

Tribute to Alan Hall

In addition to being a remarkable scientist (as described by Chris Marshall in this issue), Alan was a kind and generous mentor, colleague, advisor, and friend. Here, several of Alan's trainees, colleagues, and fellow JCB editors share their memories of him. What is clear from their accounts is that the scientific community and JCB have lost a beloved colleague—a gentleman scientist of sharp intellect and wry humor, who was a tireless champion of cell biology.

A generous and supportive mentor

Pontus Aspenström

I find it painfully difficult to talk about Alan in the past tense. I had the favor of spending a postdoc period with him during an extraordinarily productive phase in his career when he had just moved to the new MRC Laboratory for Molecular Cell Biology at the University College London campus. Looking back on the photos from that time, we all, including Alan, were amazingly young. Alan was extremely modest and supportive but he possessed a sixth or even seventh sense for what is actually important in the flood of scientific noise produced on an everyday basis in the laboratory. This is something I experienced when I worked with the so-called yeast two-hybrid system to identify novel binding partners for the Rho GTPase family member Cdc42. My sequencing data revealed that most of the positive clones encoded a strange protein associated with a rare disease called Wiskott-Aldrich syndrome. I was hesitant and Alan was much confounded when I talked to him, but he almost immediately got back to me and, based on the scarce information of cells from patients, concluded that this must be the real thing! And he turned out to be right! After returning to Sweden, I often invited him to our seminar series. Once, the two of us went to a downtown restaurant. We got a

table for two with candlelight in a quiet area of the premises. Alan said, "Pontus, you should be on a date with your wife rather than with me." However, looking back, I am really happy that I had this "date" with Alan.

Vania Braga

Alan was an exceptional scientist and was inspirational to all that came in contact with him. I was extremely grateful to Alan for his mentorship when I started my own laboratory at the MRC Laboratory for Molecular Cell Biology at University College. During the transition between postdoc and independent group leader, Alan was instrumental in guiding me toward successful approaches at all levels of my scientific career. Personally, I remember most vividly two things: first, how stimulating it was to discuss science with Alan (over coffee or a gin and tonic); and second, his generosity. He always took time from his busy schedule to talk to different people, had genuine interest in the different projects around and gave excellent advice, but was reluctant to take credit for his intellectual contributions. His passion for science was contagious and has shown me what scientific leadership should be.

Ridhdi Desai, Dan Jin, Tatiana Omelchenko, Louisiane Perrin, M. Angeles Rabadan, Yun-Yu Tseng, and Xian Zhang

As the current members of Alan Hall's laboratory, we are deeply saddened by his untimely passing. We have lost an enthusiastic scientist, an exceptional mentor, and an unforgettable friend. Alan's scientific discoveries of Rho, a Ras-related GTP-binding protein, paved the way to understanding the role of the actin cytoskeleton in many aspects of biology including cancer cell motility. While the significance of Alan's scientific achievements are transparent throughout the research

community, Alan's enthusiastic but humble personality was also second to none and can be echoed throughout the network of Alan Hall's "children"—all those who had the chance to obtain scientific training from him. He'll be forever remembered for his noble character and for his ability to be fair, calm, and supportive, especially during some of the most difficult personal decisions that some of us have had to make during our scientific careers. His famous words of advice, which we believe every member of Alan's scientific family can relate to, were "I am here to financially support you and provide you with the scientific expertise and resources to fulfill and test your research ideas. The rest depends on you and the decisions you make to successfully complete your research." Overall, his training allowed us to have ownership of our projects and help to build an unbreakable bond of friendship between every member of his laboratory.

Sandrine Etienne-Manneville

I first visited Alan's laboratory in February 1999, just after finishing my PhD. It was my first time in London, my first postdoc interview, and I, of course, had already heard and read a lot about Alan's work. I was terrified when I entered his office, but five minutes later I was sitting comfortably, discussing my results and projects in front of a totally attentive and interested Alan and already feeling incredibly confident about my ideas. Alan had this uncanny ability to make you feel that your thoughts and opinions mattered to him, that they were important and worth discussing. Whether you were a student, postdoc, or a more senior colleague, you could similarly discuss with

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him on an equal footing. I was lucky to be able to join his laboratory later that year. Over the four years that I spent in his laboratory, his office door was always open for all laboratory members to come and discuss at any time, until 6:40 p.m., when he had to run and catch his train. Sometimes, we were queueing up in the corridor to have a quick word. Often though, I would simply pop my head in just to ask his opinion on my latest result or hypothesis. But this one-minute question could easily turn into an hour-long intense discussion. He would listen to your ideas and of course discuss and challenge them. It was then a kind of ping pong game, ideas, good or bad, being exchanged, revisited, modified. Sometimes, these discussions could go on for an hour or more and I would come out exhausted, but full of new hypotheses and strategies. After leaving his laboratory, I have profoundly missed these frequent discussions. Luckily, meetings and seminars gave me new opportunities to discuss with him since then. I have thoroughly enjoyed hundreds of scientific exchanges with him, and I am already missing the next ones.

Nathalie Lamarche-Vane

I had the privilege to spend my postdoctoral years in the Hall lab at the time of the fundamental discoveries of Rho, Rac, and Cdc42 regulating the actin cytoskeleton. During this exciting period, many hours were spent in the darkroom developing images of cells (before the era of digital cameras!). Alan was not only a great scientist who rewrote the textbook of molecular cell biology but he was also an inspiring mentor who kept the future of his trainees at heart. His exceptional guidance launched the careers of many of us throughout the world, from Japan to America and Europe.

I have always been touched by his immense generosity and humility. Having a busy travel schedule, he even took the time to stop by Montreal to visit the laboratory and meet my students and laboratory members. Thank you, Alan, for all these wonderful opportunities and insightful inputs into our science. We will miss you so much. The scientific community has lost one of its giants too early.

Laura M. Machesky

I arrived in Alan's laboratory as a postdoc in 1995, a very exciting time for the unraveling of how Rho-family GTPases connect with the actin cytoskeleton. I'd heard Alan speak at a meeting of the British Society for Cell Biology and immediately contacted him for a postdoc position. We initially looked for direct connections between actin and cytoskeletal proteins with GTPases, and Alan and I had many inspiring chats about how GTPases might control actin dynamics. Alan would enthusiastically drop whatever he was doing for a science chat during the day; he always put science and the young scientists around him first. Alan traveled to scientific conferences around the world, and when he came back, we would gather around him to hear about the latest developments. Friday afternoons were often times for a gin and tonic in his office, with much storytelling and joking. Alan was a soft-spoken and gentle person, but with an underlying extremely sharp wit and sense of humor that could surprise us. He supported me at a crucial time in my career, during my transition to independence. Among his many contributions, he allowed me the freedom to set my own directions. Alan was a great role model, a friend, and a brilliant scientist, and his passing is a huge loss for his family, his many friends and colleagues, and for the scientific community.

Koh-ichi Nagata

So many things occur to me when I think of Alan. In particular, it was a huge surprise to discover that excellent science and a high-minded personality could be harmonized in one person. Alan taught me that no hierarchy should exist in science and that everyone is equal before the truth. As for my family life in London, I remember his warmth when I started working with him. We had no credit because we were short-term immigrants. Alan volunteered to co-sign the applications. (After two or three days of our first meeting! How incredible!) I am afraid he was sometimes at a loss with his first-ever non-English speaking postdoc—it was really hard for me to understand that the language spoken in the laboratory was “English.” My “English” education was from Japanese teachers in the countryside.



Alan Hall and Koh-ichi Nagata in 1997.
Photo courtesy of Koh-ichi Nagata.

I also remember his warmth when I returned to Japan. He expressed concern about my scientific future and made me a very kind offer. Memories about him flow on and on. Alan has been and always will be the real mentor for me. I will try to do my best to emulate him, although I do not know how my young colleagues see me now. . .

Michael F. Olson

While in graduate school, I read Alan's 1990 review in *Science*, which convinced me that small GTPases were the future and that his laboratory was the place to be. I sent him my CV, asked for a postdoc job, and he said “OK.” Just like that. With his help, I wrote several fellowship applications and was eventually awarded a Canadian research council grant that covered two years' salary and one-way plane fare. I moved to London before having written my PhD thesis, and was immediately hit with a problem: journals were only found in hard copy in those days and I had no access to them. I went to see Alan, and the solution was that he signed me in to his Institute's library when I needed access and gave me his photocopy card each time so I didn't have to pay to copy papers. When I started working in his laboratory, the environment was fantastic. Everyone had their own interesting projects and collaborated freely. Alan's door was always open. I remember a few times that our long

discussions made him miss his train home. And he was also happy to talk about the Rossoneri's successes (Alan was a big fan of Italian football). Since becoming a group leader, I've strived to replicate the same laboratory atmosphere and to be as nice and supportive as Alan was to me.

Anne Ridley

Alan Hall was an inspirational mentor for his laboratory members. When I joined his laboratory at the Institute for Cancer Research in 1990, I knew him as an expert on Ras signaling. However, he had recently changed his allegiance to the Ras-related and little-known Rho GTPases. He had just published a paper with Hugh Paterson, showing that RhoA induced cell shape changes in fibroblasts. After scouring the literature on the actin cytoskeleton in the musty Institute library, I decided to test many different extracellular signals, from serum to bombesin, for their effects on the actin cytoskeleton. Serum had the strongest effect in inducing Rho-mediated stress fibers in fibroblasts, and this is where Alan's biochemical expertise and detective skills came to the fore. He sent me into the cold room to purify the stress fiber-inducing factor from serum. When we realized the factor was associated with serum albumin and was not destroyed by heat, we decided it could be a lipid, and had great discussions on how to prove this. By process of elimination, we found it was lysophosphatidic acid (LPA). This was the most exciting time of my life in research—working with someone who was really driven to find the answer to a problem, and who had expertise in the many approaches needed to work out this answer.

Nic Tapon and Dagmar Tapon (née Diekmann)

Nic. Alan was the kind of boss you worked hard for, not because he told you to, but because you wanted to make him proud. He was excited with you when the science went well, and unfailingly supportive in the difficult moments. Most of all, I remember always coming out of his office with fresh ideas and feeling excited about my project. His patient, kind, and calm leadership and sense of humor were what made him special as a supervisor, and I often think of what he would have

done when I have to deal with a tricky situation as I run my own laboratory.

I remember when I started the final year of my PhD, Alan took me out for a gin and tonic (a favorite Hall laboratory tippie!) at the faculty club for a quiet chat about my future. He wanted to make sure I gave it plenty of thought and didn't leave looking for a job until the last minute. (How well he knew me!) This is typical of the thoughtful person he was.

Dagmar. Alan was a caring and supportive supervisor. As a scientist, he upheld moral principles over fame, ethical behavior over personal advancement. He was always modest about his achievements. We are grateful to have met such a wonderful person and to have had a chance to work with him. His passing creates a huge hole but his memory will always live on in us.

Alan changed our lives in more ways than just through science. In addition to our careers, we both owe him our happy marriage and three gorgeous sons. It was Alan who introduced us and suggested we work together during the time we overlapped at University College London in the 1990s while doing our PhDs in his laboratory. One of our most treasured memories is when he and his lovely wife Eileen attended our wedding one sunny May day a few years later in Heidelberg. We will miss him immensely.



Alan at Nic and Dagmar's wedding. Photo courtesy of Nic Tapon.

An exemplary colleague

Filippo Giancotti

I have known Alan for two decades and I won't forget the countless times we sat in our offices quietly discussing science or the countless chats we had about family life and politics over recruitment dinners and on other occasions. Alan was

a scientist's scientist but also a remarkable human being. I do not think I have ever heard him raise his voice no matter how irritated he may have been. And it was impossible to disagree with him; he was so reasonable. Alan made one of the most important discoveries in cell biology and continued to aim for the extraordinary, all along remaining focused on helping others achieve their best. His scientific presentations were terse and lucid. He wanted the data to speak for itself without embellishments. Our conversations often revolved around the state of our discipline and the often underappreciated importance of fundamental science. We have lost a great cell biologist and a fun and uplifting colleague.

Cole Haynes, Michael Overholtzer, and Bryan Tsou

Alan recruited us along with three others as junior faculty to the Cell Biology Program at Memorial Sloan Kettering Cancer Center. While his many scientific accomplishments are well documented, we hope to highlight here Alan's attributes as a colleague. Alan was a wonderful chair. Humility, grace, and endless generosity defined him. Somehow he had time for, and interest in, everyone, including us. His fascination and love for exciting new science was always on display. While Alan was clearly a world expert in all things related to small GTPases and the cytoskeleton, he recruited six individuals interested in wider aspects of cell biology, including centrioles, cell death, wound healing, mitosis, and mitochondria. Alan was, on many occasions, the sharpest and clearest thinking person in the room. But his questions (and there were many) or comments never came off as grandstanding. Rather, he strived to make others better while seeking no attention for himself. He was generous with his time, always happy to read a grant application or manuscript, but also confident in those he had hired and happy to provide plenty of space. As chair, he ran our department with a level of grace and generosity to which we should all strive. As a colleague, he was to us, as to seemingly everyone, a friend, and we miss him terribly.

Rick Horwitz

In the early '90s, the focus of cell migration research was on actin organization and dynamics, with adhesion just beginning to enter the picture. Alan's seminal publications, with Anne Ridley and others, on Rho and Rac introduced molecules that regulated all of these processes that we now know are intimately connected. By identifying a signaling convergence point that used a "known unknown," Ras-related GTPases, their discoveries greatly simplified the field conceptually and shifted interest to Rho GTPase effectors and regulators, an active field that continues today. No one anticipated that a small suite of related molecules would control such apparently diverse cellular processes and biological phenomena.

With this backdrop, I was very eager to meet Alan and invited him to speak at the first Keystone Symposium on Cell Migration in 1996 that Doug Lauffenburger, Mike Sheetz, and I organized. His amazing science, outstanding insight, soft-spoken manner, and warm, engaging smile captured me immediately, and he subsequently became a valued colleague and friend. A few years later, Tom Parsons and I asked Alan to serve on the Scientific Advisory Board for the Cell Migration Consortium. He was a joy to work with, making a major impact on the Consortium's research direction, urging us to initiate RNAi screens, among other suggestions. More recently, I was thrilled when Alan took over as the Editor-in-Chief of *JCB*, knowing that his insight and integrity would serve the journal well, implementing timely and insightful changes.

The news of Alan's passing was shocking and something that I am still processing. We have lost a great one—a great scientist, colleague, friend, and gentleman.

Joan Massagué

I was so pleased back in 2006 when Alan Hall was recruited to succeed me as chair of the Cell Biology Program at the Sloan Kettering Institute. "A true cell biologist at last!" I thought to myself, as my own research was moving more toward the problem of cancer. Not only was Alan an eminent cell biologist, but he was also a man of wisdom, ethics, discretion,

sincerity, and elegance—one with no agenda other than the pursuit of excellence and fairness in science. Alan remains an exemplary master, among the best of the best. A grande of science.

Erich Nigg and Michael N. Hall

At the "Biozentrum" (University of Basel), we highly appreciated Alan as a member of our scientific advisory board. He was an outstanding scientist, the recipient of many highly deserved honors, but, of equal importance, he was an exceptionally caring person. For many of us, Alan was a highly cherished colleague, a friend whom we deeply admired. We often took advantage of his wise counsel, his rigor, and his clarity. His serenity belied a very demanding schedule, and his modesty masked an exceptionally successful career. We will miss his easy smile and humorous quips that always brought joy. They would have helped dispel the profound sorrow we now feel.



The two Halls. Alan and Mike at the Biozentrum in 2011. Photo courtesy of the Biozentrum.

Harold Varmus and Thomas Kelly

A little over a decade ago, Memorial Sloan Kettering Cancer Center (MSKCC) needed someone to run a program in basic cell biology after the research programs of the Sloan Kettering Institute were reorganized. We found the perfect person in Alan Hall. Alan was British to the core, but still sufficiently adventurous to be uprooted from the UK to bring fresh views to New York. He was a superb cell biologist, whose work on regulation of the cytoskeleton was justly celebrated; moreover, as his work helped to explain the behavior of cancer cells and examined the regulatory roles of Rho family GTPases, he was ideally suited to lead cell biology at a cancer center. Most importantly, he was an engaging, sympathetic, and generous human being—someone who

seemed to know instinctively how to get along with others, encourage his junior faculty and trainees, and build his program in the spirit of institutional loyalty, as repeatedly displayed over the 11 years that he devoted to MSKCC. He was also a constructive, critical, and patient advisor to his faculty colleagues, as we learned personally when we needed help with scientific problems involving cytoskeletal dynamics. People who combine brilliance and personal strength with modesty and tact are rare in any society, and Alan's premature death is a loss to us all.

A thoughtful and dedicated editor

Elaine Fuchs

Alan was among the leaders in the cell biology community. He was the pioneer and world-renowned leader of Rho GTPases, and was credited with having built the field from the ground up. He was also a gifted educator, having trained many of the scientists who now work in this arena. Most of all, Alan was a beloved colleague and a soft-spoken giant of fairness, excellence, and generosity. Alan was a priceless gem, and he leaves a void in our cell biology community that simply cannot be filled.

Ian Macara

I knew Alan for nearly 30 years, since the early days of Ras and the discovery that it was one of a large family of small GTP-binding proteins. The late 1980s and early 1990s were exciting times in signal transduction research. At a Cold Spring Harbor meeting circa 1990, for instance, I remember spending a rainy afternoon in the cafeteria discussing Alan's first studies on the Rho GTPase, and Tony Pawson stopped by to tell us about his discovery that SH2 domains bind to phosphorylated tyrosine residues. Two years later Anne Ridley and Alan published their seminal back-to-back papers in *Cell* on the regulation of the actin cytoskeleton by Rho and Rac. Our paths continued to cross as it became evident that these small GTPases—and particularly Cdc42—are central to the control of polarity, and we each worked on different aspects of this connection. I was always astonished by how young Alan looked,

and as the years passed he never seemed to grow older! (This must have been connected somehow to working on the Ras family, because Julian Downward has the same phenotype.) Alan was always soft-spoken and polite, but firm in his scientific arguments, always smart enough to see the flaws in someone's arguments but diplomatic in pointing them out. He also strongly supported women in science—indeed, when I visited him in London the female/male ratio in his laboratory was about 18 to 1!—and many of his female trainees went on to very successful careers in biomedical research. We worked together on the editorial board of *JCB* for several years, and I was pleased when he became the Editor-in-Chief and asked me to join the very impressive group of academic editors. He put a great deal of effort into rebuilding the staff of *JCB*, and I fully expected to continue working with him for many years into the future. It was not to be. Cell biology has lost a gentleman and a scholar.

Ira Mellman

Alan Hall was a member of a small and exclusive club: current and former Editors-in-Chief of *JCB*. In the journal's 60-year history, there have been only five members, and now only two of us remain alive. Sadly, Alan served as our Editor-in-Chief for all-too-short a period of time, and his premature passing has deprived *JCB* and the entire community of cell biologists of what would have been a notable tenure. Alan was one of our best cell biologists. A rarefied figure who was responsible for discovering the function of Rho family GTPases in regulating actin function, Alan was not intimidating but approachable. He was humble, collaborative, thoughtful, and dedicated to getting it right. Alan was a long-time friend and a true gentleman of science. Of the many memories I have of our times together, the most vivid is of the time we met for lunch and a couple of pints at a small country pub outside of Oxford. We sat for several hours deep in discussion over whether Cdc42 might have a role in regulating polarity in epithelial cells, as it had just been shown to regulate polarized budding in yeast. We did produce one paper together on the topic, but I like to think of this conversation having

launched Alan on a path toward multiple transformational discoveries over many years. Invariably, Alan used a deceptively simple approach to generate a dataset that at first glance appeared childlike in its simplicity but was in fact profoundly deep in its implications. Alan was an understated man, but one who never underappreciated. In this, he was a member of a club of one. I fear that like his work, Alan's absence will likely become all the more apparent as time passes.

Tom Misteli

Alan left an early, lasting impression on me as I listened to one of his seminars on his groundbreaking work on Rho and Rac, when I was still a first-year graduate student in London. What struck me was the elegance of his science, the ambition of the questions he was asking, the clarity of his arguments, and the rigor of the experimental approaches. Little did I know that years later I would come to rely on Alan as a calm, wise, fair, and thoughtful advisor on the senior editorial board of *JCB* and as someone whose sage advice I always trusted while I served as the Editor-in-Chief of *JCB*. I was relieved to know that the journal would be in good hands as he succeeded me in that position. Alan was the epitome of thoughtfulness and integrity both as a scientist and as a man. There is much we have lost with his passing, not the least his unforgettable witty and knowing smile that seemed to have the power to solve problems small and large and always put us all at ease.

Jodi Nunnari

Alan was a complete class act. Every comment was always right on point and delivered in his unique, understated manner. I respected him and greatly valued his excellent judgement and opinion, which he used to guide *JCB* always in the correct direction. I will miss him very much.

Ken Yamada

We all knew Alan Hall as a marvelous scientific innovator, conscientious editor, and warm friend to many. He was particularly renowned for characterizing the central importance of Rho GTPases in cell and tissue dynamics, but his characteristically rigorous, creative work

extended into many other research areas. Both in his own research and in evaluating the work of others, he displayed impressive clear-eyed, critical rigor and concern about appropriate scientific approaches. As some very recent concrete examples, here are Alan's original words as we collaborated on an editorial about research reproducibility. He first commented almost wistfully about the best practices for reproducibility: "These used to be integral to any serious study, but now seem to be given less consideration." Referring to a commonly used approach, he wrote, "while this is expedient and often satisfies reviewers, it is likely to account for much irreproducibility in the literature."

This idealism without illusions and concerns about rigor were complemented by an understated style of presenting his own work that contrasted with the showmanship in other talks. Yet accompanying his quiet, gentlemanly demeanor were frequent delightful flashes of a wry and sometimes sly sense of humor.

Alan took his *JCB* editor responsibilities unusually seriously. His comments to authors to help them understand and respond to reviews were remarkably specific, in-depth, and helpful. Using his knowledge of the best reviewers in multiple fields and providing even-handed, thoughtful opinions, he contributed importantly for decades to improving and then briefly leading *JCB*.

Alan leaves us an inspiring legacy of ideals in science, both for how we should perform our own studies and for constructively strengthening biomedical research in general. We should honor him by doing our best to sustain this impressive legacy.