substrates for the cell's DNA repair machinery (*11*).

An evolutionarily related protein with a very similar function, Taz1, has been identified in fission yeast (see the figure) (*12*). TRF2 and Taz1 have no sequence similarity to TEBP α or β, and no TRF2/Taz1 ortholog has been found in the budding yeast genome. Indeed, unlike Cdc13p and TEBP, TRF2 has no affinity for single-stranded DNA and binds to the double-stranded region of telomeres. How could such a protein protect the telomere terminus? It turns out that TRF2 can remodel telomeric DNA into a duplex lariat structure called the t loop (see the figure) (*13*). T loops are formed by the single-stranded telomeric overhang invading the double-stranded region of the telomere. These t loops are found at high frequency in the telomeres of mammals and protozoa. Obviously, invasion of the duplex telomeric tract by the 3′ overhang provides an efficient way to protect chromosome ends. The cell cycle arrest of cells in which TRF2 is inhibited could result from inappropriate unfolding of the t loops.

Such diverse solutions to a common problem create the unsettling feeling that some critical feature, common to all three strategies, has somehow escaped notice. Baumann and Cech now provide evidence for a common theme in telomere protection among ciliates, yeast, and mammalian cells. Their findings indicate that all eukaryotes use a single-stranded DNA binding protein to cap the telomere. Apart from telomere synthesis by telomerase, this may be the first truly conserved aspect of eukaryotic telomeres. Taking advantage of the complete fission yeast genome, the authors found a distant ortholog of TEBPα. Deletion of this gene resulted in complete loss of telomeric DNA and reduced growth of the fission yeast. They called the gene encoding this capping factor *pot1*$^{+}$ (protection of telomeres). Fission yeast have the unique ability to live without telomeres altogether by circularizing each of their three chromosomes, and this is what happens in a *pot1*$^{-}$ strain. In vitro, Pot1 protein binds specifically to the single-stranded G-rich telomeric overhang of fission yeast; biochemical analysis suggests that this capping factor might bind along the length of the single-stranded DNA tail of the telomere, as well as at its end.

Using human sequence databases, Baumann and Cech identified a human ortholog of Pot1 and found that, like its fission yeast counterpart, this protein binds specifically to the G-rich DNA overhang of human telomeres in vitro. Mammalian telomeres end in a very long 3′ overhang (up to 300 nucleotides), so that multiple copies of Pot1 may have to bind along the single-stranded tail. In addition, Pot1 could bind to the G-rich telomeric DNA in the D loop and stabilize the t loop configuration (see the figure).

The new work suggests that protecting chromosome ends with a single-stranded DNA binding protein may well be a universal principle. It is even possible that TEBPα, Pot1, and Cdc13p are all evolutionarily related. The structure of the TEBPα protein reveals the presence of three OB-folds, a β-barrel oligonucleotide/oligosaccharide binding motif present in a wide variety of nucleic acid binding proteins (for example, RPA subunits, gene V SSB, and S1 nuclease) (*5*). Pot1 has sequence similarity to TEBPα in a region that partially overlaps the first OB-fold. However, OB-folds cannot be predicted on the basis of the amino acid sequence of the protein, so that it is not possible to determine whether Pot1 or indeed Cdc13p contain the same motifs. We eagerly await the three-dimensional structures of both Pot1 and Cdc13p.

We still need to know whether human Pot1, like its fission yeast counterpart, actually binds and protects telomeres. Another question requiring urgent attention is whether fission yeast telomeres form t loops and whether such t loops predominate or alternate with an unfolded Pot1-capped state. Finally, it will be important to learn more about the possible activities of Pot1. Cdc13p not only caps telomeres but also recruits telomerase to the ends of chromosomes (*14*); perhaps Pot1 engages in this dual task. Now that a common theme has emerged, it is comforting that the otherwise divergent solutions to the telomere-capping problem are neither loopy nor potty.

**References and Notes**

1. F. Ishikawa, T. Naito, *Mutat. Res.* **434**, 99 (1999).
2. M. J. McEachern, A. Krauskopf, E. H. Blackburn, *Annu. Rev. Genet.* **34**, 331 (2000).
3. P. Baumann and T. R. Cech, *Science* **292**, 1171 (2001)
4. D. E. Gottschling, T. R. Cech, *Cell* **38**, 501 (1984); D. E. Gottschling, V. A. Zakian, *Cell* **47**, 195 (1986).
5. M. P. Horvath, V. L. Schweiker, J. M. Bevilacqua, J. A. Ruggles, S. C. Schultz, *Cell* **95**, 963 (1998).
6. B. Garvik, M. Carson, L. Hartwell, *Mol. Cell. Biol.* **15**, 6128 (1995).
7. J. J. Lin, V. A. Zakian, *Proc. Natl. Acad. Sci. U.S.A.* **93**, 13760 (1996); C. I. Nugent, T. R. Hughes, N. F. Lue, V. Lundblad, *Science* **274**, 249 (1996).
8. E. Pennock, K. Buckley, V. Lundblad, *Cell* **104**, 387 (2001).
9. N. Grandin, C. Damon, M. Charbonneau, *EMBO J.* **20**, 1173 (2001).
10. J. Karlseder, D. Broccoli, Y. Dai, S. Hardy, T. de Lange, *Science* **283**, 1321 (1999).
11. B. van Steensel, A. Smogorzewska, T. de Lange, *Cell* **92**, 401 (1998).
12. M. Godhino Ferreira, J. Promisel Cooper, *Mol. Cell* **7**, 55 (2001).
13. J. D. Griffith *et al.*, *Cell* **97**, 503 (1999).
14. S. K. Evans, V. Lundblad, *Science* **286**, 117 (1999).
15. I thank J. Petrini, V. Lundblad, and members of my laboratory for helpful comments.

PERSPECTIVES: GEOPHYSICS

# Oceanic Crust When Earth Was Young

**Jeffrey A. Karson**

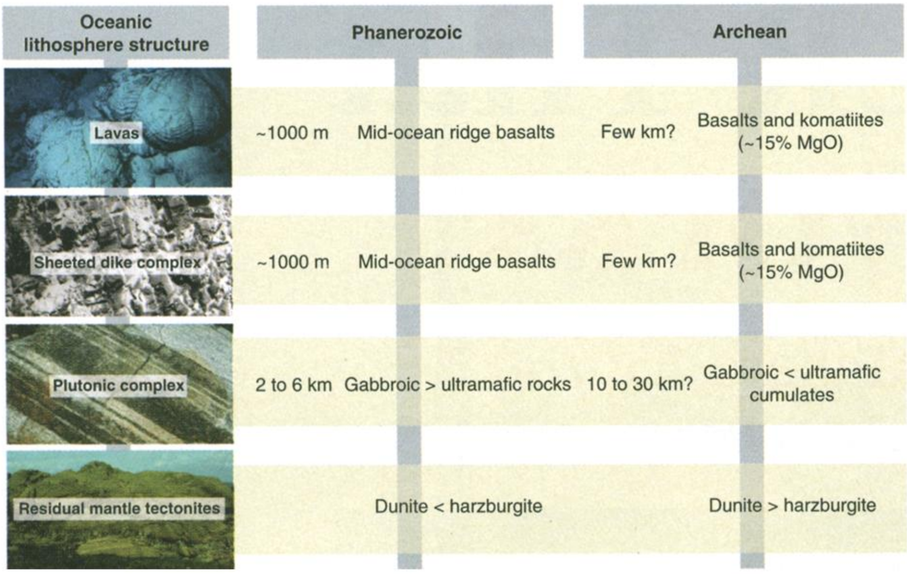
Oceanic lithosphere makes up about two-thirds of Earth's outer rigid shell and has probably done so since early in Earth's history (*1–4*). New oceanic crust and mantle are created by sea-floor spreading, which is controlled by thermally sensitive processes such as partial melting of the mantle, melt segregation and transport, and crustal magmatic construction. It has therefore been suggested that during the Archean (more than 2500 million years ago), when Earth's mantle may have been as much as three times hotter than today, a somewhat different oceanic crust should have been generated (*3–5*).

This hypothesis can be tested directly with surviving samples of Archean oceanic lithosphere. Oceanic lithosphere is usually "recycled" back into the mantle through subduction, but a few fragments of ancient oceanic lithosphere ("ophiolite complexes") survive in collisional mountain belts (*6*). The discovery of a ~2500-million-year-old ophiolite complex, reported by Kusky *et al.* on page 1142 of this issue (*7*), represents an important new chapter in this continuing line of inquiry.

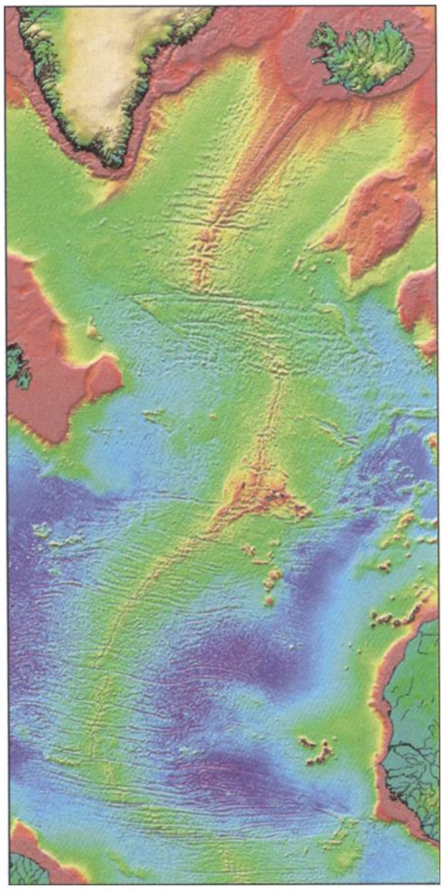
There are two very good reasons why this area is steeped in controversy. First, we do not know all that much about contemporary oceanic crust and how it varies from one tectonic and magmatic setting to the next. Second, whether we recognize Archean ophiolites depends on what we are looking for, and this in turn depends on which of the various models we use to describe plate tectonics on early Earth.

Over the past few decades, studies of Phanerozoic (544 million years ago to present) ophiolite complexes and of contem-

The author is with the Division of Earth and Ocean Sciences, Duke University, Durham, NC 27708, USA. E-mail: jkarson@duke.edu




**Deciphering the past.** Comparison of key differences between Phanerozoic and Archean oceanic crust and ophiolites based on highly generalized results of geological, geophysical, and geochemical studies of oceanic crust and ophiolites (*6, 8–11*) and anticipated characteristics of Archean oceanic crust generated by enhanced mantle melting and crustal construction (*2, 5*) at spreading rates on average three times greater than present. Ophiolites are distinctive layered assemblages of rocks (*14*) formed by magmatic construction in various extensional tectonic settings. They include submarine lavas, sheeted dike complexes, and plutonic complexes overlying upper mantle material. Plutonic complexes are rock bodies that crystallized from magma deep in the crust.



**Shaded bathymetric map of the northern Mid-Atlantic Ridge.** Elevated mantle temperatures have resulted in increased magmatic production and creation of a 25-km-thick oceanic crust near the Iceland hot spot. Thick oceanic crust similar to this may have formed extensively at Archean mid-ocean ridge spreading centers when Earth's mantle was hotter than today.

porary oceanic crust have demonstrated that tectonic extension and magmatism can produce very similar crustal structures in a wide range of settings—not just mid-ocean ridge spreading centers (*8–10*). Many ophiolite complexes appear to have formed above subduction zones or as ocean islands. Their origin is obscured by non–setting-specific geochemical characteristics, tectonic transport from their point of formation, and postformation damage.

It was long thought that spreading rate and spreading center morphology were the key factors governing oceanic crustal structure, but it has become clear that the regional magma budget is also important (*10*). For example, despite its slow spreading rate (less than 20 mm per year), Iceland has a ~25-km-thick magmatic crust (*9*, *11*), whereas in other, colder parts of the Mid-Atlantic Ridge (see the map) and other slow-spreading ridges, there is little or no magmatic crust (*10*). In these magma-starved areas, intense faulting shuffles the expected ophiolite sequence. In contrast, fast-spreading ridges appear to generate a more uniform, generally thicker crust (*9*).

The bottom line is that today, the products of mid-ocean ridge spreading centers are very diverse and reflect a wide range of setting-specific characteristics. Similar crust formed, for example, in a subduction zone is likely to be even more varied. There is no reason to think that things were simpler in the Archean.

Additional uncertainties are likely to arise from spreading conditions specific to the Archean, when convective heat loss through enhanced sea-floor spreading was large (*1–5*). This could have been accomplished either by globally elevated spreading rates or by a greater overall ridge length. Furthermore, the hotter mantle may have generated more melt, promoted by rapid mantle ascent and enhanced melting. An increase in mantle temperature by some 200°C, possible for the Archean, is likely to result in a much greater volume of melt coming to the surface (*11*, *12*). In addition, at modern spreading centers, thicker, more uniform magmatic crust is generated by faster spreading, compared with the sputtering magma supply of most slow-spreading ridges. The 25-km-thick crust of Iceland illustrates the huge increase in magmatic thickness that can result from heating of the mantle (by about 200°C) beneath the Mid-Atlantic Ridge (see the figure), in this case by a mantle plume heat source (*11*). The higher temperatures would also promote the generation of more Mg-rich magmatic material and more melt-depleted upper mantle residue (see the table). In contrast, contemporary fast-spreading oceanic crust is only about 5 to 7 km thick, and its magmatic material has a lower Mg content (see the table). Although Iceland has been suggested as a modern analog for Archean oceanic crust (*5*), it is not clear what sort of crustal structure might result from the combination of very robust magmatism and very fast spreading.

Given the diversity of contemporary oceanic crust and the limited knowledge of Archean tectonics, it is likely that Archean ophiolites created at mid-ocean ridge spreading centers may be difficult to recognize. Many Archean-age ophiolite-like assemblages have been interpreted as oceanic crust formed at mid-ocean ridge spreading centers, but their geological and geochemical characteristics have proven problematic or at best ambiguous (*5*). The newly discovered Dongwanzi ophiolite complex (*7*) appears to be the best candidate for Archean oceanic crust to date. It includes all of the major rock units found in typical Phanerozioc ophiolites (*6*) and is not so dismembered or metamorphosed that it cannot be reconstructed as a complete section through Archean oceanic crust. It thus provides at least a starting point for testing some of the ideas outlined

CREDIT: SEAFLOOR MAP, W. H. F. SMITH AND D. T. SANDWELL

above. One exciting possibility is that Archean ophiolites may hold clues to the nature of an early subsurface biosphere at ancient mid-ocean ridges, at the time of the earliest known life on Earth (*13*).


**References and Notes**

1. K. Burke, W. S. F. Kidd, *Nature* **272**, 240 (1978).
2. N. H. Sleep, B. F. Windley, *J. Geol.* **90**, 363 (1982).
3. D. H. Abbot, S. E. Hoffman, *Tectonics* **3**, 429 (1984).
4. M. J. Bickle, *Earth Planet. Sci. Lett.* **80**, 314 (1986).
5. M. J. Bickle, E. G. Nisbet, A. Martin, *J. Geol.* **102**, 121 (1994).
6. Anonymous, *Geotimes* **17**, 24 (1972).
7. T. M. Kusky, J.-H. Li, R. D. Tucker, *Science* **292**, 1142 (2001).
8. E. M. Moores, *Rev. Geophys. Space Phys.* **20**, 735 (1982).
9. C. Z. Mutter, J. C. Mutter, *Earth Planet. Sci. Lett.* **117**, 295 (1993).
10. J. A. Karson, in *Faulting and Magmatism at Mid-Ocean Ridges*, W. R. Buck, P. T. Delaney, J. A. Karson, Y. Lagabrielle, Eds. (American Geophysical Union, Washington, DC, 1998), pp. 177–218.
11. R. S. White, D. P. McKenzie, R. K. O'Nions, *J. Geophys. Res.* **97**, 19683 (1992).
12. D. P. McKenzie, M. J. Bickle, *J. Petrol.* **29**, 625 (1988).
13. J. W. Schopf, *Earth's Earliest Biosphere: Its Origin and Evolution* (Princeton Univ. Press, Princeton, NJ, 1983).
14. Lavas: Basaltic pillow lavas, Mid-Atlantic Ridge, about 3 m wide; photo taken from submersible Alvin. Sheeted dike complex: exposed on a steep cliff, Hess Deep Rift, eastern Pacific Ocean, about 6 m wide; mosaic of digital images from Argo II ROV, about 6 m wide. Plutonic complex: interlayered gabbroic and ultramafic plutonic rocks from the Smartville Ophiolite Complex, California, about 1 m across. Residual mantle tectonites: depleted upper mantle peridotite from Bay of Islands Ophiolite Complex, Canada, about 4 m across.


PERSPECTIVES: ASTRONOMY

# How to Find a Stellar Black Hole

**Joseph F. Dolan**

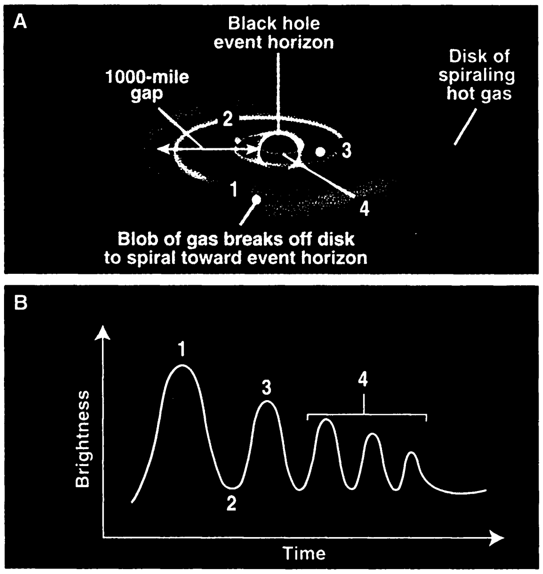
Black holes are now widely accepted as the cause of many phenomena in astrophysics, from supermassive black holes at the centers of galaxies to stellar-mass–sized black holes in x-ray binaries (*1*). Black holes are the simplest objects physics can think of to explain the behavior of these systems. There remains the theoretical possibility, however, that these objects may be more exotic than black holes. Recent observations have come tantalizingly close to ruling out more exotic objects in x-ray binaries, providing the best evidence yet that stellar-mass–sized black holes must exist.

In compact stars, the inward force of gravity acting on the star's outer layers is balanced by the pressure generated by the Pauli exclusion principle acting on its electrons (in white dwarfs) or nucleons (in neutron stars). The star is in equilibrium when its total energy, $E$ (the sum of the positive energy associated with the pressure generated by the Pauli exclusion principle and the negative gravitational energy), is at a minimum. Chandrasekhar first showed (*2*) that compact stars have a maximum mass, $M_{max}$, beyond which they are not stable. If the mass is more than about 1.5 times the mass of the sun, $M_{sun}$, then $E$ can be decreased without being bound by decreasing the star's radius and increasing its (negative) gravitational energy. No equilibrium radius exists, and general relativity predicts gravitational collapse to a point singularity—a black hole.

The black hole is not visible to the outside world, however. Schwarzschild found (*3*) that according to general relativity, no signal can reach the region of space-time outside the Schwarzschild radius

$$R(S) = 2GM/c^2 \sim 3\ M/M_{sun}\ \text{km} \qquad (1)$$

from the region inside, where $M$ is the mass of the black hole, $c$ is the speed of light, and $G$ is the gravitational constant. (The time coordinate also goes to zero at this distance.) The boundary between the two regions is called the event horizon. Every black hole will have an event horizon, so the naked point singularity is forever shielded from our view. But because any object with an event horizon must be a black hole, detection of such a horizon would prove the existence of a black hole.




**Dying pulse trains.** (**A**) A luminous clump of material detaching from the inner edge of the accretion disk spirals into the event horizon and disappears. (**B**) Photometric signature of the clump's emission.

Observations of Cyg XR-1 and other x-ray binary systems have shown that the x-ray source is a compact object with a minimum mass above $M_{max}$; for example, $M > 6\ M_{sun}$ for Cyg XR-1 (*4*). This ruled out a white dwarf or neutron star but still allowed more unusual objects, such as a Q star (*5*). Two recent studies now report what are likely to be signatures of an event horizon, and thus of a black hole, in such x-ray binary systems.

Garcia *et al.* (*6*) used the Chandra satellite to monitor the x-ray luminosity of six candidate black-hole transients in quiescence. (Transient x-ray sources exhibit episodes of outburst lasting several weeks separated by long periods of extremely low luminosity, a behavior connected to episodic mass transfer from a companion star.) Quiescent black-hole transients were 1/100th as luminous in x-rays as quiescent neutron-star transients with similar orbital periods. The authors attribute the effect to the fact that most of the radiation generated locally in the quiescent accretion disk disappears across the event horizon of the black hole.

This method for detecting an event horizon requires knowledge of the local luminosity that the system produces in the accretion disk. Garcia *et al.* use an advection-dominated accretion flow (ADAF) model of the disk to calculate its local luminosity. It has been suggested (*7*) that adiabatic inflow-outflow solutions (ADIOS) may instead be operating in transients during quiescence. In this case, most of the energy generated by accretion would be carried away from the central object by mass outflow above and below the plane of the disk. The low luminosity observed would not be directly related to the existence of an event horizon, or possibly even a black hole. Theoretical work still needs to be done on the nature of the accretion in black-hole transients (*8*).

Another approach to detecting the event horizon of a black hole was proposed by Stoeger in 1980 (*9*). He proposed that individual flare patches—

The author is in the Laboratory for Astronomy and Solar Physics, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA. E-mail: tejfd@stars.gsfc.nasa.gov