, the rapid-fire chattering of an agitated pine squirrel, the heat of the midday sun contrasting with the cool of the shade, the dappled play of sunlight on the forest floor, especially in the fall when the grasses turn a golden pastel color and the dwarf huckleberry leaves blaze softly in subdued reds and yellows. In early summer you will be enchanted by the ethereal, flute-like call of the hermit thrush; a dark-eyed junco may flush suddenly from a tiny nest beneath a yellow arnica flower; and looking up you may be rewarded by the sight of a great gray owl gazing down in silence from a tree branch. A muddy spot may reveal the track of elk, or bear, or wolverine, and a curious pine marten may follow you for a short distance.

So, what would Yellowstone be without its lodgepole pine? Still an interesting place, no doubt; the geothermal features are sufficient to provide interest. But a wild and romantic and magical place? Probably not. Let us enjoy and praise this remarkable tree and this remarkable place.

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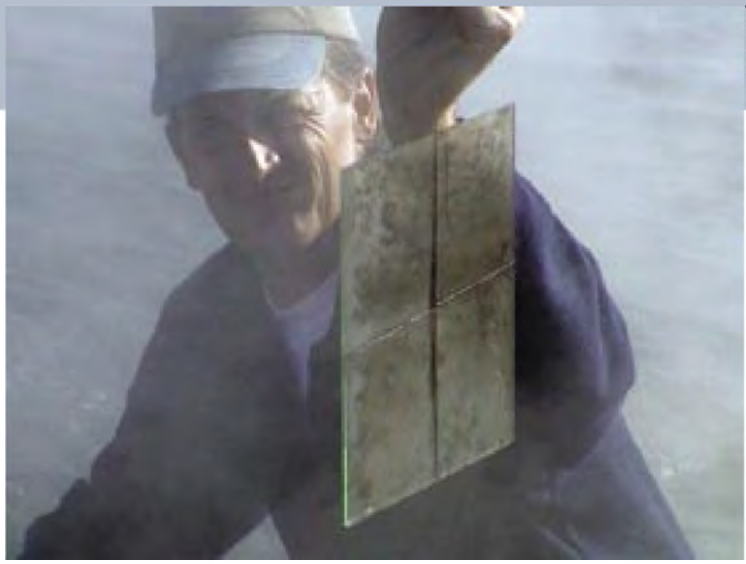
BILL COTTON

BILL ROMME

Bill Romme (left) is a professor of fire ecology in the Department of Forest, Rangeland, and Watershed Stewardship at Colorado State University in Fort Collins, Colorado. **Dan Tinker** (right) is an assistant professor of forest and fire ecology in the departments of Botany and Renewable Resources at the University of Wyoming in Laramie, Wyoming. Bill and Dan have been conducting research in lodgepole pine forests throughout Yellowstone and Grand Teton national parks for many years, including studies of the history of forest fires in Yellowstone; the mechanisms by which lodgepole pine and other plants regenerate after forest fires; the effects of fire on ecosystem productivity and nutrient cycling; and the role of fallen logs and other large wood in the functioning of coniferous forest ecosystems. Both received PhD degrees in botany from the University of Wyoming.

Microbial Ecology and Energetics in Yellowstone Hot Springs

John R. Spear, Jeffrey J. Walker, and Norman R. Pace



JEFF WALKER

John Spear holds a large glass slide used as a growth surface for microbiota in a Hayden Valley-region hot spring (76°C). The slide is clear when first inserted into the hot spring, hung with fishing line. After three days, the slide is heavily colonized with microbiota—the darkly colored, thick biofilm that can be seen covering the slide. The material is collected with a sterile razor blade and used for the kind of culturing, microscopy, and molecular microbial analyses described in this article.

ANY ECOSYSTEM on Earth is comprised of all living things (plants, animals, etc.) and non-living things (rocks, soil, water, etc.) in a given geographic area. That area can be on the scale of a landscape, such as the Greater Yellowstone Ecosystem (GYE, multiple states in size), to the local area around a single hot spring, to the area within some minute distance between bacteria. There is a constant exchange of materials between the living and non-living components in any of these ecosystems. One of the most important of these exchanged materials is energy. When we walk around the GYE, the energy source for the richness of life we can see is apparent: photosynthesis, the capture of light energy from the sun into usable form. This capture is made possible by the fixation of the sun's photons into useful chemical energy by plant cell chloroplasts.

The living components of an ecosystem are composed of a blend of organisms we now know to occupy three domains of life. In the first of these three domains, members of *Eucarya* make up most of the world we see, including plants, animals, and fungi. Members of the other two domains, *Bacteria* and *Archaea,* are all microbial, and perform many ecosystem services, such as primary productivity, waste recycling, weathering, and mineralization. Microbial capture of the sun's energy by photosynthesis is conducted by algae, a group of microbial organisms within the domain *Eucarya,* and cyanobacteria, a group of organisms within the domain *Bacteria.* Components of the third domain of life, *Archaea,* are not known to engage in traditional photosynthesis at this time. Once photosynthesis converts light energy into biomass, many other organisms, including animals, then thrive by consuming this energy. Photosynthesis thus provides the energy foundation for our macrobial-visible, eukaryotic world.

Photosynthesis by bacteria is visible all over Yellowstone, in the form of the many colors in and around hot springs (Figure 1). A walk around the park reveals a multitude of colorful microbial mats (whole assemblages of microorganisms) living at various temperatures and pHs under different site-dependent chemical regimes. These colors are often the product of photosynthetic pigments within the microbial cells. The green, black, orange, brown, and yellow mats around Grand Prismatic Spring, or around the boardwalks of the Lower Geyser Basin, are examples of photosynthetic mats. These microbial mats form their own complex ecosystems, composed of mixed communities of microorganisms living together with a few photosynthetic members supplying energy to others. However, while photosynthesis is visible at the plant and microbial mat level, it is not the only kind of energetic fixation mechanism.

Yellowstone, with its more than 10,000 thermal features, is full of life at temperatures that exceed the limit of photosynthesis (~72°C; 158°F) (Figure 1, bottom). Some form of microbial life, generally bacteria or archaea, probably occurs in all Yellowstone hot springs, many of which are at boiling temperature. A different kind of energy, a chemical energy mechanism, must be available for life to thrive at these high temperatures. To survive anywhere, life needs four things: water, a carbon source, an electron donor—something to provide electrons (energy)—and an electron acceptor. Humans consume water, carbon, and electron donors; we inhale oxygen to accept the electron transfer from the donors, and exhale waste in the form of CO_2. Microbes in a Yellowstone hot spring do the same, but instead use CO_2 or small organic molecules for carbon, hydrogen sulfide (H_2S) or molecular hydrogen (H_2) as an electron donor, and molecules such as oxygen (O_2), sulfate (SO_4^{2-}), phosphate (PO_4^{2-}), nitrate (NO_3^{2-}), or various metals as electron acceptors. The result is that microorganisms can thrive both on the walls and in the water of hot springs (Figure 2).

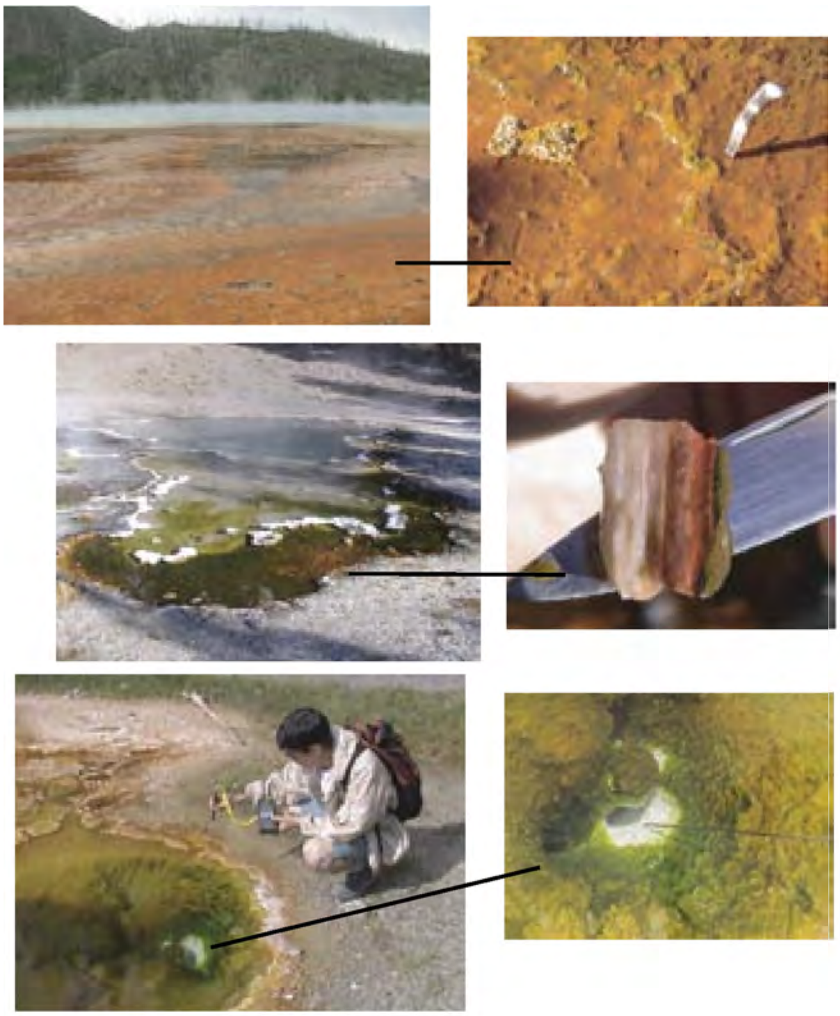


Figure 1. *Top:* Grand Prismatic Spring as viewed from the boardwalk. The presence of multiple colors around the edge of the world's largest hot spring are due to microbial mats. *Top right:* When viewed up close, oxygen bubbles from photosynthesis can be seen trapped within the multiple layers of the mat. *Middle:* Octopus Spring in the White Creek region, with colors imparted by microbial mats along its southern edge. *Middle right:* A close-up view of these beautifully laminated mats as seen on the blade of a pocket knife. *Bottom:* The green color of this hot spring in the White Creek region is due to the presence of photosynthetic microorganisms lining the walls of the spring. However, the photosynthetic temperature limit of ~72°C (158°F) is exceeded at the source vent, and a clear color delineation is observed along the walls from green (photosynthesizing) to white (if cells are there, living on chemical energy).

Until recently, little was known about microorganisms in any environment. Traditional microbiology has relied upon cultivation techniques. These have taught us a number of lessons about what organisms look like, how they metabolize different substrates, and how they live with each other. As more and more whole genomes from these cultured organisms emerge, information on their genetics and potential capabilities is also becoming available. We now know that <1% of Earth's microbes are able to thrive in a culture situation, simply because it is nearly impossible to duplicate an organism's natural environment in the lab (Amann, Ludwig, et al. 1995). With the advent of new molecular identification methods for microbes, we have gained a much broader knowledge of the microbial world than was possible with traditional cultivation methods. However, it is important to remember that modern microbiology relies upon information obtained from culture studies to infer information from molecular identification.

Molecular identification examines a gene, an amount of DNA sequence on a microorganism's chromosome. Differences in the DNA sequence on the 16S ribosomal RNA (rRNA) gene can be used to map relatedness between organisms and within groups (kingdoms within the *Bacteria, Archaea,* and *Eucarya* domains). The power of this process is that it can provide a definitive determination of who is who, provides data-baseable

Figure 2. *Top:* A hot spring in the West Thumb area. *Top right* provides a close-up view of the black color lining the walls of this 88°C hot spring. The color is imparted by non-photosynthetic pigments within microbial cells living on the sub-aqueous surfaces. *Bottom:* Octopus Spring in the White Creek region as seen from above. In addition to microbial mats, as seen in Figure 1, there are also organisms living within the water column itself, such as the many inch-long, white-to-pink filaments found in the immediate outfall channel of the hot spring (*bottom right*).

information (DNA sequences), and can be subject to thorough analysis (advanced statistical approaches).

The last decade has seen a number of these kinds of phylogenetic studies applied to several Yellowstone hot springs (Barns, Fundyga, et al. 1994; Reysenbach, Wickham, et al. 1994; Huber, Eder, et al. 1998; Hugenholtz, Pitulle, et al. 1998; Reysenbach, Ehringer, et al. 1998; Ward 1998; Ward, Ferris, et al. 1998; Reysenbach, Ehringer, et al. 2000; Blank, Cady, et al. 2002; Norris, Wraith, et al. 2002; Spear 2002). Upon review of the results, we observed a common theme. Several studies showed an abundance of members of the *Aquificales* bacterial division. Also present were representatives from the *Thermotogales*, *Thermus,* and *Proteobacteria* divisions. We know from traditional cultivation studies that many cultivars from each of these groups prefer or can only use H_2 as an electron donor. This is a surprising result, because when you walk around Yellowstone, you smell sulfide and see sulfur, both of which can act as strong electron donors for microbial life. It seemed as though, and was long thought to be, that the underlying energetic basis for life above the photosynthetic limit of 72°C was the microbial oxidation of these reduced sulfur compounds (Madigan, Martinko, et al. 2003). The phylogenetic results from these studies seemed to suggest otherwise. Could it be that instead, molecular hydrogen provides the electron

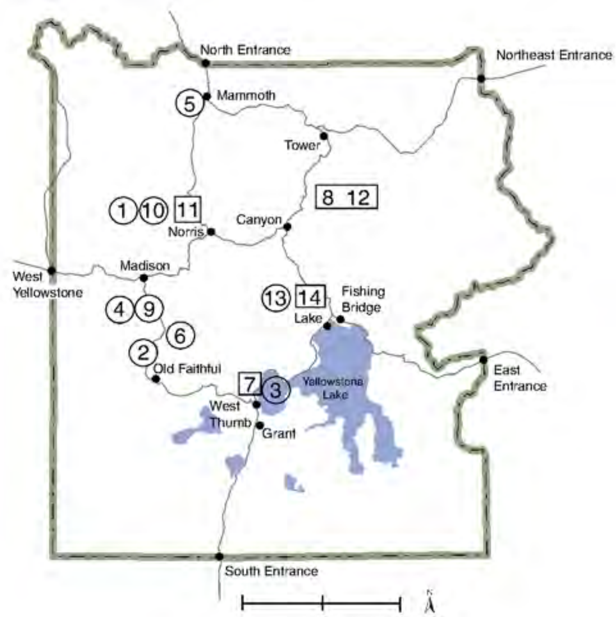


Figure 3. Map of Yellowstone National Park showing the authors' research locations by site number. Hydrogen measurements were conducted in the field by the method described at all sites. Site numbers in boxes represent sites with associated phylogenetic analyses conducted in the laboratory at the University of Colorado.

donor, the fuel, for these microbes in their environments? Thus began our study (Spear, Walker, et al. 2005).

Methodology

Sample collection and DNA extraction. Care was taken in the field to adhere to the idea of minimum impact research (Spear 2004). Samples for DNA extraction were collected from individual source springs in different regions of the park (Figure 3) by one of several methods, depending on the nature of the spring. In some hot springs (Washburn Spring, Queens Laundry), gram amounts of sediment could be collected, frozen in cryovials of liquid nitrogen in the field, and stored at –80°C in the lab. In others, glass slides were suspended in spring pools for periods ranging from 48 hours (Obsidian Pool Prime, Mud Volcano region) to two months (a West Thumb hot spring). Biofilms were then scraped from the slides and frozen in liquid nitrogen. Samples for analyses were collected in different seasons from 1999 to 2003. Total community DNA was prepared from ~1g of frozen samples (Dojka, Hugenholtz, et al. 1998). DNA was purified further to remove substances that could inhibit polymerase chain reactions (PCR) (Barns, Fundyga, et al. 1994).

PCR amplification of rDNA. Initial PCR amplifications of environmental DNAs were conducted to obtain the 16S rRNA genes from all members in the source community. This was conducted with the universal PCR primers 515F and 1391R (Lane 1991) that can amplify the small sub-unit rRNA gene from all three domains of life—*Bacteria, Archaea,* and *Eucarya.* Full-length bacterial rRNA gene sequences were obtained with the PCR primers 8F and 1492R (Lane 1991). Archaeal libraries were constructed with the PCR priming pairs 4Fa or 333Fa, with 1391R (Lane 1991). These primers were each combined with the environmental DNA sample in a PCR mixture including the enzyme *Taq* polymerase, which, when subjected to a certain temperature regime, makes many copies of each of the 16S rRNA genes in the sample. The end result of these amplifications is a tube full of many copies of mixed 16S rRNA genes representative of the source community.

Glossary

Air-bubble stripping: A method of measuring the amount of dissolved gases in water. Similar to the way that CO_2 carbonation dissolves in soda or beer, most gases dissolve in water. Gases such as hydrogen and methane dissolve in Yellowstone's hot spring waters. To measure those, hot spring water is run through a plain atmospheric air bubble. In the process, gases leave the water and enter the air bubble. The air bubble is then extracted and analyzed for the types of gas it contains.

Anion: A negatively charged ion. Chloride (Cl-) and nitrate (NO_3-) are examples of anions.

Cation: A positively charged ion. Metals like copper (Cu_2+), Manganese (Mn_2+) and Sodium (Na+) are cations.

Dissociation constant: A value (K) that expresses the extent to which a substance (e.g., sodium chloride, NaCl) dissociates in solution. The smaller the value of K, the less dissociation. The value varies with temperature, ionic strength, and the nature of the solvent (water, in Yellowstone's case).

Environmental DNA: DNA extracted from the environment.

nM: Nanomolar. A molar solution is one mole of a substance in one liter of water. For example, there are 58 grams in one mole of sodium chloride, NaCl. If those 58 g are dissolved in 1 liter of water, the result is a 1M solution. One-billionth of that concentration is an nM solution.

Nucleotide: Basic structural units of nucleic acids (as RNA and DNA).

Obsidian Pool Prime: Obsidian Pool is a hot spring in the Mud Volcano region that has yielded enormous bacterial diversity, as shown by previous molecular analyses. Obsidian Pool Prime is a hot spring right next to it; the two have a common outfall channel.

Peristaltic pump: A mechanical pump used to pump fluid. The pump has no direct contact with the source fluid to be pumped. Instead, a mechanical wheel rubs a section of plastic tube in a pulse fashion to move the fluid through the tube. The pump head can have a variable-speed motor attached, in order to pump quickly or slowly.

Reduction gas chromatography: A method of separating the gases that comprise a source gas into their separate components. When a source gas is heated and passed through an analytical column, the different gases in the source gas separate into their constituent parts at different rates. From this, the types and amounts of gases that comprise the source gas can be determined. A reduction gas analyzer is used for gases like hydrogen and methane that contain several hydrogen atoms.

SSU: Small sub-unit, as in SSU rRNA, which stands for "small sub-unit ribosomal RNA." Ribosomes are the protein manufacturing facilities of all cells. They are composed of several sub-units, or components. Bacteria for example, have two RNA sub-units, and 52 protein sub-units that make up the ribosome. The authors of this article are tracking the genetic information (the DNA sequence that codes for the RNA) of one of those RNA sub-units.

Thermister: A temperature-sensing device, typically a thermally sensitive resistor that exhibits measurable change in electrical resistance. This can be read as temperature on a meter, much like a thermometer.

Cloning and sequence analysis. Before DNA sequences can be obtained from PCR products, separation of the PCR product has to occur, because it is a mix of the many genes present in the source community. To do this, PCR products are cloned into *E. coli* cells with a virus-like vector that only puts one PCR product into each cell. The result is many

E. coli colonies, each containing a unique PCR product sequence. PCR products were cloned for sequencing.

Sequencing reactions were prepared and sequenced in 96-well format. Unique sequences were assembled and put through the Basic Local Alignment Search Tool (BLAST) algorithm (Altschul, Madden, et al. 1997) to determine approximate phylogenetic position.

Figure 4. Field-portable, bubble-stripping apparatus for measurement of H_2 in geothermal waters. An intake tube is wrapped in insulation to keep the water hot. A peristaltic pump pumps water through a glass jar (*right*) with a 20-ml atmospheric air bubble inside. After an amount of pump time at a given rate of flow, the bubble is withdrawn for analysis.

Phylogenetic analysis. Chimeric sequences—two gene sequences from two different sources that appear as one—were identified using secondary-structure analyses in addition to software (Maidak, Cole, et al. 2001). Sequences that showed ≥99% identity to common contaminants of rRNA-based molecular surveys were excluded from further analyses (Tanner, Goebel, et al. 1998). The remaining environmental rRNA gene sequences were then aligned to other known SSU rRNA sequences.

Hydrogen and water chemistry. To survey the distribution of hydrogen concentrations in high-temperature Yellowstone waters (pools, streams, geothermal vents, and a well; Spear 2002), we pumped source waters and performed air-bubble-stripping with H_2, CH_4, and CO_2 analysis by reduction gas chromatography (Chapelle 1997). A peristaltic pump was used to pump source waters through H_2-impermeable tubings into a 250-ml, glass-bottle, bubble-stripping device for triplicate analyses. A 20-ml atmospheric air bubble was introduced into the bottle after it was completely filled with the source water to be measured. Temperature of the bubble was measured by a thermister attached to a digital thermometer. Tubes were insulated from the hot spring water surface to the pump to maintain source water temperature in the bubble-strip apparatus (Figure 4). After bubble-stripping, bubbles were collected with an air-tight syringe and transferred to nitrogen-charged, H_2-impermeably sealed glass septum vials and sent to a geochemical research company in Pittsburgh, Pennsylvania, for immediate analysis on a reduction gas analyzer.

Sulfide measurements were conducted. Samples for water chemistry were collected by pumping water out of each spring, syringe-filtering it through a 0.2-µm filter, and acidifying it with ultra-pure nitric acid to

Polymerase Chain Reaction (PCR)

IN MOLECULAR BIOLOGY, it is often necessary to know what one particular segment of DNA, a gene, does for a cell. However, the cell may contain only one copy of that gene (consisting of, e.g., 1,500 base pairs of nucleotides—A+T and C+G repeated in a certain order). One copy is a miniscule amount—too little to work with. In these cases, a process known as **Polymerase Chain Reaction,** or **PCR,** is used to repeatedly amplify a segment of DNA. PCR enzymatically replicates the one copy of the gene into millions or billions more copies.

To facilitate this process, PCR **primers** are applied to the source DNA sequence on either side of the gene. These primers consist of the building blocks of DNA (the A, T, C, and G nucleotides), appropriate to the gene being analyzed. From obtained DNA sequences, these oligonucleotide sequence primers (chains of up to 20 nucleotides) have come to be teased out of genomic DNA. For some genes, it has been observed that these sequences are often quite common between organisms. In the case of *Bacteria* and *Archaea,* for example, it is evident that on either side of the 16S rRNA gene, there is a like code of 15–20 base pairs that is always the same, no matter what kind of *Bacteria* or *Archaea* is examined. In fact, the 16S gene is very similar in actual base pair sequence among most organisms, with the occasional base difference.

It is the sum of these slight differences that allows geneticists to distinguish between organisms and infer relatedness to one another. PCR primers are used to match that 15–20 base pair difference on either side of the gene, thereby providing a starting point in PCR to amplify that one gene. To make the multitude of copies necessary for understanding the genetic function of the gene, the PCR reaction replicates the source gene many times in a series of heating and cooling reactions in the presence of an enzyme called DNA polymerase, commonly Taq polymerase—originally isolated from a Yellowstone hot spring.

preserve the sample. Samples were placed at 4°C for transport back to the lab. Anions, cations, and elemental analyses were conducted in the Laboratory for Environmental and Geological Studies of the Geology Department at the University of Colorado at Boulder.

Thermodynamic modeling. The amounts of chemical energy available from chemical primary producers were quantified with thermodynamic computer models. Species distributions for dissolved inorganic carbon and sulfide were calculated from the measured total amounts for these compounds, together with appropriate dissociation constants and the measured pH, assuming the species were in equilibrium.

Results and Discussion

Chemistry of Yellowstone hot springs. The first step in this work was to provide a chemical context to aid in the interpretation of the phylogenetic results of others (Reysenbach, Wickham, et al. 1994; Hugenholtz, Pitulle, et al. 1998; Reysenbach, Ehringer, et al. 2000; Blank, Cady, et al. 2002). We conducted chemical analyses of hot springs of different kinds of chemistries in different geological areas of the park. Hot springs in the Upper Geyser Basin, for example, contained little or no sulfide and had higher, alkaline pH (pH 8–9). Hot springs in Norris Geyser Basin and the Mud Volcano region sometimes contained higher concentrations of sulfide, and had low-to-neutral pH.

When we measured molecular hydrogen concentrations in hot springs in these different areas around the park, we found concentrations that ranged from 3 nM to over 325 nM of aqueous, dissolved, hydrogen (Spear, Walker, et al. 2005). From cultivation studies of microbes that oxidize hydrogen as an energy source, we know that these concentrations are in the range of, and often far exceed, the 5–10 nM concentrations sufficient to maintain growth in culture. We also measured carbon dioxide, methane (CH_4), and the light hydrocarbons ethane, butane, and butene that we will not cover here (Spear, Walker, et al. 2005).

Each hot spring has its own geochemistry. The H_2 concentrations are spring-dependent, and seasonally consistent when measured over time. Other potential energy sources for microbes in Yellowstone hot springs, such as iron (Fe(II)), manganese (Mn(II)), and aqueous ammonia (NH_4), also occur variably in hot springs. However, because of the chemistry of the springs, the potential for energy yield from such compounds is low relative to other sources like sulfide and hydrogen.

The results from these chemical analyses indicate that aqueous, dissolved hydrogen gas is ubiquitous in Yellowstone hot springs. The concentration varies from spring to spring for a number of possible reasons. But in most of the hot springs we tested, there was enough H_2 present to fuel the microbial cells that live there. The source of the H_2 in the water is probably chemical, not biologic—a geologic process in which heated waters in Yellowstone's subsurface react with iron-bearing rocks to produce H_2 (Gold 1992; Stevens 1995; Sleep, Meibom, et al. 2004). The actual measured presence of H_2 in Yellowstone waters provides our first line of inference that H_2 may be a common fuel for life at >72°C.

Phylogenetic analyses. For a second line of inference, we phylogenetically examined the microbes present in hot springs of >72°C, with both low and high hydrogen and low and high sulfide, to test the impact of reduced sulfur compounds on community composition. If sulfide or hydrogen is a dominant electron donor for the microbial community, this dominance should be reflected in the community composition. Microbes that use the dominant electron donor should be most abundant. To determine the community composition associated with these different chemical regimes, we PCR-amplified, cloned, and sequenced rRNA genes from crust and sediment communities. We also looked at pioneer communities that colonized on glass slides placed in hot springs for from two days to three months. We screened >2,500 randomly chosen clones from five different hot springs, and determined >400 new rRNA gene sequences for submittal to GenBank, a public repository of DNA sequence information.

To determine the phylogenetic types of organisms present

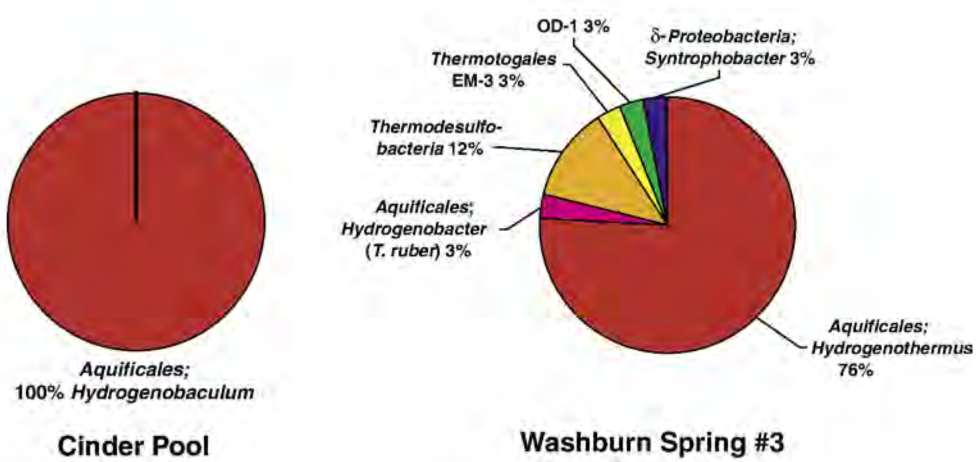


Figure 5. Results of phylogenetic analyses from Cinder Pool, Norris region, and a lower Washburn Spring, Canyon region, Yellowstone National Park. Cinder Pool is 88°C, pH 4.2, and contains 77 nM H_2, 1.2 μM CH_4, 47 μM sulfide, and 1 μM sulfate. One of the Lower Washburn Springs, #3, is 86°C, pH 6.2, and contains 19 nM H_2, 5.8 μM CH_4, 167 μM sulfide, and 44 μM sulfate.

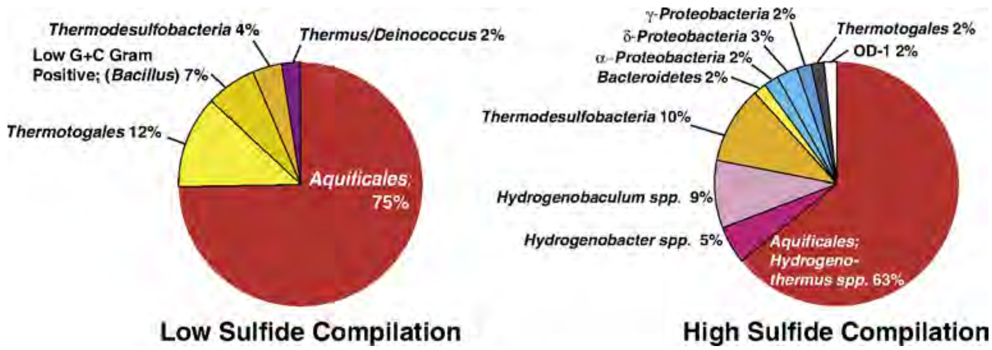


Figure 6. Results of community compilations from low- and high-sulfide Yellowstone hot springs. Left chart describes the phylogenetic distribution of rRNA gene sequences obtained from two low-sulfide springs in this study (a West Thumb hot spring and Obsidian Pool Prime), combined with the five low-sulfide springs of Blank et al. (Octopus Spring, Queens Laundry, Eclipse Geyser, Spindle Spring, and Boulder Spring) (Blank, Cady, et al. 2002). Right chart describes the phylogenetic distribution of rRNA gene sequences obtained from three high-sulfide springs in this study (Cinder Pool, Washburn #1, and Washburn #3).

in a given hot spring, we compared the obtained sequences to sequences of known organisms in public databases. Although the detail of hot spring composition varied, all of the five communities examined contained sequences representative of the same kinds of phylogenetic groups. As in previous studies (Hugenholtz, Pitulle, et al. 1998; Blank, Cady, et al. 2002), communities were dominated by bacterial rRNA genes. *Archaea* are considered common in these and other "extreme" environments, but as in the previous studies, our surveys indicated that these organisms are about one-tenth as abundant as bacteria. Most of the *Archaea* encountered in this study were relatives of an environmental Crenarchaeote observed in an earlier study of Obsidian Pool (Barns, Fundyga, et al. 1994; Barns, Delwiche, et al. 1996).

The several hundred unique rRNA gene sequences determined in this study fell into only a few phylogenetic groups. Sequences representative of the three main sub-groups of the bacterial division *Aquificales* (hydrogenobacter, hydrogenobaculum, and hydrogenothermus) were the most abundant in the five hot springs examined. The results of these analyses for two individual springs are presented in Figure 5. Sequences representative of the bacterial divisions *Thermotogales, Thermus/Deinococcus,* and *Thermodesulfobacteria* were also common. Cultivated representatives of organisms from all of these groups either exclusively or preferentially utilize molecular hydrogen as an electron donor. Collectively, >90% of the sequences obtained from these two hot springs came from these groups. If a characteristic is present in all of the cultivated members of a group, then other representatives of that group are assumed to also have those properties. Therefore, we can assume that the sequences obtained from the hot springs indicate that the organisms in the springs primarily use molecular hydrogen as their electron donor.

Communities of hot springs with both low and high sulfide concentrations did include some organisms of the kinds that can oxidize sulfide as an electron donor. However, these organisms were not as numerically abundant in the clone libraries as the H_2-oxidizers mentioned. Analytical results for hot springs of both high and low sulfide grouped together by spring type are shown in Figure 6. We did find a number of rRNA gene sequences representative of the δ-Proteobacteria, a group that includes many organisms that reduce sulfate to sulfide, often with molecular hydrogen as an electron donor. This would suggest that when sulfate is present in a Yellowstone hot spring, sulfate-reducing bacteria could then contribute to the energy budget of the community. As in the first two hot springs examined, the collected data from all of the springs indicate that, in hot springs of >72°C, >90% of community composition favors hydrogen oxidation independent of sulfide concentration.

Thermodynamic modeling. For a third line of inference that H_2 provides the fuel for microorganisms in Yellowstone hot springs >72°C, we thermodynamically modeled the potential energy available to the microbial communities present in a given hot spring. This model was based on the chemical compositions that we measured for the hot springs. Because photosynthesis does not occur at >72°C, most microbes in Yellowstone hot springs have to get their energy from reduced compounds, e.g., molecular hydrogen, sulfide, or methane (CH_4). The potential energy for the oxidation of these reduced compounds depends heavily on the availability of an electron acceptor in these hot springs. Molecular oxygen, O_2, diffusing into hot spring waters from the atmosphere, is the likely electron acceptor for most of the kinds of organisms we found in our phylogenetic survey.

Oxygen, however, is difficult to measure accurately in hot water, because of the low solubility of this gas at high temperature. Generally, the concentrations of this important electron acceptor are low, in the nM range, and we used a range of reasonable oxygen concentrations for our model. When we modeled the potential energy available in hot springs across a range of oxygen concentrations, the results indicated that the oxidation of H_2 was always favored under oxygen-limited conditions. This third line of experimental inference is consistent with the apparent dominance of H_2 oxidizers in our clone libraries of five hot springs examined.

Conclusions

With the combined use of chemical analyses, phylogenetic analyses, and thermodynamic modeling, we have shown that microbial life in Yellowstone hot springs at >72°C is most likely fueled by aqueous molecular hydrogen, not sulfide. While actual hydrogen concentrations vary, along with microbial community structure and geochemistry in each spring within the park, we observed a trend that nevertheless indicates a favorable role for hydrogen to fuel microbial life. The importance of hydrogen-metabolizing microorganisms in environmental microbiology has long been recognized (Madigan, Martinko, et al. 2003). We have now determined that biologically significant levels of hydrogen occur in the waters of Yellowstone hot springs, and that there are a large number of organisms present of the kinds that oxidize hydrogen. This theme of hydrogen as a main fuel for Yellowstone hot springs likely resonates to other geothermal ecosystems around our globe, and maybe elsewhere in the universe. YS

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John Spear is an assistant professor in the Division of Environmental Science and Engineering at the Colorado School of Mines. John performed the work described here as a postdoctoral fellow in the laboratory of Dr. Norman Pace at the University of Colorado–Boulder. His laboratory at the Colorado School of Mines continues to focus on microbial diversity and energetic mechanisms relevant to environments such as those that occur in Yellowstone hot springs, as well as those of hypersaline microbial mats found near Guerrero Negro, Baja California Sur, Mexico.

Jeff Walker is a postdoctoral fellow in the laboratory of Dr. Larry Gold in the Department of Molecular, Cellular and Developmental Biology at the University of Colorado–Boulder. Jeff worked on the microbial communities associated with Yellowstone endolithic communities (life in the pore space of rocks) as a graduate student with Norman Pace.

Norman Pace is a Professor of Molecular, Cellular and Developmental Biology at the University of Colorado–Boulder. His laboratory has long been involved with microbial community characterization by applied molecular methodologies and has, for a number of years, focused on extreme environments like those found in Yellowstone hot springs. Dr. Pace is a member of the National Academy of Sciences and is a Fellow of the MacArthur Foundation.

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From the Archives

YNP, PHOTO ARCHIVES, YELL #331

Two men at the largest pool of Five Sisters Springs in the Lower Geyser Basin, circa 1893.

"...[S]pectacular advances in microbiology have opened new avenues in our search for the origins of life itself and...hot-water organisms like Taq polymerase [an enzyme extracted from a microscopic bacterium discovered in Yellowstone's Mushroom Pool, which ultimately led to the development of DNA fingerprinting], hold vast promise for a host of other revelations and applications....[T]he scientific consensus is that less than one percent of the organisms in Yellowstone's 10,000 thermal features have even been identified, much less studied or put to work. Yellowstone's fabulous reach seems only to grow longer as time passes and as we learn more about what the creation of the park may yet mean."

—*Paul Schullery,* Searching for Yellowstone,
Helena: Montana Historical Society, 2004

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