

IN MEMORIAM

A life in pictures—Marilyn Gist Farquhar

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The world lost a pioneering cell biologist on November 23, 2019, with the passing of Marilyn Gist Farquhar, PhD, at age 91. With a career-long immersion in electron microscopy, it was befitting that Marilyn was still active as the director of the Electron Microscopy Core at the University of California San Diego at the time of her death. Her fascination with electron microscopy stemmed from the early times of this exacting art in the 1950s, initially leading her from a PhD in experimental pathology at UC Berkeley to the crucible of electron microscopy at the Rockefeller University, where she undertook postdoctoral work with George Palade. Drawn back to California in 1962, Marilyn started her own research laboratory at UC San Francisco, applying electron microscopic cytochemistry to study the secretory process in pituitary cells and leukocytes, but subsequently returned to the Rockefeller University in 1970 where she would be appointed as their first ever woman professor. In 1973, Farquhar and Palade, now married, moved to start a new section of cell biology at Yale University School of Medicine, where Marilyn became the Sterling Professor of Cell Biology and Pathology (Fig. 1).

A classic paper of 37 pages revealed and documented the morphology of complexes of adherens junctions and tight junctions. Published in *JCB* in 1963 by Marilyn Farquhar and George Palade (Farquhar and Palade, 1963), the work is emblematic of the meticulous and forensic dissection of cell fine structure and function that would follow over many years from the separate, and sometimes joint, research efforts of the Farquhar and Palade laboratories. In 1974, Palade shared the Nobel Prize in Physiology or Medicine. Up to and beyond his death in 2008, the life-long collection of George's electron micrographs remained one of Marilyn's most treasured possessions, documenting for her the journey of the scientist and partner she revered (Farquhar, 2012) and illustrating the cells that were their shared source of wonder.

At Yale, Marilyn's own research spanned her long-term interests, first the Golgi apparatus, which she studied early on by labeling resident cisternal enzymes and following membrane recycling and receptor trafficking (Fig. 2). She took a keen interest in the Golgi literature, reviewing it over the decades



Figure 1. **Marilyn Farquhar, in her element at Yale.** Photo courtesy of Yale University School of Medicine.

(Farquhar and Palade, 1981; Farquhar, 1985). A picture of the Golgi complex, painted by her mother, hung in her office for all to see. Her second main interest was in the architecture of the kidney, where she would reveal the structure and proteoglycans of the glomerular basement membrane and examine the "feet" of podocytes, describing their roles in glomerular filtration. Indeed, at Yale, her laboratory always had "Golgi people" and "kidney people," with Viennese pathologist Donscho Kerjaschki serving as a long-time colleague in the latter realm. Together with their co-workers, they identified the Heymann nephritis antigen as gp330 (Kerjaschki and Farquhar, 1982; now known as the endocytic receptor megalin) and they uncovered the podocyte sialomucin, podocalyxin (Kerjaschki et al., 1984). The 1980s at Yale was a heady time in cell biology and we were fortunate to serve as postdocs in Marilyn's laboratory during this period. We

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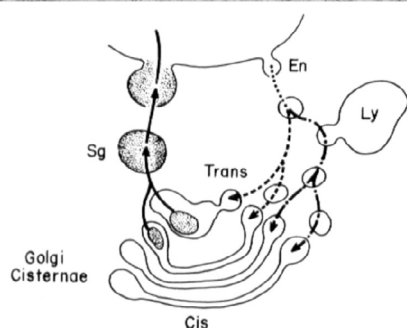
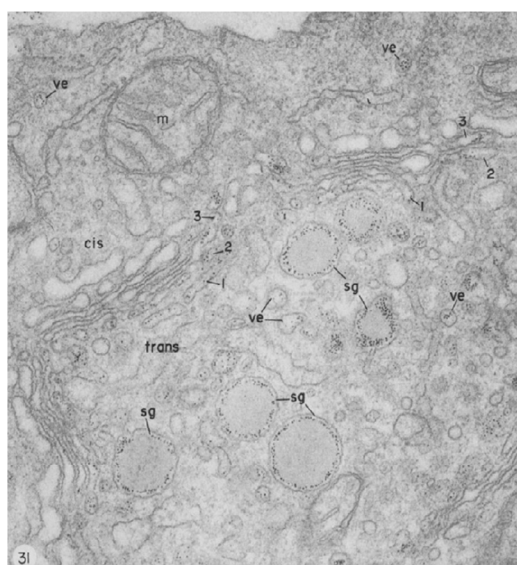


Figure 2. **Traffic in and out of the Golgi.** (Top) Membrane recycling in secretory cells followed by plasma membrane-bound cationized ferritin. Micrograph originally from Farquhar (1978) and reproduced in Farquhar and Palade (1981). (Bottom) Diagram reproduced from Farquhar and Palade (1981).

learned tough lessons from a tough microscopy master (Fig. 1). Mostly, however, the take-home messages were those of persistence, precision, and presentation, practiced unwaveringly by Marilyn herself and imposed upon her research. These principles have guided the research careers of many fortunate Farquhar laboratory trainees, then and since.

Marilyn's singular focus on science was inexhaustible and legendary. As a dinner guest at their house or a walking companion on their annual treks in Colorado, you might find yourself, before long, watching Marilyn absorbed in reading scientific papers or hearing about a new paper. Meanwhile, with great eloquence and drawing from his deep trove of worldly knowledge, George would be recounting a vibrant history of art, or of any country in Europe; such were their intense passions and pastimes.

In 1990, Farquhar and Palade headed west, back to Marilyn's much-loved California, where at UC San Diego School of Medicine

they established a new division of cellular and molecular medicine, followed in 1999 by Marilyn's appointment as founding chair of the by now upgraded Department of Cellular and Molecular Medicine, which she led until 2008. There, the Farquhar laboratory went on to contribute to other important areas of cell biology, turning to cell signaling and charting new families of regulators for heterotrimeric G proteins.

Marilyn was a pioneer in science long before being a "woman in science" came to the fore as a public issue. She rarely gave voice to the doubtless trials and challenges of her own career progression, combined as it was with her roles as a proud mother and grandmother, but she remained a strong and effective advocate for women in research and academia throughout her career. Her achievements were many. She was recognized by membership of the National Academy of Sciences and the American Academy of Arts and Sciences and awards including the E.B. Wilson Medal of the American Society of Cell Biology, Homer Smith Medal of the American Society of Nephrology, Distinguished Scientist Medal of the Electron Microscopy Society of America, and Rous-Whipple Award of the American Society for Investigative Pathology. In 2017, she became the recipient of the Revelle Medal, UC San Diego's highest honor. She served as president of American Society of Cell Biology (1981), denoting a career-long involvement with the society and the cell biology field.

The world is indebted to Marilyn Gist Farquhar for the volumes of detailed knowledge she extracted from cells over a lifetime as a microscopist and scientist, and for the many scientific careers she launched for others. Above all else, the one burning passion that defined her teachings and should frame her legacy was her exuberant, unquenchable fascination with the biology of cells.

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