

well, and there is controversial evidence from the martian meteorite ALH84001 that supports this view (23). But there are possible abiotic sources for CH₄, too, on both Mars and early Earth. The one that was probably most important is that identified by Sagan and Chyba, namely, submarine outgassing at mid-ocean ridges. Submarine volcanism favors CH₄ over CO₂ by shifting the chemical equilibrium to the right in the reaction $\text{CO}_2 + 2\text{H}_2\text{O} \leftrightarrow \text{CH}_4 + 2\text{O}_2$. Today, the CH₄/CO₂ ratio in hydrothermal vent fluids is only ~1% (24), but it could have been much higher in the past if the primitive mantle were more reduced. Evidence for a reduced early mantle is provided by thermodynamic analyses of diamond inclusions (25) and by recent studies of metal-silicate partition coefficients of siderophile elements (26), which indicate that the upper mantle could originally have been in equilibrium with metallic iron. Applying these same arguments to early Mars is speculative but not outside the realm of possibility.

I note, parenthetically, that maintaining $f(\text{CH}_4) = 0.01$ in the primitive martian atmosphere would require a CH₄ source comparable to that on modern Earth, which would almost certainly have to be biological. It would also require that hydrogen be bottled up at the exobase so that it escaped at less than the diffusion-limited rate (18). This latter constraint seems physically plausible in light of the cold temperatures expected in a CO₂-rich upper atmosphere, but it has not been demonstrated that the escape of H would have been slow. So, it is far from obvious that high CH₄ concentrations are the solution to the early Mars climate problem. It does seem likely that Sagan and Chyba are on the right track, however: Reduced gases probably were present in significant concentrations on both early Earth and Mars, and they played an important role in climate evolution on both planets. Sagan himself had been fond of this idea for many years. It seems likely that his excellent scientific intuition will once again be found to be correct.

References

1. C. Sagan and C. Chyba, *Science* **276**, 1217 (1997).
2. T. Owen, R. D. Cess, V. Ramanathan, *Nature* **277**, 640 (1979); J. C. G. Walker, P. B. Hays, J. F. Kasting, *J. Geophys. Res.* **86**, 9776 (1981).
3. R. Rye, P. H. Kuo, H. D. Holl, *Nature* **378**, 603 (1995).
4. J. F. Kasting, *Icarus* **94**, 1 (1991).
5. R. T. Pierrehumbert and C. Erlick, in preparation.
6. C. Sagan and G. Mullen, *Science* **177**, 52 (1972).
7. W. R. Kuhn and S. K. Atreya, *Icarus* **37**, 207 (1979).
8. J. F. Kasting, *J. Geophys. Res.* **87**, 3091 (1982).
9. B. N. Khare, C. Sagan, J. E. Zumberge, D. S. Sklarew, B. Nagy, *Icarus* **48**, 290 (1981).
10. H. D. Holland, *The Chemical Evolution of the Atmosphere and Oceans* (Princeton Univ. Press, Princeton, NJ, 1984).
11. K. J. Zahnle, private communication.
12. J. F. Kasting, *Origins Life* **20**, 199 (1990).
13. J. L. Bada, C. Bigham, S. L. Miller, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 1248 (1994).
14. J. W. Schopf, *Earth's Earliest Biosphere: Its Origin and Evolution* (Princeton Univ. Press, Princeton, NJ, 1983).
15. L. Brown, thesis, Pennsylvania State University, in preparation.
16. Y. L. Yung, M. Allen, J. P. Pinto, *Astrophys. J. Suppl. Ser.* **55**, 465 (1984); C. P. McKay, J. B. Pollack, R. Courtin, *Icarus* **80**, 23 (1989).
17. J. T. Kiehl and R. E. Dickinson, *J. Geophys. Res.* **92**, 2991 (1987).
18. J. C. G. Walker, *Evolution of the Atmosphere* (Macmillan, New York, 1977).
19. J. F. Kasting, K. J. Zahnle, J. C. G. Walker, *Pre-cambrian Res.* **20**, 121 (1983).
20. U. Fink, D. C. Benner, K. A. Dick, *J. Quant. Spectrosc. Radiat. Transfer* **18**, 447 (1977); L. P. Giver, *ibid.* **19**, 311 (1978).
21. J. B. Pollack et al., *Icarus* **65**, 442 (1986).
22. J. B. Pollack, J. F. Kasting, S. M. Richardson, K. Pollakoff, *ibid.* **71**, 203 (1987); M. H. Carr, *J. Geophys. Res.* **100**, 7479 (1995).
23. D. S. McKay et al., *Science* **273**, 924 (1996).
24. J. A. Welhan, *Chem. Geol.* **71**, 183 (1988).
25. J. F. Kasting, D. H. Egger, S. P. Raeburn, *J. Geol.* **101**, 245 (1993).
26. M. J. Walter and Y. Thibault, *Science* **270**, 1186 (1995); K. Richter and M. J. Drake, *Earth Planet. Sci. Lett.* **146**, 541 (1997).

UPDATE: CELL BIOLOGY

Sticky Endings: Separating Telomeres

R. Scott Hawley

The ends of eukaryotic chromosomes are capped by telomeres, which facilitate the replication of the ends of the DNA molecule. The telomeres of both homologous and nonhomologous chromosomes can easily self-associate, perhaps as a simple consequence of their structure—repeated arrays of a sequence at the ends of all of an organism's chromosomes. Indeed, the clustering of telomeres at one point in the nucleus, creating a so-called "bouquet" of chromosomes, has been noted in a variety of organisms (1). As discussed in a recent Perspective (2), these associations are sufficiently strong that the separation of telomeres presents a special problem for the meiotic and mitotic segregational systems.

Evidence that cis- and trans-acting functions are required for the separation of telomeres at cell division has been recently obtained in *Tetrahymena* and *Drosophila* (3,4). In this issue (page 1252), Conrad et al. (5) report a gene (*NDJ1*) that encodes a telomere-associated protein required for meiotic chromosome segregation in a third organism, the yeast *Saccharomyces cerevisiae*. This protein accumulates at the telomeres of chromosomes during meiotic prophase, and its absence results in high levels of failed meiotic chromosome segregation (meiotic nondisjunction). The failure of homolog separation at meiosis is observed whether or not the homologs have undergone genetic recombination. However, there is no effect of the absence of the Ndj1 protein on the segregation of telomere-less ring chromosomes, arguing that Ndj1 protein is not required for meiotic chromosome separation per se, but

rather that the Ndj1 protein is essential to separate segregational partners that have telomeres.

The Ndj1 protein is also required for the completion of homologous synapsis. Loss of the Ndj1 protein delays the formation of the axial elements of the synaptonemal complex, a structure that connects homologous meiotic chromosomes along their length, without affecting recombination. The mechanism by which the Ndj1 protein facilitates synapsis remains unclear, but the normal clustering of telomeres into a bouquet may create three-dimensional chromosome arrangements, such as interlocked bivalents, that would impede proper synapsis. An inability to dissolve telomere-telomere interactions, especially those between nonhomologous telomeres, might prevent the chromosomal movements required to resolve those problems and facilitate homologous alignments. Such a model nicely explains both the effects of Ndj1 deficiency on synapsis and segregation, and the rather curious lack of effect of this deficiency on ring chromosomes.

Thus, even as cells have used telomeres to neatly solve the problem of replicating chromosomal ends, they have introduced difficulties for chromosomal movement because of the inherent stickiness of telomeres. Perhaps not surprisingly, cells have evolved ways to cope.

References

1. A. F. Dernburg et al., in *Telomeres*, E. H. Blackburn and C. W. Greider, Eds. (Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 1996), pp. 295–338.
2. R. S. Hawley, *Science* **275**, 1441 (1997).
3. K. E. Kirk et al., *ibid.*, p. 1478.
4. G. Cenci et al., *Genes Dev.* **11**, 863 (1997).
5. M. N. Conrad et al., *Science* **276**, 1252 (1997).

The author is in the Department of Genetics, Section of Molecular and Cellular Biology, University of California at Davis, Davis, CA 95616, USA. E-mail: shawley@netcom.com