Carol Widney Greider (1961-) [1]

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Carol Widney Greider studied telomeres and telomerase in the US at the turn of the twenty-first century. She worked primarily at the University of California, Berkeley in Berkeley, California. She received the Nobel Prize in Physiology or Medicine[3] in 2009, along with Elizabeth Blackburn and Jack Szostak, for their research on telomeres and telomerase. Telomeres are repetitive sequences of DNA at the ends of chromosomes that protect chromosomes from tangling, and they provide some protection from mutations. Greider also studied telomerase, an enzyme that repairs telomeres. Without telomeres, chromosomes are subject to mutations that can lead to cell death, and without telomerase, cells might not reproduce fast enough during embryonic development. Greider's research on telomeres helped scientists explain how chromosomes function within cells.

Carol Greider was born 15 April 1961 in San Diego, California, to Jean Foley Greider and Kenneth Greider. Greider also had a brother named Mark, one year older than she. Greider's parents both received their PhDs from the University of California, Berkeley, her mother in botany, and her father in physics. During the early 1960s, the Greider family moved often as Greider's parents accepted different academic teaching positions. In 1965, the family moved to Davis, California. In 1967, when Greider was in first grade, her mother died. Greider later reported that her mother's death played a role in learning how to take responsibility to do things on her own. In her statement for the Nobel Prize, Greider also notes that the death of her mother contributed to difficulties Greider had in school, especially after learning she had dyslexia.

In 1971, Greider's father took a sabbatical from his position at the University of California, Davis, and moved to Heidelberg, Germany, with the family. As Greider states in her Nobel Prize biography, the foreign environment enabled her to make new friends and to recognize and enjoy differences between people. In 1972, the family left Germany and returned to Davis, where Greider attended junior high schools. Greider reported discovering an aptitude for biology in her junior year of high school. In 1979, she started an undergraduate program to study marine ecology at the University of California, Santa Barbara in Santa Barbara, California.

In 1982, Greider participated in a study abroad program at the University of GÖttingen, in GÖttingen, Germany, where she worked at the Max Planck Institute for Biophysical Chemistry. During her second semester, Greider attended a course on chromosomes taught by Ulrich Grossbach. Greider later said that she was entranced by the work being done on chromosomes in *Chironomus* [4] flies. She finished her work on microtubules and switched to chromosomal work with Grossbac and others. Greider returned to Santa Barbara for her senior year, and she received her undergraduate degree in Biology in 1983.

Greider then applied to graduate schools, and the University of California, Berkeley accepted her as a graduate student in molecular biology. Greider met Elizabeth Blackburn, a faculty member in the Department of Molecular Biology. After hearing about Blackburn's work on telomeres Greider planned to work with Blackburn.

As a first-year graduate student, Greider worked in different labs and did not immediately work with Blackburn. She first worked with Richard Calendar, who studied the interactions between bacteriophages, or viruses that infect bacteria, to learn more about the properties of DNA. Next, Greider worked with Blackburn. Greider cloned telomeres to try to determine why those chromosomal ends did not shorten when the cell replicated. Her work was based on research conducted by Blackburn and Jack Szostak, who in 1982 were the first to identify telomeres in *Tetrahymena* [5], a ciliated single-celled protozoan. For that research, Szostak worked at Harvard Medical School [6] in Boston, Massachusetts. In 1984, Greider joined Blackburn's lab to work on a telomere [7] elongation project. Greider began work on making extracts of the enzymes from *Tetrahymena*, the same organism that Blackburn and Szostak had used to identify telomeres. Greider made extracts of the enzymes from the cells in *Tetrahymena* to identify the enzyme responsible for telomere [7] elongation.

At the end of December 1984, Greider and Blackburn identified telomere [7] terminal transferase as the enzyme that replicated telomeres in *Tetrahymena*, and in 1985 they published their results. Shortly after publishing their article, Greider and Blackburn shortened the name of the enzyme to telomerase, after Greider received feedback from a fellow student that the name was too long. In 1987, Greider and Blackburn began studying how genes [8] produce the telomerase enzyme. After conducting experiments, Greider and Blackburn found that telomerase contains an RNA component, which is a template that enables telomerase to repair telomeres on chromosomes. Repaired telomeres enable organisms to replicate cells without potentially harmful mutations or without apoptosis [9]. Greider and Blackburn published their results in 1987, the same year that Greider received her PhD in molecular biology.

In 1987, Greider was hired as an independent researcher at Cold Spring Harbor Laboratory (CSHL) in Cold Spring Harbor, New York by CSHL president Bruce Stillman. Greider studied the sequence of nucleotides that comprise telomerase RNA, and she cloned and isolated the RNA sequence of telomerase. She published her results in 1989. Then the CSHL hired her as a faculty member. She continued to research telomeres and telomerase activity in cells and their roles in the cell cycle through the late

1980s and early 1990s.

While at CSHL, Greider met Nathaniel C. Comfort, a historian of biology, who was working in the public affairs office at CSHL. The two married in 1993. In 1996, when Greider was pregnant with their son she suggested that CSHL should have a childcare facility. Officials of the laboratory agreed to her request, and Greider participated in the ground breaking of the facility while pregnant. Once her son Charles was born, Greider enrolled him in the childcare facility, and she often brought him to meetings and to her office. She also encouraged other women with children at CSHL to do the same.

In 1997, Greider was offered a faculty position at Johns Hopkins University in Baltimore, Maryland. Her husband was concurrently offered a faculty position in George Washington University [10], in Washington, D.C. Greider and Comfort accepted their positions and the family moved to Baltimore, Maryland. At Johns Hopkins, while working with mice and yeast, Greider studied how cells function without telomerase. Greider and Comfort's second child was born in Baltimore in 1999. According to Greider, her job as a mother came before her work in the laboratory and the flexible work environment of her lab helped ensure that priority. In 2003, she became director of molecular biology and genetics, where she continued to work as of 2014.

Greider received numerous awards, including the Albert Lasker Award for Basic Medical Research in 2006, and the Nobel Prize in Physiology or Medicine, which she received in 2009 along with Blackburn and Szostak. Greider received the awards in recognition for her accomplishments in telomere [7] and telomerase research. She and Comfort divorced around the same time she received the Nobel Prize.

As of 2014, Greider was the youngest woman to receive the Nobel Prize in Physiology or Medicine, at the age of forty-eight. Some also recognize Greider as a leading woman scientist at a time when there were relatively few. Into the first decades of the twenty-first century, Greider researched telomeres in relation to cellular death, regenerative disease, DNA stability, and the relationship between stem cells [11] and telomerase.

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