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IN MEMORIAM

In memoriam: Catherine Rabouille (1962–2025)

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The cell biology community mourns the loss of Catherine Rabouille, an exceptional scientist whose determination, innovation, and fearless engagement with ideas reshaped how we think about cellular organization. After a brave battle with metastatic breast cancer, Catherine chose to bring her life to a peaceful close on 7 August 2025, in a manner consistent with the clarity, resolve, and agency that defined her approach to science and life. She was an extraordinary mentor, whose generosity, attentiveness, and unwavering support shaped generations of scientists and left a profound mark on all those she guided. Catherine leaves behind a legacy defined by intellectual courage and an enduring passion for science.

The scientist

Catherine's passion for science was evident from the outset of her career. She completed her PhD in 1988 at the Université de Technologie de Compiègne (France), where colleagues recognized traits that would define her scientific life: fierce determination, strong intuition, and a deep curiosity about the inner workings of the cell. Early in her career, she distinguished herself by thinking independently and daring to challenge accepted ideas.

Following her PhD, Catherine undertook a postdoctoral position at Harvard University (USA) at the Laboratory for Biomembranes and Carbohydrate Chemistry at the Joslin Diabetes Center. In 1989, during a cryosectioning course in Heidelberg (Germany), she met her future husband, Adriaan Oprins, together with whom she had a life in harmony thereafter. In 1990, she moved to the Department of Cell Biology at University Medical Center (UMC) Utrecht (the Netherlands) for a postdoctoral position, where under the guidance of Jan W. Slot she developed exceptional skills and knowledge in EM and applied it to the study of autophagic processes (Rabouille et al., 1993), laying the technical foundations that would underpin much of her later seminal research on the secretory pathway.

In 1993, Catherine moved to the Imperial Cancer Research Fund in London (UK) for a postdoctoral position in the laboratory of Graham Warren, where she made a major breakthrough. For around 5 years, Catherine spearheaded pioneering research on the reassembly of the Golgi complex after mitosis. She succeeded in reconstituting the Golgi in a cell-free *in vitro* system, which was a feat that had never before been achieved for such a complex membrane-bound organelle (Rabouille et al., 1995a; Rabouille et al., 1995b)—see Fig. 1. In vitro reconstitution transformed the complexity of the Golgi into a tractable, testable system, allowing the fundamental organizing principles and components of Golgi structure and function to be uncovered. This research was carried out during a uniquely competitive period in Golgi research, when the question of whether the Golgi complex was a stable organelle or a highly dynamic, self-organizing structure was the subject of intense debate (Emr et al., 2009). Against this backdrop of conceptual controversy and rapid technical progress, her contributions fundamentally advanced our understanding of the Golgi complex. Her exceptional microscopical skills and unending enthusiasm allowed her to succeed where many others would have failed. Graham recalled that while he had been trained to approach problems by building step-by step on experimental observations, Catherine taught him the value of something she strongly believed in: intuition. She pursued bold hypotheses and speculations, such as implicating the ATPase p97 in Golgi reassembly, based initially on a hunch, to be proven correct (Rabouille et al., 1998; Rabouille et al., 1995a). Through this, she became an unusually independent and unconventional researcher.

After her time in London, Catherine made a decision to acquire new expertise with *Drosophila melanogaster* through a postdoctoral position at the Department of Biochemistry at Oxford University (UK). This brave decision to switch model systems paid off and laid the foundations for her independent career, which started as a group leader at the Wellcome Center for Cell Biology at the University of Edinburgh (UK) in 1999. Catherine's output during these early years as a group leader was prolific. With her first PhD student, Vangelis Kondylis, she provided foundational contributions to our understanding of transitional ER (tER)-Golgi units as functional and organizational entities of the early secretory pathway in *Drosophila* (Kondylis and Rabouille, 2003; Kondylis and Rabouille, 2009).

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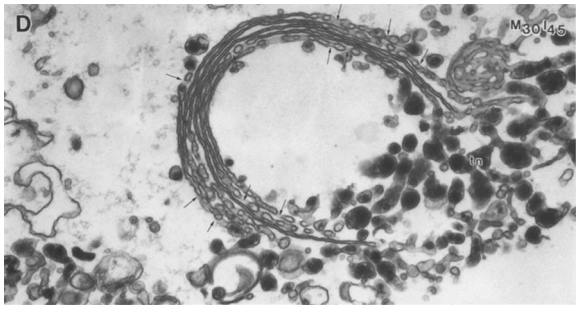

Figure 1. **An electron micrograph of in vitro reconstitution of the Golgi complex (from Rabouille et al., *J. Cell Biol.* 129:605–618, 1995)**.

Their studies challenged the view of the Golgi as a static organelle by showing that, while its spatial coupling to tER sites maintained organelle function and identity, its architecture was plastic and adaptable to cellular need. In 2002, she moved back to the UMC Utrecht to continue working on the regulation of the early secretory pathway (Ivan et al., 2008; Zacharogianni et al., 2011) and subsequently became a group leader at the Hubrecht Institute in 2010, while also holding a professorship at the UMC Groningen (the Netherlands) from 2016.

Catherine's research at all three Dutch institutions exemplified her remarkable ability to forge new scientific territories: first with unconventional secretion (Rabouille, 2017), and second, in the discovery of Sec bodies (Zacharogianni et al., 2014). Her long-standing interest in Golgi organization led her to study the Golgi reassembly and stacking proteins, or GRASPs. Working on the *Drosophila* ortholog, dGRASP, her lab made the striking discovery that certain transmembrane proteins, such as integrin α subunits, can reach the plasma membrane by bypassing the Golgi apparatus altogether (Schotman et al., 2008). At the time, the idea that proteins could be secreted without traversing the classical ER–Golgi route was highly controversial. However, since then more evidence has emerged that GRASP proteins are evolutionarily conserved regulators not only for the unconventional secretion of transmembrane proteins such as integrins and mutant CFTR, but also for the release of soluble proteins lacking signal peptides (Lerche et al., 2026; Rabouille, 2017). This body of work, together with that of others, laid the conceptual foundations of a now established and rapidly expanding field of unconventional secretion, encompassing multiple distinct pathways that are often engaged under cellular stress.

Catherine's interest in how the secretory pathway adapts to stress led directly to the discovery of a membraneless organelle: the Sec body, which forms in response to adverse cellular conditions such as nutrient scarcity (Zacharogianni et al., 2014). While it was well known that conventional secretion is downregulated during stress, Catherine showed that key components of the early secretory pathway do not simply disperse or degrade. Instead, selected proteins, such as dSec16, reversibly coalesce into Sec bodies through liquid–liquid phase separation, where they are protected and stored for rapid redeployment once normal conditions are restored. This discovery coincided with the emergence of phase separation as a unifying principle of cellular organization, highlighting Catherine's instinct for identifying pioneering biological concepts (Rabouille, 2019).

Rather than following the field, Catherine consistently demonstrated remarkable innovation, developing frameworks and ideas that paved the way for new fields of research. It is particularly notable that such groundbreaking achievements were often accomplished with a small, tightly focused team of one or two researchers. Besides contributing conceptual ideas, Catherine and her colleagues often developed novel techniques to address research questions, often involving her favorite technique: EM. An example of which was in situ hybridization-immuno-EM for the detection of individual mRNAs at the ultrastructural level (Herpers et al., 2010). These inventive approaches and her expertise led to many collaborations and contributions to many fields in cell biology, including mRNA localization and axis specification in oocytes. In addition to her research, Catherine made lasting contributions to the scientific community by organizing multiple workshops and minisymposia, which fostered exchange across disciplines and brought together researchers to tackle emerging questions in the field. Her fair, direct, and rigorous assessment of science was also invaluable on grant review panels; a fellow reviewer remembered "she said things that many of us had thought, but never dared to say." Ultimately, Catherine's collegiality and her contributions to the cell biology community were recognized when she was elected as an EMBO member in 2009.

The mentor

Across all of her roles, Catherine was known as an engaged and outspoken colleague, who thrived on discussion and debate. Her incisive questions brought energy and momentum to every seminar and group meeting she joined, and she never approached things half-heartedly. With her characteristic "OK, let's go," she would dive into problems with infectious enthusiasm. Exchanges with Catherine were always lively and thought provoking; she sharpened ideas and challenged assumptions. Widely sought out for her insight, she was incredibly generous with her time and often helped colleagues think more clearly over their science through rounds of writing and rewriting (sessions she fondly called 'ping-pong'). Drafts would frequently be returned littered with comments such as "I'm confused," followed by "NOW I'm REALLY confused," "rewrite," "not clear," or "what are you telling me?" These confronting remarks and subsequent discussions invariably led to a stronger and more refined piece of work, driven by Catherine's genuine need to understand the science herself. She often said, "Two people can have a conversation and walk away hearing completely different things." Catherine made sure the scientific message was clear to all; if she understood your writing, others would too. These qualities made Catherine an exceptional mentor and advocate. Be it scientific or personal problems, she took time to listen, saw issues clearly, and provided measured advice. Her deep commitment to mentoring and supporting colleagues through professional challenges was unwavering. It is for this reason that she was an active member of several career development committees. Even when ill health limited her ability to engage fully in scientific work, she continued to prioritize the needs of her

Figure 2. **Catherine (image taken in 2024)**.

mentees, particularly those at early career stages. During her cancer treatment, sometimes when she had only an hour or two of energy each day, Catherine often chose to spend that time meeting online with her mentees, offering scientific feedback and thoughtful career advice.

The human

Catherine was always unmistakably herself, and she approached science much as she approached life: with deep commitment and dogged determination. She cared profoundly about her trainees, friends, and colleagues. She knew the names of partners and children, remembered their birthdays, and had a genuine interest in the lives of those around her. If Catherine worked with you, she wanted to know you as a person, not just as a colleague (Fig. 2).

She also cared deeply about nature and the environment. Catherine was acutely concerned about climate change and was deliberate in doing her part to limit her carbon footprint and help preserve the world for future generations.

The way she faced her cancer diagnoses reflected who she was: determined, resilient, and unwilling to give in. She won the first battle. The second time, she fought for years. In 2020, after being told she had only a few months to live, once again she defied statistics. She was determined not only to see her students graduate but to spend that time forging deeper, meaningful connections with her friends and family.

Despite being in pain, Catherine's energy and creative spark never faded. She herself was a singer, and she loved art, literature, music, and film. When her lab closed, she redirected her energy elsewhere. She wrote reviews of the films she watched (which were sometimes delightfully damning). She also created a website documenting the street art of Utrecht, bringing the same curiosity and care to these pursuits as she did to her science and colleagues.

Final word

We live in an academic culture increasingly defined by metrics that attempt to quantify academic worth but inevitably fail to capture its full substance. Measures such as the H-index cannot account for the intangible yet profound contributions scientists make to the intellectual lives and careers of one another. Catherine cared deeply about people and invested enormous energy in sharpening their thinking and the clarity of the way they expressed their ideas. She did so not quietly or passively, but through direct and often challenging discussions that pushed their science to become clearer, stronger, and more honest. While her research alone has left an indelible mark on our understanding of secretion pathways and organelle dynamics, it is an irony Catherine herself would have appreciated—given her lifelong fascination with numbers—that perhaps her most enduring influence lies in contributions that resist quantification, carried forward in the work, confidence, and clarity of thought of those she trained, challenged, and inspired.

Catherine Rabouille is survived by her husband, Adriaan, her daughters Lila and Neve, and a global community of colleagues and friends who will continue to feel her influence. Her legacy lives on in the discoveries she made, the concepts she introduced, and the many people whose thinking she transformed through her passion, intuition, and fearless engagement with ideas. All of us, colleagues and friends of Catherine, will celebrate her memory with a glass of Malbec, her favorite wine, as she urged us to do!

- In remembrance of Catherine Rabouille, a force of nature in science and in life.

Author contributions: All authors contributed to the article.

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