

## ASPB Pioneer Member

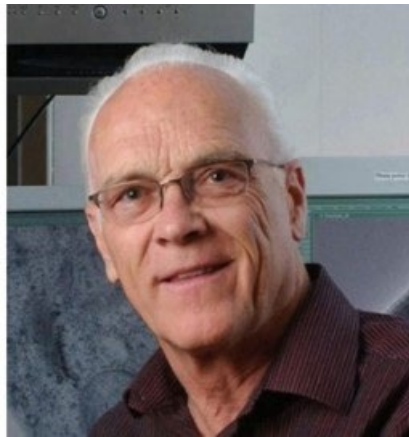
### L. Andrew Staehelin

#### Remembering Pioneering Cell Biologist Lucas Andrew Staehelin (1939-2022)

L. Andrew Staehelin died at the age of 83 on September 28 of 2022. He was a professor in the Department of Molecular, Cellular and Developmental Biology (MCDB) at the University of Colorado Boulder.

Andrew was born in Sydney, Australia, on Feb. 10 of 1939. His family moved to Switzerland in 1948, where he grew up and attended the Gymnasium in Bern. To pursue his broad interests in natural sciences and biology, Andrew attended the Swiss Federal Institute of Technology. He completed his undergraduate studies between 1959 and 1963, and obtained his PhD in plant cell biology in 1966 under the supervision of Kurt Mühlethaler. He then moved to New Zealand where he worked at the Physics and Engineering Laboratory of the Department of Scientific and Industrial Research between 1966 and 1969. Deeply interested in pushing the boundaries of biological electron microscopy, Andrew moved to Boston in 1969 to pursue his postdoctoral training with Keith Porter at Harvard University.

In 1970 and at the age of 31, Andrew became an Assistant Professor in the newly formed Department of MCDB at the University of Colorado Boulder where he spent all his professional career. He was promoted to associate professor in 1973, then to full professor in 1978, and to professor emeritus in 2006. In addition, he held visiting professorship positions in several academic institutions such as Albert-Ludwigs University of Freiburg, the Swiss Federal Institute of Technology, and University of Melbourne. But Boulder and the surrounding mountains



were Andrew's home. He often came to the lab with exciting tales of a ski, hiking, or biking adventure that he had with his children and wife, Margrit, the previous weekend, and he often recounted that he had some new biological insights on a project while out in the wilderness.

Andrew's academic career revolved around two of his passions, teaching and discerning the structure of plant cells to better understand their function. He was an inspiring and devoted teacher, who enjoyed interacting with undergraduate students in the challenging settings of large introductory courses at CU Boulder. He was recognized with two teaching awards for his impact in undergraduate teaching. He had endless patience for undergraduate students in his classes, and he was very supportive and generous with his time and professional advice when they came to his office hours. Andrew's passion for teaching was contagious, and it spread to everyone he trained, influencing their own careers and the scores of students they would eventually train at colleges and universities everywhere.

He trained and mentored many graduate students and postdoctoral researchers from all over the world in his laboratory. All those who were lucky to be part of his research group, learned cell biology and electron microscopy from a mentor whose rigorous attention to detail and perfectionism were only matched by his

optimism, enthusiasm, good humor, generosity, and endless energy. There was always a smile on his face. He kept a magnifying glass in his desk drawer for inspecting the little details of electron micrographs. The poor student or post-doc would cringe when he reached for this magnifying glass. One never knew if the results would be a gentle scolding on astigmatism or a triumphant "AHA! Notice the clathrin coats on the trans-Golgi network!" In the years before digital cameras, he would examine draft figures, then send us back to the darkroom yet again to make subtle adjustments to the contrast and composition of the micrographs. Despite the momentary frustration of having to go back and start over and over again, we always had to agree with him that the final product was far better than what we originally had deemed sufficient.

Andrew also had amazing people skills. He understood that a happy, cohesive lab group is a productive group. He fostered a team spirit through annual lab ski outings and the legendary holiday fondue party that Andrew and Margrit hosted at their home each year. People from both inside and outside the lab regularly turned to Andrew for wise advice on careers and personal challenges, often years after leaving Boulder.

Andrew understood early on in his career that the preservation of the biological material under study was crucial to uncover the function of cells and their organelles. He recognized the limitations of chemical fixation and devoted his efforts to develop and optimize cryofixation methods for plant material. In the early 70's and 80's, Andrew used rapid freezing and freeze fracture to address two major topics in plant biology, the organization of photosynthetic membranes and the site of cellulose synthesis. His lab provided decisive evidence in favor of the indirect coupling of electron transport to ATP synthesis by demonstrating that the ATP



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synthase enzyme (then known as the coupling factor) was confined to the stromal (unstacked) regions of the photosynthetic membrane (Miller & Staehelin, 1976). His work on spinach chloroplasts showed the relationship between stroma and grana thylakoids and the dynamic distribution of photosystem complexes (Staehelin, 1976). By applying rapid freezing and freeze-fracturing to plant cells and green algae, and by drawing on his previous research on cellulose deposition at the plasma membrane (Kiermayer and Staehelin, 1972), Andrew and his students were able to visualize plasma membrane-localized rosette complexes actively synthesizing cellulose (Giddings et al., 1980). The lab's pioneering work not only showed the production of microfibrils from cellulose synthase complexes at the plasma membrane but made important predictions about the assembly of the cellulose synthase complexes in the endomembrane system and their mobility at the plasma membrane as an essential aspect of cellulose synthesis and deposition.

At atmospheric pressure, effective cryofixation (with no detectable ice crystal damage) can only be achieved within ~10  $\mu\text{m}$  from the sample surface. To successfully preserve the interior of plant cells, Andrew optimized and introduced high-pressure freezing, rapidly cooling samples to cryogenic temperatures in a few milliseconds while applying high pressure (~2,000 atm) (Dahl and Staehelin, 1989). This is still the best available technique for the preservation of eukaryotic cells and tissues. Using high-pressure freezing and immunolabeling, Andrew's group showed novel structural features of Golgi stacks (Staehelin et al., 1990), the response of Golgi stacks and vesicles to trafficking inhibitors and the compartmentalization of their glyco-enzymatic activities (Moore et al., 1991, Zhang and Staehelin 1992, Zhang et al., 1993, Driouich et al., 1993) and vacuole biogenesis (Zheng and Staehelin, 2011).

By applying high-pressure freezing to dividing plant cells, Andrew's lab also revealed a series of previously uncharacterized intricate membranous intermediates that occur during the assembly of plant cell plates (Samuels et al., 1995) and a specialized form of cortical endoplasmic reticulum in gravity-sensing root tip columella cells (Zheng and Staehelin, 2001).

In the late 90's and the first decade of the 21st century, with the development of electron tomography and 3D modeling at CU Boulder, Andrew successfully introduced 3D tomographic reconstructions as a critical new tool in his research. Electron tomography allowed the Staehelin lab to further push Andrew's passion for structure-function connections leading to a prolific time with breakthrough publications on preprophase band assembly (Karahara et al., 2009; Takeuchi et al., 2016), phragmoplast organization (Austin et al., 2005), cell plate formation (Otegui et al., 2001; Seguí-Simarro et al., 2004), Golgi structure and function (Otegui et al., 2006; Donohoe et al., 2007; Kang and Staehelin, 2008; Kang et al., 2011; Donohoe et al. 2013), and the architecture of thylakoid membranes in plant chloroplasts (Austin and Staehelin, 2011). 3D modeling of cell reconstructions based on serial sections allowed for the study of the cell cycle-dependent dynamics of membranous compartments (Seguí-Simarro and Staehelin, 2006, Seguí-Simarro et al. 2008).

Andrew and his students and post-docs wrote almost 300 scientific papers and book chapters. He also edited several books with his always clear style and fabulous illustrations. The broad range of cell biology topics that he pushed forward through his career reflected his broad interest and endless curiosity for all aspects of cell biology. He had an outstanding knowledge of plant cell biology he shared with all of us. He was widely acknowledged as the "go-to"

person for investigations of membrane dynamics in plant cells and had many collaborations with national and international colleagues. Significantly, he continued to publish through the year of his passing.

Andrew was a master at interpreting plant cell structures through the lens of the latest advances in yeast and animal cell biology. This sometimes meant that he would go out on a limb to propose some ideas that were controversial. His interpretations were creative, integrating new molecular genetics and biochemical insights. Andrew pushed the envelope, with thoughtfully constructed arguments, and challenged the field to do better.

In recognition to his scientific contributions, Andrew received several awards, including membership in the German National Academy of Sciences Leopoldina, fellow of the American Association for the Advancement of Science (AAAS), a faculty recognition award from CU Boulder, the Haselkorn Scholar Award from the University of Chicago, and fellow of the Society of Plant Biologists.

His service to the research community included serving as editor of major journals and establishing the Plant Cell Wall Gordon Conference.

After retirement, Andrew devoted efforts to educate the public about genetically modified crops and agricultural practices and wrote several op-ed articles for local newspapers. He was also a keynote speaker at the Plant Cell Dynamics Meeting in Madison WI in 2017 and wrote several articles reviewing major challenges and breakthroughs in plant cell biology (Staehelin and Paolillo, 2020; Cheung et al., 2022).

Andrew is survived by his wife, Margrit, who has been his hiking and travel companion all around the world, as well as his sons and grandchildren.

He will be greatly missed as a beloved and inspirational mentor, colleague, and friend. His scientific and friendly spirit



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will live on.

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