Burgers vectors of the involved dislocations (*24*), a jog is produced on each threading dislocation when the stacking boundary crosses the "forest" of threading dislocations (Fig. 4D). In turn, the stacking-boundary dislocation acquires a kink for each crossing. The production of a jog on each threading dislocation costs energy, and the total energy barrier of all the needed crossings is much larger than the Peierls glide barrier encountered for pure glide within a rotational domain. Thus, the threading dislocations impede the stacking-boundary motion. Because the threading dislocations only occur at the rotational-domain boundaries, we explain the experimental observation that the stacking boundaries become stuck at the rotational boundaries. The crossing of the threading dislocations is temperature activated: The lower the temperature, the longer the stacking boundaries are pinned at the rotational boundaries. In contrast, the glide motion within rotational boundaries is independent of temperature in the observation range.

We can also understand why stacking boundaries preferentially advance (Fig. 2) along the unique direction of the misfit dislocations within each rotational domain. The array of misfit dislocations within each rotational domain constitutes a periodic array of obstacles for stacking-boundary motion unless, as observed, the stacking-boundary dislocation moves along the misfit dislocations themselves.

The experiments under sulfur exposure can also be explained by the atomistic details of the dislocation structures. When sulfur is deposited on a 2-ML Cu/Ru(0001) film, the striped pattern of misfit dislocations responsible for the rotational domains breaks down (fig. S3), and a well-ordered triangular pattern appears (*18*, *19*) that lacks rotational domains (fig. S4B). The unit cell of this pattern (fig. S4) is a small triangular unit with sides composed of misfit dislocations and threading dislocations at the three corners (*18*). Nevertheless, the stacking domains still persist and are observed as before in bright-field conditions (Fig. 3). As in 2-ML Cu/Ru(0001) without sulfur (Fig. 1A), there are still two different possibilities for stacking the second Cu layer on top of the first. However, the threading dislocations are now uniformly distributed within the film. The stacking boundary dislocations now encounter a closely spaced (<7 nm apart) distribution of threading dislocations, so the stacking domains evolve smoothly at our observation scale, which is larger than the film's threading dislocation spacing (the LEEM resolution is ~10 nm). Therefore, the stacking boundaries move smoothly with no preferred directions (Fig. 3).

In summary, we have shown how observing thin-film microstructure evolution in real time and in real space can determine what process controls the healing of crystallographic defects. In the Cu on Ru system, all the microstructure interactions can be observed and understood; it serves as a model of thin-film evolution in which the detailed interactions can be fully modeled (*25*). Given the ubiquity of dislocations in heteroepitaxial films, we anticipate that our key finding, that dislocations interactions control the rate at which extended defects heal themselves, will hold in many other metal and nonmetal systems.

References and Notes

1. W. Cochrane, *Proc. Phys. Soc.* **48**, 723 (1936).
2. E. Bauer, *Appl. Surf. Sci.* **11**, 479 (1982).
3. O. L. Alerhand, D. Vanderbilt, R. D. Meade, J. D. Joannopoulos, *Phys. Rev. Lett.* **61**, 1973 (1988).
4. R. Q. Hwang, M. C. Bartelt, *Chem. Rev.* **97**, 1063 (1997).
5. O. Rodríguez de la Fuente *et al.*, *Phys. Rev. Lett.* **88**, 036101 (2002).
6. J. de la Figuera *et al.*, *Mat. Sci. Forum* **426-432**, 3421 (2003).
7. F. El Gabaly, R. Miranda, J. de la Figuera, *Phys. Rev. B* **70**, 012102 (2004).
8. R. Phillips, *Crystals, Defects and Microstructures: Modeling Across Scales* (Cambridge Univ. Press, Cambridge, 2001).
9. C. Busse, T. Michely, *Surf. Sci.* **552**, 281 (2004).
10. E. Bauer, *Rep. Prog. Phys.* **57**, 895 (1994).
11. C. Günther, J. Vrijmoeth, R. Q. Hwang, R. J. Behm, *Phys. Rev. Lett.* **74**, 754 (1995).
12. C. Ammer, K. Meinel, H. Wolter, A. Beckmann, H. Neddermeyer, *Surf. Sci.* **375**, 302 (1997).
13. H. Zajonz, D. Gibbs, A. P. Baddorf, V. Jahns, D. M. Zehner, *Surf. Sci.* **447**, L141 (2000).
14. H. Zajonz, A. P. Baddorf, D. Gibbs, D. M. Zehner, *Phys. Rev. B* **62**, 10436 (2000).
15. J. de la Figuera, A. K. Schmid, N. C. Bartelt, K. Pohl, R. Q. Hwang, *Phys. Rev. B* **63**, 165431 (2001).
16. Materials and methods are available as supporting material on *Science* Online.
17. T. Giessel, A. K. Schmid, N. C. Bartelt, J. de la Figuera, R. Q. Hwang, *18th European Conference on Surface Science*, Vienna, 21 to 24 September 1999 (European Physical Society, Paris, 1999), abstr. Th-P-151.
18. J. de la Figuera *et al.*, *Surf. Sci.* **433-435**, 93 (1999).
19. J. Hrbek *et al.*, *J. Phys. Chem. B* **103**, 10557 (1999).
20. C. B. Carter, R. Q. Hwang, *Phys. Rev. B* **51**, 4730 (1995).
21. J. de la Figuera *et al.*, *Phys. Rev. Lett.* **86**, 3819 (2001).
22. M. S. Daw, S. M. Foiles, M. I. Baskes, *Mat. Sci. Rep.* **9**, 251 (1993).
23. S. M. Foiles, M. I. Baskes, M. S. Daw, *Phys. Rev. B* **33**, 7983 (1986).
24. J. P. Hirth, J. Lothe, *Theory of Dislocations* (Krieger, Malabar, FL, 1992).
25. S. J. Zhou, D. L. Preston, P. S. Lomdahl, D. M. Beazley, *Science* **279**, 1525 (1998).

26. This research was partly supported by the Office of Basic Energy Sciences, Division of Materials Sciences, U.S. Department of Energy, under Contract DE-AC04-94AL85000, by the Comunidad Autónoma de Madrid through Project 07N/0041/2002, and by the Spanish Ministry of Science and Technology through Project MAT2003-08627-C02-02. J.d.l.F gratefully acknowledges additional support through a "Ramón y Cajal" contract from the Spanish Ministry of Science and Technology.

Supporting Online Material

www.sciencemag.org/cgi/content/full/308/5726/1303/DC1
Materials and Methods
Figs. S1 to S4
Movies S1 and S2

18 January 2005; accepted 23 March 2005
10.1126/science.1109889

A Microbial Arsenic Cycle in a Salt-Saturated, Extreme Environment

Ronald S. Oremland,[1]* Thomas R. Kulp,[1] Jodi Switzer Blum,[1] Shelley E. Hoeft,[1] Shaun Baesman,[1] Laurence G. Miller,[1] John F. Stolz[2]

Searles Lake is a salt-saturated, alkaline brine unusually rich in the toxic element arsenic. Arsenic speciation changed from arsenate [As(V)] to arsenite [As(III)] with sediment depth. Incubated anoxic sediment slurries displayed dissimilatory As(V)-reductase activity that was markedly stimulated by H_2 or sulfide, whereas aerobic slurries had rapid As(III)-oxidase activity. An anaerobic, extremely haloalkaliphilic bacterium was isolated from the sediment that grew via As(V) respiration, using either lactate or sulfide as its electron donor. Hence, a full biogeochemical cycle of arsenic occurs in Searles Lake, driven in part by inorganic electron donors.

The microbial life that exists in brines of exceptionally high salinity has been a topic of fascination to microbiologists (*1*, *2*). Primary productivity in hypersaline ecosystems is driven by oxygenic photosynthesis, as typified by salt-adapted microbes like *Dunaliella parva* that provide the organic carbon needed to sustain a microbial food chain. Typical heterotrophs obtained from such locales are either obligate aerobes or fermentative anaerobes (*3*). Some also have the ability to respire nitrate, but the importance of this scarce anion as a respiratory electron acceptor in high-density brines has not been studied. In extremely hypersaline environments that have

[1]U.S. Geological Survey, ms 480, 345 Middlefield Road, Menlo Park, CA 94025, USA. [2]Department of Biological Science, Duquesne University, Pittsburgh, PA 15282, USA.

*To whom correspondence should be addressed. E-mail: roremlan@usgs.gov

salt concentrations that approach saturation (e.g., ≥300 g/liter), the otherwise ubiquitous process of sulfate reduction is either notably absent or greatly diminished (*4*–*6*). Likewise, methanogenesis is either feeble (*7*) or undetectable (*6*). The most likely reason for this is that the metabolic pathways of these two processes generate insufficient energy to meet the higher requirements of maintaining an internal osmotic gradient against the strong external salt milieu (*4*). Hence, any anaerobe with a respiratory metabolism that can live at extremely high salinities must be able to link its oxidation of carbon substrates to biological oxidants considerably stronger than sulfate or carbonate so as to yield more energy. For example, the selenate-respiring bacterium, *Selenihalanaerobacter shriftii*, was isolated from Dead Sea sediments (*8*), but the scarcity of this element in the brine means that this process is probably not of quantitative importance to the biogeochemical cycling of carbon.

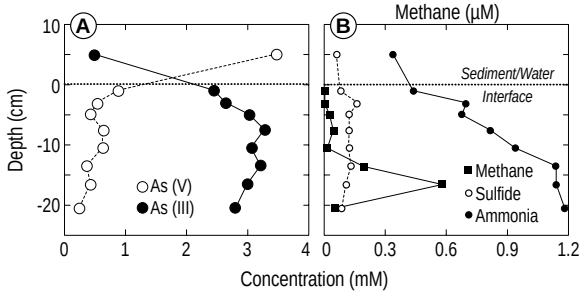


Fig. 1. Searles Lake vertical sediment depth pore-water profiles of (**A**) arsenate [As(V)] and arsenite [As(III)] and (**B**) sulfide, methane, and ammonia.

In comparison to sulfate (SO_4^{2-}/HSO_3^-: electrochemical potential $E_o' = -516$ mV) (*9*) or carbon dioxide (CO_2/CH_4: $E_o' = -244$ mV (*9*), arsenate [As(V)] reduction to arsenite [As(III)] is a more robust bio-oxidation (*10*), with a much higher electrochemical potential (arsenate $[HAsO_4^{2-}]$/arsenite $[H_2AsO_3^-]$: $E_o' = +60$ mV) (*11*). Although arsenic is usually thought of only for its toxic properties, several prokaryotes metabolize arsenic oxyanions to gain energy for growth. Arsenate respiration and chemoautotrophic arsenite oxidation occur in prokaryotes from broadly diverse phylogenetic groups and a variety of environments (*12*).

Relatively high concentrations of arsenic oxyanions occur in several soda lakes of the western United States (*13*), originating from hydrothermal springs that are common in this volcanically active region. Arsenate acts as an important respiratory electron acceptor in Mono Lake, second only to sulfate, for the oxidation of organic carbon by anaerobic bac-

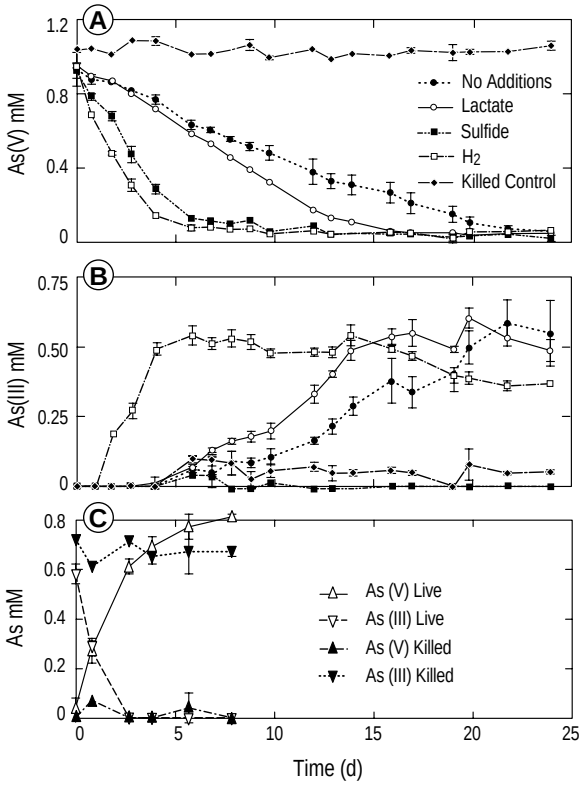
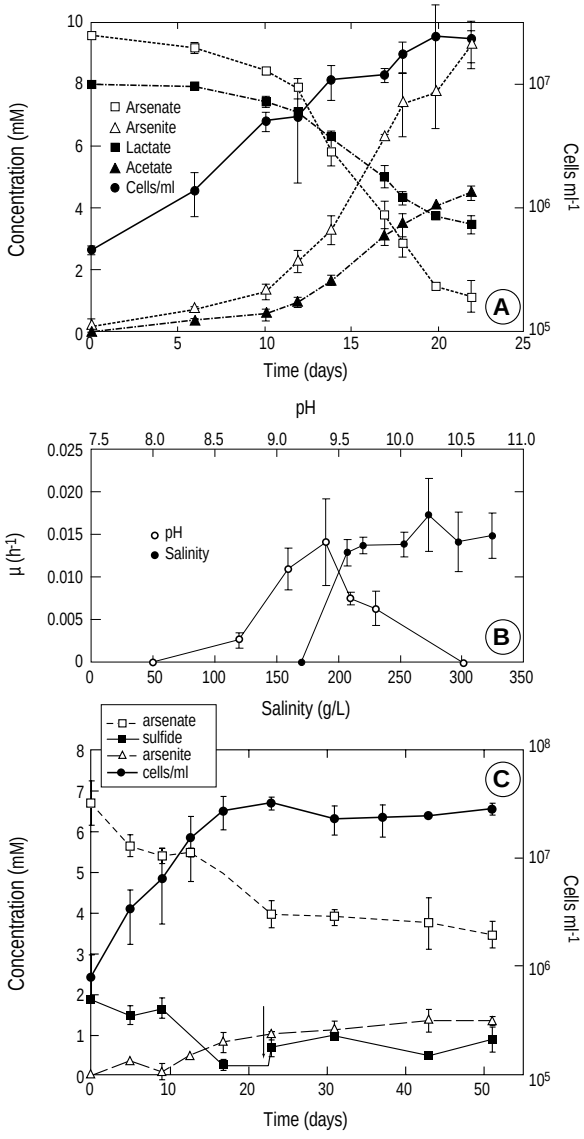


Fig. 2. (**left**) Incubation experiments with sediment slurries from Searles Lake under anoxic (**A** and **B**) or oxic (**C**) conditions. (A) Reduction of arsenate; (B) formation of arsenite; (C) oxidation of arsenite to arsenate. Symbols represent the mean ± 1 SD of three slurries. **Fig. 3.** (**right**) (**A**) Anaerobic growth of strain SLAS-1 on lactate plus arsenate at a salinity of ~330 g/liter and pH 9.8. (**B**) Salinity and pH range for growth of strain SLAS-1. (**C**) Anaerobic growth of strain SLAS-1 with sulfide as the electron donor. Arrow indicates addition of more (0.5 mM) sulfide to samples after 23 days of incubation. In all of the panels, symbols represent the mean ± 1 SD of three experimental growth cultures.



teria (*14*). Searles Lake is located in the Mojave Desert about 270 km south-southeast of Mono Lake. The major ionic constituents of the Searles Lake subsurface brine are (given as molality, *m*; moles per kilogram of solvent) Na^+ (7.43), K^+ (0.78), $HCO_3^- + CO_3^{2-}$ (0.64), Cl^- (5.25), SO_4^{2-} (0.73), and BO_3^{3-} (0.46), as reported previously (*15*, *16*).

Searles Lake surface brine is unusually enriched in arsenic [ΣAs = ~ 3.9 mM; for methods, see (*17*)]. In a sediment core pore-water profile, the speciation of dissolved arsenic oxyanions changed from predominantly As(V) (88%) in the overlying water to predominantly As(III) (84%) by 7-cm sediment depth (Fig. 1A). The As(V) + As(III) content of the pore waters ranged from 84 to 97% of the overlying water, indicating that only minor loss of arsenic oxyanions was attributable to the formation of thioarsenites (*18*, *19*), by adsorption onto mineral surfaces or by chemical precipitation as a mineral phase (e.g., arsenopyrite). Other relevant major anionic brine constituents were chloride (range = 4.7 to 5.0 *m*), sulfate (range = 0.66 to 0.79 *m*), and phosphate (range = 16 to 20 mM), but none displayed any trended variation with core depth (*20*). Nitrate was not detected, but traces of sulfide, methane, and ammonia were present (Fig. 1B), indicating generally reducing conditions in the sediments, which contrasted with the slightly oxic conditions (dissolved oxygen = 6.3 μM) found in the overlying water. For comparison, the sulfide and methane concentrations were roughly a factor of 10 and 100 less, respectively, than what we reported in the anoxic bottom waters of Mono Lake (*14*), and a factor of 10 to 100 less for the methane concentrations in Mono Lake sediments (*21*). This supports Oren's hypothesis (*4*) of a near-absence of sulfate reduction and methanogenesis in salt-saturated (i.e., Searles Lake), anoxic environments (*6*). The arsenic speciation patterns in Searles Lake sediments were consistent with our observations of the stratified water column of Mono Lake, which were attributable to microbial reduction of As(V) in the anoxic zone and oxidation of As(III) in regions where dissolved oxygen, or nitrate, were present (*14*, *22*, *23*). To test whether the pore-water arsenic speciation observed in Searles Lake sediments was also attributable to microbiological processes, we conducted sediment incubation experiments (*17*).

Anaerobic sediment slurries reduced As(V) to As(III), whereas no activity was noted in autoclaved controls (Fig. 2, A and B). Addition of lactate, an electron donor used by many As(V) respirers (*10*, *12*), modestly increased the rate of As(V) reduction. When inorganic electron donors sulfide or hydrogen were added, As(V) reduction was even more rapid, suggesting that these may be important in situ lithotrophic electron donors in this system, similar to other extreme systems (*18*, *24*). Recovery of As(III) from added As(V) was generally only about 60 to 70% and was only ~10% in the slurries amended with sulfide (Fig. 2B), because of the formation of thioarsenites (*20*), which are soluble in alkaline, carbonate-rich solutions (*18*, *19*). Live aerobic slurries rapidly oxidized As(III), whereas no oxidation occurred in the killed controls (Fig. 2C). Thus, a full biogeochemical cycling of arsenic occurs in Searles Lake, mediated by microbial aerobic oxidation of As(III) and anaerobic reduction of As(V).

We cultivated enrichments of anaerobic, As(V)-respiring prokaryotes adapted to the "extreme" conditions of Searles Lake by using our artificial brine (*17*) plus As(V) as the electron acceptor. Because this study preceded the sediment slurry investigations, we did not attempt to cultivate enrichments of cultures using inorganic electron donors. We used lactate as the electron donor based on our earlier success at isolating As(V)-respiring heterotrophs from Mono Lake (*25*). Over the course of 1 year, a stable population grew that was transferred every other week into fresh medium and subsequently purified by serial dilution. The isolate, strain SLAS-1, was a curved, motile rod that grew (doubling time ~48 hours) by oxidizing lactate to acetate plus HCO_3^- while reducing As(V) to As(III) (Fig. 3A), according to the stoichiometry noted previously (*25*) but recalculated for the actual concentrations used in the medium (*17*):

$$\text{Lactate}^- + 2\text{HAsO}_4^{2-} + \text{H}^+ \rightarrow \text{Acetate}^- + 2\text{H}_2\text{AsO}_3^- + \text{HCO}_3^- \quad \Delta G_r = -201.7\ \text{kJ}$$

Strain SLAS-1 did not grow at salinities below 200 g/liter and had roughly equivalent growth rates at salinities >200 g/liter (Fig. 3B). Optimal growth was at pH 9.5, with little growth below pH 9.1 (Fig. 3B). Thus, strain SLAS-1 was well adapted to the extreme chemical conditions of Searles Lake. We also demonstrated that strain SLAS-1 could grow by using sulfide as its electron donor with As(V) as its electron acceptor (Fig. 3C). We noted, but did not quantify, the production of thioarsenites during this growth. Thioarsenites probably accounted for half of the reduced form of arsenic (+3 oxidation state) present by the end of growth because the ratio of As(V) consumed to As(III) produced was 2:1 rather than the expected 1:1. Hence, this microbe has a capacity for either heterotrophy or lithotrophy with regard to its ability to use either an organic (lactate) or inorganic (sulfide) electron donor to sustain its growth while respiring As(V). Further proof that strain SLAS-1 was able to grow as a chemolithoautotroph came from its ability to carry out dark HCO_3^- fixation into cell material when grown on sulfide plus As(V). Dilute washed suspensions (2.2×10^7 cells ml^{-1}) of sulfide-grown

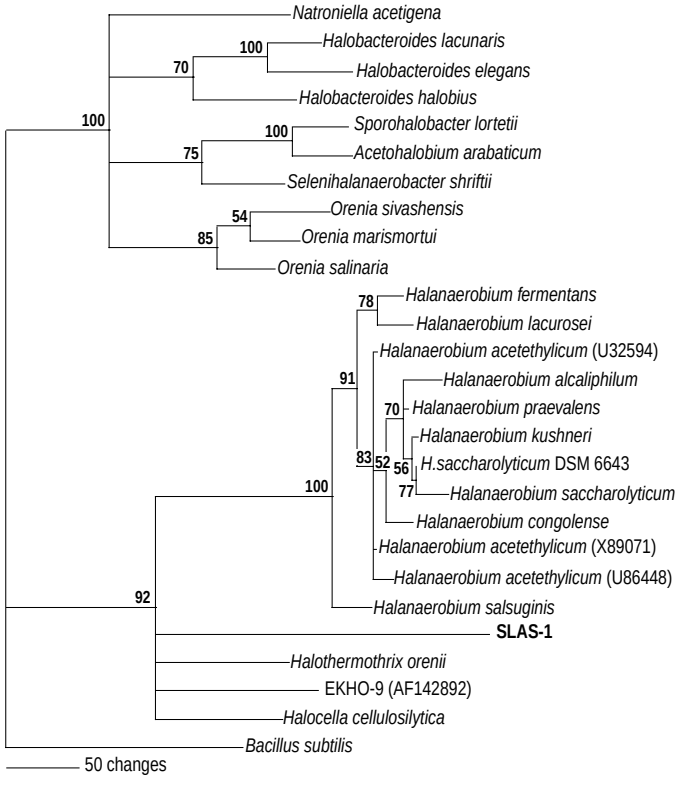


Fig. 4. Phylogenetic tree of Halanaerobiales showing the affiliation of SLAS-1 based on 16S rRNA gene sequence (920 bases) using maximum parsimony analysis (*28*). The species of Halanaerobiales used for the tree (with their GenBank accession numbers in parentheses) were *Halanaerobium congolense* (U76632), *Halanaerobium salsuginis* (L22890), *Halanaerobium kushneri* (U86446), *Halanaerobium alcaliphilum* (X81850), *Halanaerobium praevalens* (AB022035), *Halanaerobium saccharolyticum* (L37424, X89069), *Halanaerobium lacurosei* (L39787), *Halanaerobium fermentans* (AB023308), *Halobacteroides halobius* (U32595), *Halobacteroides lacunaris* (U32593), *Halanaerobium acetethylicum* (U32594, X89071, U86448), *Halobacteroides elegans* (AJ238119), *Halocella cellulosilytica* (X89072), *Halothermothrix orenii* (L22016), *Orenia salinaria* (Y18485), *Orenia sivashensis* (AF152595), *Orenia marismortui* (X89073), *Natroniella acetigena* (X95817), *Sporohalobacter lortetii* (M59122), and *Acetohalobium arabaticum* (X89077). Bootstrap numbers are given at the branch nodes.

cells (*17*) fixed ^{14}C-HCO_3^- into cell carbon (2051 ± 1282 dpm; $n = 3 \pm 1$, mean ± SD) when provided with both sulfide and As(V), whereas no activity occurred with live controls incubated without sulfide (80 ± 69 dpm; $n = 2$) or in a heat-killed control containing both sulfide and As(V) (30 dpm). Strain SLAS-1 was unable to metabolize H_2; however, we have subsequently cultivated enrichments from Searles Lake sediments that use H_2 as an electron donor to support chemolithoautotrophic growth on As(V) (*20*).

Phylogenetic alignment by 16*S* ribosomal RNA (rRNA) gene sequences taxonomically assigned strain SLAS-1 within the order *Halanaerobacteriales* in the Domain Bacteria (Fig. 4). With the exception of the selenate-respiring *Selenihalanaerobacter shriftii* isolated from the Dead Sea (*8*), all other strains are moderate or extremely halophilic, fermentative anaerobes. Strain SLAS-1 was only remotely related to these other species, having the closest sequence similarity to *Halothermothrix orenii* (83.9%) and *Halocella cellulytica* (83.5%). Clearly, strain SLAS-1 is sufficiently genetically distant from these other strains to merit eventual designation as a new species.

Our results show that a full biogeochemical arsenic cycle is operative in the sediments of this salt-encrusted lake, and we have isolated at least one bacterium that can account for some of these observed dynamics. Our demonstration that the abundant As(V) oxyanions present in the brine can be used as a terminal electron acceptor broadens our understanding of the types of processes occurring in such extreme environments, which has implications for possible exobiological life in dense brines (*26*). However, basic research can also aid our interpretation of the interaction of hydrologic and microbial processes affecting arsenic solubility and partitioning in less extreme environments, such as drinking-water aquifers (*27*).

References and Notes

1. B. Javor, *Hypersaline Environments* (Springer, Berlin, 1989).
2. A. Oren, in *Microbiology and Biogeochemistry of Hypersaline Environments*, A. Oren, Ed. (CRC Press, Boca Raton, FL, 1999), pp. 1–12.
3. A. Oren, *Adv. Microb. Ecol.* **10**, 193 (1988).
4. A. Oren, *Microbiol. Mol. Biol. Rev.* **63**, 334 (1999).
5. K. K. Brandt, F. Vester, A. N. Jensen, K. Ingvorsen, *Microb. Ecol.* **41**, 1 (2001).
6. K. B. Sørensen, D. E. Canfield, A. Oren, *Appl. Environ. Microbiol.* **70**, 1608 (2004).
7. M. A. Marvin-DiPasquale, A. Oren, Y. Cohen, R. S. Oremland, *Microbiology and Biogeochemistry of Hypersaline Environments*, A. Oren, Ed. (CRC Press, Boca Raton, FL, 1999), pp. 149–159.
8. J. Switzer Blum, J. F. Stolz, A. Oren, R. S. Oremland, *Arch. Microbiol.* **175**, 208 (2001).
9. R. K. Thauer, K. Jungerman, K. Decker, *Bacteriol. Rev.* **41**, 100 (1977).
10. D. K. Newman, D. Ahmann, F. M. M. Morrell, *Geomicrobiol. J.* **15**, 255 (1998).
11. A. J. Bard, R. Parsons, J. Jordan, *Standard Potentials in Aqueous Solutions* (Dekker, New York, 1985).
12. R. S. Oremland, J. F. Stolz, *Science* **300**, 939 (2003).
13. R. S. Oremland, J. F. Stolz, J. T. Hollibaugh, *FEMS Microbiol. Ecol.* **48**, 15 (2004).
14. R. S. Oremland *et al.*, *Geochim. Cosmochim. Acta* **64**, 3073 (2000).
15. G. I. Smith, *U.S. Geol. Surv. Prof. Pap.* **1043**, 143 (1979).
16. A. R. Felmy, J. H. Weare, *Geochim. Cosmochim. Acta* **50**, 2771 (1986).
17. Materials and methods are available as supporting material on *Science* Online.
18. S. E. Hoeft, T. R. Kulp, J. F. Stolz, J. T. Hollibaugh, R. S. Oremland, *Appl. Environ. Microbiol.* **70**, 2741 (2004).
19. J. T. Hollibaugh *et al.*, *Geochim. Cosmochim. Acta* **69**, 1925 (2005).
20. T. R. Kulp, unpublished data.
21. R. S. Oremland, L. G. Miller, M. J. Whiticar, *Geochim. Cosmochim. Acta* **51**, 2915 (1987).
22. S. E. Hoeft, F. Lucas, J. T. Hollibaugh, R. S. Oremland, *Geomicrobiol. J.* **19**, 1 (2002).
23. R. S. Oremland, S. E. Hoeft, N. Bano, R. A. Hollibaugh, J. T. Hollibaugh, *Appl. Environ. Microbiol.* **68**, 4795 (2002).
24. A. E. Liu, E. Garcia-Dominguez, E. D. Rhine, L. Y. Young, *FEMS Microbiol. Ecol* **48**, 323 (2004).
25. J. Switzer Blum, A. Burns Bindi, J. Buzzelli, J. F. Stolz, R. S. Oremland, *Arch. Microbiol.* **171**, 19 (1998).
26. P. W. J. J. van der Wielen *et al.*, *Science* **307**, 121 (2005).
27. R. S. Oremland, J. F. Stolz, *Trends Microbiol.* **13**, 45 (2005).
28. J. Felsenstein, *Annu. Rev. Genet.* **22**, 521 (1988).

29. We are grateful to D. Hamel, J. Fairchild, C. Hartwig (Searles Valley Minerals Corp., Trona, CA) and to M. Phillips for assistance with access, sampling, and logistics at Searles Lake. We thank H. Dalton, C. Murrell, A. Oren, R. Tabita, and M. Levandowski for constructive criticism of an earlier draft of this manuscript, and H. Cook for initiating our interest in Searles Lake. This work was supported by the U.S. Geological Survey National Research Program and by a grant from NASA's Exobiology Research Program. The GenBank accession number for strain SLAS-1 is AY965613.

Supporting Online Material

www.sciencemag.org/cgi/content/full/308/5726/1305/DC1
SOM Text
Materials and Methods
References

8 February 2005; accepted 22 March 2005
10.1126/science.1110832

Physical Limits and Design Principles for Plant and Fungal Movements

Jan M. Skotheim[1,2] and L. Mahadevan[2,3]*

The typical scales for plant and fungal movements vary over many orders of magnitude in time and length, but they are ultimately based on hydraulics and mechanics. We show that quantification of the length and time scales involved in plant and fungal motions leads to a natural classification, whose physical basis can be understood through an analysis of the mechanics of water transport through an elastic tissue. Our study also suggests a design principle for nonmuscular hydraulically actuated structures: Rapid actuation requires either small size or the enhancement of motion on large scales via elastic instabilities.

From the twirling circumnutation of growing tendrils to the opening and closing of stomata to the growth of fungal hyphae (*1*), plants and fungi are moving all of the time, often too slowly to notice. Rapid movements, though rarer, are used by many plants in essential functions such as seed or sporangium dispersal (Dwarf mistletoe, *Hura crepitans*, and the fungus *Pilobulus*); pollen emplacement (*Catasetum* orchids and *Stylidium* triggerplants); defense (*Mimosa*); and nutrition (Venus flytrap, carnivorous fungi). The mechanisms involved in these movements are varied: *Hura crepitans* (*2*) uses explosive fractures to disperse seeds at speeds as great as 70 m/s, the Venus flytrap (*3*) uses an elastic buckling instability to catch insects in 0.1 s, and the noose-like carnivorous fungus *Dactylaria brochophaga* (*4*) traps nematodes in less than 0.1 s by swelling rapidly.

The diversity of these nonmuscular hydraulic movements, often referred to as nastic movements, raises two related questions: Is there a physical basis for their classification? What, if any, are the principles underlying the biological designs for rapid movements in plants and fungi? To address these, we note that plants and fungi have a common feature that allows us to consider them together here: a cell wall that allows their cells to sustain a large internal (turgor) pressure of up to 10 atmospheres that can be harnessed for growth and motion. Indeed, movements are eventually driven by differential turgor, which may be regulated actively [e.g., by osmotic control as in stomata (*5*)] or passively [e.g., by differential drying as in *Hura crepitans* (*2*)]. In either case, the speed is limited by the rate of fluid transport. Thus, a biophysical charac-

[1]Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences, University of Cambridge, Cambridge CB3 0WA, UK. [2]Division of Engineering and Applied Sciences, Harvard University, Pierce Hall, 29 Oxford Street, Cambridge, MA 02138, USA. [3]Department of Organismic and Evolutionary Biology, Harvard University Biological Laboratories, 16 Divinity Avenue, Cambridge, MA 02138, USA.

*To whom correspondence should be addressed. E-mail: lm@deas.harvard.edu.