# Marilyn Gist Farquhar

1928–2019

BIOGRAPHICAL *Memoirs*

*A Biographical Memoir by*
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NATIONAL ACADEMY OF SCIENCES

# MARILYN GIST **FARQUHAR**

*July 11, 1928–November 23, 2019*

Elected to the NAS, 1984

*By Dorothy Ford Bainton, Pradipta Ghosh, and Samuel C. Silverstein*

Marilyn Farquhar will be remembered professionally for her original contributions to the fields of intercellular junctions, which she discovered and described in collaboration with George Palade, membrane trafficking (endocytosis, regulation of pituitary hormone secretion, and crinophagy), localization, signaling, the pharmacology of intracellular heterotrimeric G proteins and the discovery of novel modulators of these G proteins, and podocyte biology and pathology. Over her 65-year career she was a founder of three of these fields (intercellular junctions, crinophagy, and spatial regulation of intracellular G-protein signaling) and was a recognized and valued leader in guiding the evolution of all of them. She sponsored, mentored, and nurtured 64 pre- and postdoctoral fellows, research associates, and visiting scientists. Her work was largely supported by uninterrupted funding from the National Institutes of Health (NIH). She was listed as one of the ten most cited women authors by Citation Index from 1981 to 1989.

She served as President of the American Society of Cell Biology (1981-1982) and received the society's prestigious E. B. Wilson Award for her many contributions to basic cell biology in 1987, the Distinguished Scientist Medal of the Electron Microscopy Society of America (1987), the Homer Smith Award of the American Society of Nephrology (1988), the Histochemical Society's Gomori award (1999), FASEB's Excellence in Science Award (2006), and the Rous-Whipple (1991) and Gold Headed Cane (2020) awards of the American Society for Investigative Pathology. She was a member of ten scientific societies. She was elected to the National Academy of Sciences (USA) in 1984 and the American Academy of Arts and Sciences in 1991. She served on the faculties of the University of California, San Francisco (1962-1970), Rockefeller University (1970-1972), the Yale School of Medicine (1973-1989) and the University of California, San Diego School of Medicine (1990-2019).

## The Early Years

Although Marilyn Farquhar's scientific productivity is well documented in 319 publications, her development as a scientist is less well known. She was born on July 11, 1928, in Tulare as a third-generation Californian. Her father, Brooke Gist, was from a pioneer family and worked as a farmer and insurance agent. Her mother, Alma Gist, was also from a pioneer family and had started at Mills College, but her father had a bad year in farming and she had to come home. She was determined that her two daughters would receive a college education. Marilyn stated, "It was my good fortune to be born in California, which has the University of California, the top public university in the nation. Thus, I was provided with a first-class education for very little money." She drew inspiration from her mother, whose own academic ambitions had been cut short by hard times, and from a family friend, Francis Zumwalt, who ran a pediatric practice out of her home.[1] After graduation from the University of California, Berkeley (UCB) in 1952 and two years of medical school at the University of California, San Francisco (USCF), she began her scientific career by working toward a Ph.D. in experimental pathology. She made this change because her husband, Dr. John Farquhar, discouraged her from taking the clinical years of medical school. Luckily for her, J. F. Rinehart, the chairman of Pathology, had just purchased an RCA 3B electron microscope and one of the first Porter-Blum microtomes and asked her to investigate tissue preparation for electron microscopic analysis. Her initial efforts using unbuffered osmic acid to fix renal tissues were relatively unsuccessful, but she soon switched to buffered osmium and achieved much better results. Her thesis project would characterize the ultrastructural changes during hormone secretion by rat anterior pituitary gland cells. She combined her newfound tissue fixation methods with the approach of an experimental endocrinologist—target organ ablation and hormone replacement—to great success.[2,3,4]

When her husband relocated to the University of Minnesota to continue his training, she followed, joining Robert Good and Robert Vernier, who were then exploring changes in human kidney structure in various diseases. It was a superb collaboration. Marilyn's skills as a renal electron microscopist complemented Vernier's clinical and Good's immunological talents. Together, they established percutaneous renal biopsy as a powerful diagnostic modality, opened a new chapter in understanding renal diseases, and initiated Marilyn's lifelong interest in renal physiology and pathology.[5,6] When her husband moved to New York City for further training, she obtained a postdoctoral traineeship in the laboratory of George Palade at Rockefeller University (1958-1962). There, she began her formal training in the new field of cell biology, in its "birthplace."

As the luck that makes science so exciting and unpredictable would have it, Palade's Romanian doctoral thesis was on the structure of urinary tubules of Black Sea dolphins, and at the time of Farquhar's arrival in his lab he was studying glomerular structure. Farquhar's postdoctoral studies of the ultrastructure of diseased kidneys complemented Palade's interests and led to a natural collaboration. Their experiments established the glomerular capillary basement membrane as a barrier to the trans-glomerular passage of large-molecular-weight plasma proteins, thereby opening an entirely new approach to renal physiology.

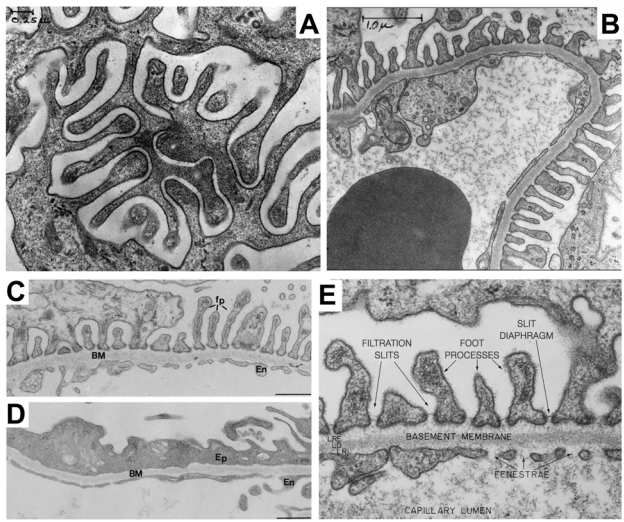


Figure 1. The Glomerulus "through Farquhar's eyes:" A. Kidney rat glomerular filtration barrier, tangential section of the fenestrated endothelium. Original magnification: x23,000. B. Peripheral area of normal rat kidney. Bar= 1.0 micron. C-D. Electron micrographs showing the loss of glomerular foot processes in rat models of nephrotic syndrome. (C) Portion of a glomerular capillary from a normal, untreated rat showing the typical organization of the foot processes (fp) of the glomerular epithelium. (D) Portion of a capillary from a nephrotic rat showing disruption of the foot process organization of GECs (Ep) and loss of the filtration slits between foot processes. BM, basement membrane; En, endothelium. Bar, 0.5 μm. (From T. Takeda et al., *J. Clin. Invest.* 2001.) E. The ultrastructure of the glomerular filtration surface, which consists of the endothelium interrupted by fenestrae; the glomerular basement membrane (GBM), and the epithelial foot processes. The latter are attached to one another at their base by slit diaphragms. The endothelial fenestrae are open and the GBM is directly exposed to the blood plasma. Magnification, x50,000. (From M. G. Farquhar and Y. S. Kanwar, 1980.)[7]

These studies led them to identify "tight junctions" as the cell structures responsible for the water and solute impermeability of epithelia and to characterize their principal structural elements (zonula occludens, zonula adherens, and macula adherens).[8]

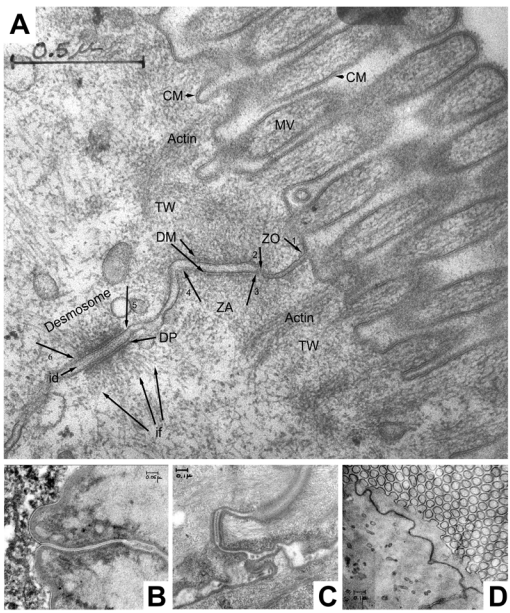


Figure 2. Cell-Cell junctions "through Farquhar's eyes": A. Transmission electron micrograph (TEM) of the junctional complex of intestinal epithelial cells of the rat showing the apical-most zonula occludens (tight junction), the zonula adherens (medium junction), and the macula adherens (desmosome). B. TEM of two frog epithelial cell cells showing the tight junction complex running horizontally. C. TEM of desmosomes (macula adherens) in the junctional complex between cells in frog skin. The upper desmosome is cut obliquely and appears much wider than the lower (vertically located) one. D. TEM of a section close to the luminal surface of the rat intestinal epithelium showing a tight junction (zonula occludens) extending diagonally across the image from upper left to lower right. (From Farquhar and Palade, 1963.)[8]

After the birth of two sons, she and her husband returned to California, where she joined the UCSF faculty (1962-1970). There, she directed her own laboratory and focused on pituitary hormone secretion. Together with her graduate students and postdoctoral fellows, she discovered the process of "crinophagy" (named by Christian de Duve), in which excess secretory granules fuse selectively with and are degraded by lysosomes.[9]

This led others to identify crinophagy in other endocrine cells, such as pancreatic alpha and beta cells. At this time, she also began studies of Golgi cisternae and the function of coated vesicles in protein uptake in the epididymis[10] and provided the first descriptions of biogenesis and heterogenicity of neutrophil granules.[11,12]

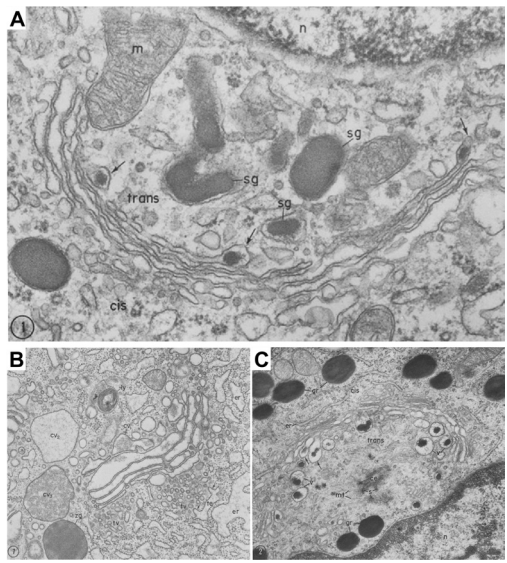


FIGURE 3. The Golgi apparatus "through Farquhar's eyes": A: Golgi region of a mammotroph, or prolactin-secreting cell, from the anterior pituitary gland of a lactating rat. Arrows point to transmost cisternae; sg, secretion granules (sg); n = nucleus; m = mitochondrion. x 67,000. B. Golgi region from an exocrine pancreatic cell (guinea pig); cv, condensing vacuoles, tv, transport vesicles; zg, zymogen granules; er, ER elements; ly, lysosome. x 38,000. C. Golgi region of a developing PMN leukocyte (promyelocyte stage) illustrating the formation of azurophil or primary granules along the trans side of the Golgi complex; ce, centriole; arrows, transmost cisternae; v, dense-core vacuoles; gr, dense azurophil granules (gr); s = centriolar satellites; mt = microtubules; n = nucleus. x 50,000. (From D. F. Bainton and M. G. Farquhar, 1968. *J. Cell Biol.*) From Farquhar (The Golgi apparatus (complex)-(1954-1981)-from artifact to center stage; Marilyn Gist Farquhar, George E. Palade).

In 1969 she returned to Rockefeller as a Full Professor and joined the Palade-Siekevitz group. In 1970 she divorced her husband and married George Palade, forming an extraordinarily happy and professionally productive partnership. Farquhar and Palade collaborated where there was mutual interest but maintained separate labs and programs throughout the rest of their careers.[13]

We pause here to reflect on the peripatetic career pathway that was common for talented and professionally committed women in the 1960s and 1970s: follow your husband, bear and nurture children, remain competitive in your field, make many compromises, and still do outstanding science. Marilyn had the brilliance and persistence to make the most of every geographic move. She was a wonderful role model for young women attempting to break into a man's world. She advised women to follow their scientific interests with passion and focus. She broke with tradition by showing them how to manage both a family with children and a scientific career. It would take negotiating with superiors for reduced time when children were very young, then returning to a regular schedule as children became more self-sufficient. Her own career, and that of her women trainees, proved the value and efficacy of such flexible career plans.[14]

## Later Years: Research, Teaching, and Administration

Now recognized as a brilliant cell biologist, she returned to Rockefeller in 1969, where she was appointed as a Professor of Cell Biology (1970-1973), Rockefeller's first female professor. In their retrospective, John Bergeron and David Castle recalled that she was clearly among the standard setters in a department and institution loaded with scientific talent.[15] Moreover, she was friendly, easily approachable, and made time for informal conversations, thereby enriching the scientific environment for numerous students, faculty colleagues, and a host of visitors and collaborators.

In 1973 Farquhar and Palade moved to Yale, where she helped build a new Cell Biology department in the medical school. In 1974 Palade was named a corecipient of the Nobel Prize in Physiology and Medicine. While at Yale, Farquhar and others discovered that "megalin" was the target of an autoimmune disease known as passive Heymann nephritis, an animal model of the human autoimmune disease membranous glomerulonephritis. Further study revealed that it was in the low-density lipoprotein (LDL) receptor superfamily and was the main proximal tubule membrane receptor for the retrieval of many filtered proteins and vitamins, thereby initiating a new chapter in understanding of renal physiology.[16,17,18]

In 1990 Farquhar and Palade moved to the University of California, San Diego (UCSD) to establish a new Division of Cellular and Molecular Medicine. With the recruitment of top scientists, the division became a full department, with Farquhar as its founding chair. She continued her two prior areas of research: Golgi secretion and glomerular biology. She also ventured into the intracellular roles of heterotrimeric G proteins, a.k.a. "molecular switches," for signal transduction. She was among the first to recognize these switches' functional activities on intracellular membranes. Whereas the field of pharmacology was primarily focused on how these switches signal at the cell surface, she asked what (if any) roles they might play on intracellular organelles (See Figure 4, upper panel). In the twenty-five years that followed, her work revealed that these G proteins were functional at multiple intracellular sites.[19] She discovered a plethora of modulators of these switches (GAPs, GEFs and GDIs; see Figure 4, lower panel)[20-25] and revealed how such modulation fine-tunes organelle functions (Golgi secretion, autophagy, growth-factor signaling from endosomes, etc.), and regulates membrane trafficking.[26-29]

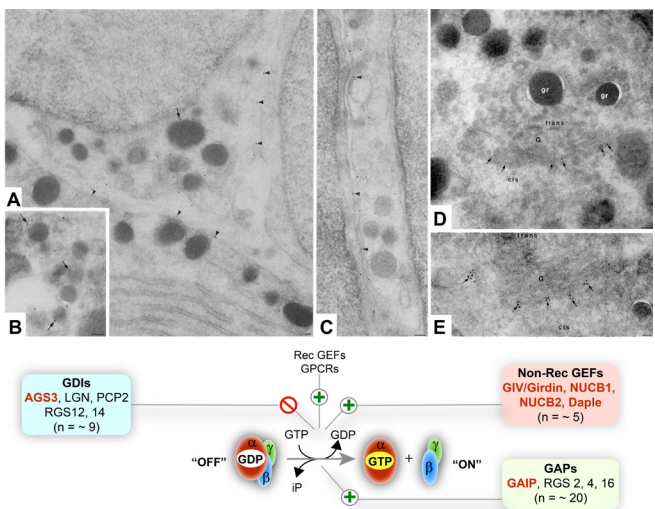


Figure 4. Roles of trimeric G proteins on endomembranes: controversy then, a trendy paradigm now. Upper panel: Farquhar was one of the first to have noted the presence of heterotrimeric G proteins at intracellular membranes. A-C. Electron micrographs show immunogold labeling of Gαs on the plasma membrane and secretory granules in lactotrophs (A), a somatotroph (B), and a gonadotroph (C, right) in the rat anterior pituitary. Gold particles at the plasma membrane are marked by arrowheads; the labeling of granules (which is sparse) is marked by arrows. Bar, 0.1 pm; magnifications: A, 20,000x; B, 50,000x; C, 45,000x. D-E. Immunogold

labeling with of Gαi3 showing its presence on Golgi membranes and concentrated on the cis-face of the Golgi complex. Ultrathin cryosections of normal rat pituitary (A) or GHB cells (B) were labeled. (From B. Wilson. et al., *Endo*, 1994.) Lower panel: Schematic summarizing Farquhar's contributions to the field of trimeric G protein signaling, populating it with distinct classes of modulators that fine-tune G protein signaling on endomembranes (hence, off-the-beaten path of GPCR-dependent canonical signaling from the plasma membrane). She discovered GAIP, which was chronologically the first in the class of RGS proteins that serve as GAPs, and did so almost simultaneously with others. She also discovered AGS3, again the first in the class of proteins that serve as GDIs, and did so nearly simultaneously with another group. Finally, she discovered GIV/Girdin, Calnuc/NUCB1 and Daple, all members of a family of proteins that serve as non-receptor GEFs; these are again the first in this class that act via a defined structural motif. Red font = proteins discovered by Farquhar in each class of modulators.

This was a remarkable feat. As a cell biologist, she was widely regarded as a quintessential "outsider" in the field of G-protein pharmacology, and yet she became one of the most significant contributors of novel molecules to that field.

She was a superb educator. Her lectures and seminars exemplified thoughtfully designed experiments, gorgeously illustrated with Ansel Adams–quality diagrams and micrographs, many of which can be reviewed in "A Life of Pictures—Marilyn Gist Farquhar."[30] Her depth of understanding and her lifetime of experience enabled her to trace the history of the fields in which she worked from their inception to the present. She was meticulous in citing the contributions of other scientists. Her inventiveness as an investigator attracted outstanding students to the field of cell biology generally, and to her laboratory in particular. Two of us, Dorothy Bainton and Pradipta Ghosh, were fortunate to have been fellows in her laboratory and to have experienced her humanity, her generosity, her high ethical standards, and her commitment to excellence.

She resigned as Department Chair in 2008 but continued to teach, mentor, and maintain a productive lab until 2015. In 2017, UCSD's Chancellor recognized her contributions to building UCSD's Medical School to a high rank among the nation's medical schools and to fifth in the nation in external research grants by naming her a "changemaker," and awarding her UCSD's highest honor, the Roger Revelle Medal. She is survived by sons Bruce and Douglas Farquhar, daughter-in-law Wendy Farquhar, and grandchildren Christopher and Brooke.

## Personal Note

As a youth, George Palade enjoyed hiking in the mountains of Romania. Marilyn gained her love of the mountains in the high Sierras of California. Following their move to UCSD, they spent a month each summer relaxing and hiking in the Elk Mountains near Aspen, Colorado. There they frequently hiked with friends and prior trainees, who enjoyed their company, shared their lunch delicacies, and were impressed by their adventurousness and stamina. More than one trainee who knew George before and after his marriage to Marilyn commented that Marilyn had a profoundly beneficial effect on him. She enabled him to relax, to shed his "European professional formality," and to express fully his playfulness and good humor. Those so fortunate to have shared these mountain adventures with Marilyn and George treasure their memories of them. They rounded out our relationships with them as the extraordinary people they were.

George Palade, a long-standing personal and professional collaborator. Palade and Farquhar took disciplined breaks from academic pressures; together they enjoyed art (paintings, music, poetry, museums, opera, theater, and fine cuisine), travel to places where art and history are irrevocably intertwined (especially their annual escape to Aspen, Colorado), natural beauty and outdoor physical activities (especially hiking mountains and taking long walks at the beach). Farquhar believed that these shared moments were the secret to their very good physical condition, portals for stress relief, and source of replenishment of the soul.

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