

A Tribute to Elizabeth D. Hay, 1927–2007

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Dr. Elizabeth Dexter Hay, born in St. Augustine, Florida, on April 2, 1927, died of cancer on August 20, 2007. Betty left behind a rich legacy, not only as a superb cell and developmental biologist, but also as an educator and beloved mentor. She was a remarkable woman.

Betty attended Smith College in 1944, and met biology professor Meryl Rose, who became her scientific mentor. In Rose's laboratory, Betty studied limb regeneration, and became so immersed in the work, that she completed substantial research while handling her college course load. Also, each summer she worked in Rose's lab in Woods Hole, Massachusetts. She graduated *summa cum laude* from Smith College in 1948 and thought of going to graduate school. Rose talked her into applying to medical school instead, because he understood that her career choices might be restricted to teaching in a women's college biology department if she had only a Ph.D. degree. Therefore, Betty applied to Johns Hopkins University Medical School and was accepted. (She considered applying to Harvard Medical School, but decided against it when she found they had no women's rest rooms.) While in her first year of medical school, her interest in regeneration, anatomy, and histology caught the eye of the department chair, Dr. Allan Grafflin, who found Betty a spot in a lab to pursue her regeneration studies. She also continued to go to Woods Hole each summer to do further work with Rose. In 1952, she was



Fig. 1. Images of Elizabeth (Betty) Hay from her medical student days using the TEM at John's Hopkins University Medical School (upper left, from the Harvard Archives); as an Assistant Professor (upper center, photo from Jean Paul Revel); in her office as the Chair and Professor of the Department of Anatomy and Cellular Biology at Harvard (lower left, photo from Jean Paul Revel); the night she accepted the E.B. Wilson Medal from the American Society for Cell Biology in 1988 (lower center and right color photos by Mark Nathanson).

awarded her MD degree, being only one of four women in the class. She stayed on at Johns Hopkins for a year of internship, then, in 1953, was appointed as an instructor of Anatomy. The next year, she attended a meeting where Keith Porter showed electron micrographs of cytoplasmic structures. This caught her attention. Betty's words were, "I came back and,

wow, from then on it was electron microscopy for me" (taken from *Int J Dev Biol* 2004;48:687-694, article entitled "The extracellular matrix in development and regeneration: an interview with Elizabeth D. Hay" by Robert L Trelstad). She located the only electron microscope at Johns Hopkins in the School of Public Health, and began using it. By 1956, Betty was appointed

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Assistant Professor of Anatomy, and was using the electron microscope to study embryological processes, but was unhappy with the quality of her micrographs. She began traveling to Rockefeller Institute for Medical Research (now Rockefeller University) to see Keith Porter and George Palade for advice. Don Fawcett, who had been working with Porter and Palade, had just been appointed chairman of anatomy at Cornell University Medical College across the street from Rockefeller. Fawcett offered Betty an Assistant professorship which she accepted in 1957. By a fortunate set of circumstances, Don Fischman entered Cornell as a medical student that year. He had worked on amphibian limb regeneration with Charles Thornton as an undergraduate at Kenyon College, thus he immediately joined Betty's laboratory. They had a very productive collaboration tracing the origin of the cells in the regeneration blastema and they proved that the osteoclast formed by fusion of circulating monocytes. In 1960, Don Fawcett was appointed Hersey Professor of Anatomy at Harvard Medical School and recruited Betty for a faculty position. She always joined him there. She always credited Fawcett with inspiring and mentoring her as a scientist. At Harvard, she transitioned from the salamander to the embryonic chick cornea model system. In 1969, she was awarded the Louise Foote Pfeiffer Professorship of Embryology, and in 1975, when Fawcett

stepped down as Chair of the department of Anatomy and Cellular Biology, Betty assumed that position. She served in this capacity for 18 years. Her greatest scientific contribution—illuminating the role of extracellular matrix in regulating cell behavior—led to the birth of a new field of cell and developmental biology and numerous honors and awards. Among these were the Centennial Award and the Henry Gray Award from the American Association of Anatomists, the E.B. Wilson Medal from the American Society for Cell Biology, and the FASEB Excellence in Science Award. In 1984, she was elected to the National Academy of Sciences. In addition to her scientific accomplishments, she contributed service and leadership to several societies associated with her discipline, including presidencies of the American Association of Anatomists (1981-1982), the American Society for Cell Biology (1976-1977), and the Society for Developmental Biology (1973-1974). Later in her career, Betty became fascinated by epithelial-mesenchymal transitions during development, and published several papers in this area. She was an idea "generator." Stephen Sugrue once noted that Betty had a small, old, beat up book that she kept in her desk, where she put notes and bits of papers on her ideas. As people came to her lab for training, she would take out this notebook and assign them one of the many ideas. Betty retired in 2005 from the Cell Biology department at Harvard

Medical School, and the location of the idea notebook is unknown. Many of her progeny would delight in reviewing the ideas it contained.

In the introduction to the book she edited, "Cell Biology of the Extracellular Matrix (first edition 1981, second edition 1991), Betty states that, "Cytoskeleton, cell shape, cell migration, control of cell growth and differentiation, these are all subjects that, to be fully understood today, require a consideration of the extracellular matrix (ECM): its composition, role in development and relationship to the cell surface." This powerful idea, coupled with Betty's dedication and passion for science, her love of teaching and mentoring, are part of her profound legacy (Fig. 1). She may no longer be with us in a physical sense, but her scientific descendants, working on many areas related to cell-matrix interactions, are well into the third generation of researchers. To Betty we say, we are sad you are gone, but we are truly better for having known you.

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