Images, Imagination, Insight

Prof. dr. A.M.C. Emons

Farewell address upon retiring as Professor of Plant Cell Biology at Wageningen University on 21 April 2011

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Mister Rector, ladies, and gentlemen,

Cell biologists make micrographs, images of cell interiors and movies of cell processes. They want to see how cells work, to gain insight in cell mechanisms.

A cell, the building block of organisms, of plants as well as of animals and humans, resembles a community with workers, engines, factories, energy plants, post offices, infrastructure, and a transport and communication system.

In the past 30 years cell biologists have seen many of their imaginations come true, from observing cell skeleton function in glass mini-containers, to filming enzymes in living cells producing cellulose microfibrils.

Introduction

Images may look alike, but represent very different things. For instance, a photograph of part of a *Tradescantia* stamen hair cell, a photograph of a woman's breast with a tumor, and a photograph of a bursting volcano may look alike. Elisabeth Pierson, postdoc in my laboratory, injected the *Tradescantia* stamen hair cell in 1996 with fluorescent actin from animal source. At the site of injection new actin filaments formed, which resemble the tumor in the breast. If the image of the volcano is turned around and with Photoshop the lava is taken away, it is not recognized as a volcano. Important is the scale bar; for the image of the volcano it is not 5 centimetres, but 5 kilometres. The take home message: we need context, as for instance a scale bar, to interpret images. Now we turn our attention to my favorite study object: plant cells.

To be useful for cell biological research, cells have to be accessible for fixation, drug treatment, signal application, and live cell imaging. I have used several cell systems but as example I show the root hairs, cells sticking out from roots. Some of my colleagues from outside the plant field find them funny. In a living plant cell a lot of activity is going on.

These cells are model systems, as can be learned from a review of a book on them, in which our colleague Nigel Chaffey says: Mendel had his peas. Morgan his fruit flies. Emons and Ketelaar have their... root hairs.

Which are the cell biological images that allowed me imagine the working of cells?

From freeze fracture images to membrane cleavage imagination

That started with my MsC work on cell wall formation in the green alga *Chlorella* at the Radboud University in Nijmegen. I freeze fractured dividing *Chlorella* cells, which work was published in 1970. We had many discussions about the fracture plane. Singer and Nicolson had already published their fluid mosaic model in which a cell membrane is a liquid lipid bilayer with embedded proteins, and in our discussions, it was my imagination that the fracturing was splitting that membrane, and that the particles we see are proteins embedded in the lipid bilayer. When I came back to science in 1980 to work for my PhD, after having three children and having been teaching biology, I had to work through a pile of literature, and found a paper in Science by Branton and other scientists, published in 1975. From then on it is established that by freeze etching and fracturing the membrane indeed splits and that the particles we see are proteins.

From cellulose microfibril deposition orientation to imagining cellulose production

This PhD work was done in Nijmegen as well, and my doctoral supervisor was André Sassen. The topic was cellulose microfibril formation. Cellulose microfibrils are the load-bearing structures of the plant cell wall, an extracellular structure all plant cells have; they help plants stand upright. The cellulose microfibrils are embedded in a matrix of other polysaccharides as steel rods in reinforced concrete, and consist of 18 cellulose chains of beta-1,4D glucose.

The images I made from cell walls of *Equisetum* root hairs – it was before *Arabidopsis* was in fashion – and which required a lot of imagination, were pictures representing cellulose microfibrils in the cell wall, combined with images of particles in the freeze fractured plasma membrane, and grouped in rosettes. We imagined that those rosettes were the cellulose synthases. A team of scientists form Texas and Japan have many years later proven that these rosettes indeed contain the enzymes that make cellulose microfibrils. So, the rosettes are cellulose synthase complexes.

I had those photographs of blown up cellulose microfibrils, and saw their angle change along the plasma membrane, while cortical microtubules remained longitudinal, and the paradigm was that cortical microtubules, tubes made of tubulin and aligned along the plasma membrane, at the other side, orient the cellulose microfibrils, in fact the hypothesis I wanted to prove.

At conferences, people asked: 'How are these cellulose microfibrils in the wall of these root hairs organized, if not by microtubules?' Though my standard answer was 'And what organizes the microtubules?' I had to come up with an idea how such a helicoidal cell wall with successive layers in which the microfibril angle rotates, could be made without a guiding principle from within the cell.

$$\sin \gamma = \frac{Nd}{2\pi R}$$

I did come up with this formula, which supposes that the cellulose synthase complexes move straight unless obstructed, if deposited in a constrained space. The main variable that determines the angle (γ) is the number of rosettes producing these cellulose microfibrils (N); d describes the ratio of cellulose microfibrils and cell wall matrix, and R relates to the geometry of the cell.

A further supposition to make this particular helicoidal cell wall was that there should be rosettes everywhere in the plasma membrane, but that insertion of them

into that membrane would occur in waves. For the production of most other cell wall textures rosette insertion into the plasma membrane should occur in the whole membrane.

With these ingredients I could imagine how a helicoidal cell wall and all other types of cell wall could be constructed without an organizing principle from inside the cell. I could make drawings on paper, and together with Henk Kieft in the computer. However, it remained my imagination difficult to communicate to other scientists.

It was after Bela Mulder from FOM Institute AMOLF, with whom I had started to collaborate in the '90s, had made this formula parameter-less, and calculated the solutions for different situations, that we could feed the data to a computer, which produced the simulations for the helicoidal cell wall. Now we had a 'virtual laboratory' in which 'experiments' can be performed under different conditions, that is, values of the parameters of the model.

By varying these values, all the different cell wall textures can be produced. Via mathematics and simulation we brought the imaginations back to images that cell biologists understand. Is this model true? YES, all wall textures can be produced from this principle, in which the number of rosettes in the plasma membrane determines cellulose microfibril orientation, unless this default mechanism is overruled, by obstructing the rosettes. The proper question is: Does it occur in nature? Whether and for what microtubules are needed to orient cellulose microfibrils cannot come from modeling, but should come from experimentation.

The dream I had as a PhD student, the experiment I wanted to do, was to follow the rosettes in the plasma membrane of living cells, but they could not be observed with the best of light microscopes, only with electron microscopes, but in the electron microscope the cells do not live anymore. I made a cartoon for a review article in 1991; it imagines that these complexes, embedded in the plasma membrane move while depositing the cellulose microfibrils in the cell wall from UDP-glucose in the cell.

More than 25 years later, Fabiana Diotallevi, PhD student of Bela Mulder, went further with imagining the movement of a rosette inside the plasma membrane while depositing a cellulose microfibril, with a simulation. It is indeed generally thought that the cellulose synthase complexes move inside the membrane by the force of their own production, not driven by the action of molecular motors, but comparable to a jet engine.

Nowadays we use a trick. We take the gene for the protein that makes the jellyfish *Aequoria victoria* fluorescent and put it onto the gene for a protein we want to visualize, in this case the cellulose synthase. Then the fusion protein will be fluorescent.

From filming cellulose synthase trafficking in vivo to insight in cellulose production

Now that we gave them that little lamp, we can see the cellulose synthase complexes and the microtubules in the light microscope in living cells. In the photobleaching experiment that my PhD student Jelmer Lindeboom did, the microtubules are red and the rosettes are green. The big green blobs are Golgi bodies with cellulose synthase complexes in them. The small particles are the rosettes in the plasma membrane moving at steady velocity, and producing cellulose microfibrils. Jelmer bleached the existing GFP-fluorescence away and looked where particles come back and whether this is along microtubules. This work done was in collaboration with Ryan Gutierrez from Carnegie Institution at Stanford. We see the cellulose synthase complexes being inserted into the plasma membrane along microtubules and subsequently moving along them. This is a big further step to INSIGHT in the process. Here we look deeply, very deeply, into cells, living cells, in which we see the movement of a protein complex of 40 nm. What can be measured is that its speed is 300 nm/min.

This is slow. Molecular motors transport structures in plant cells at velocities up to 12 μm/min. However, while moving the complexes produce those big polymers the cellulose microfibrils. You should not compare this process to a car driving on a road, but to a road-paving machine producing the asphalt of the road.

If we remove the microtubules from the cell, rosettes change their orientation of movement, but still move in orderly patterns, which can be seen in a time stack of them. Thus, there is an intrinsic default ordering mechanism, which microtubules can overrule.

What about root hairs? In a photobleaching experiment on *Arabidopsis* root hairs my PhD student Ying Zhang showed that cellulose synthase complexes are inserted into the plasma membrane in the tip as well as in the tube of the hair, and move on microtubules, and between them.

Ying studies the distribution of angles of cellulose synthase complexes in relation to microtubules in fully-grown root hairs. Histograms show orientation of movement of them with microtubules, microtubule orientation itself, cellulose synthase complexes in cells from which microtubules have been removed, and with prolonged removal, complexes on microtubules, and complexes in between microtubules. What's the difference? All are helical with a slight deviation from the long axis of the hair, but the dispersion, the variation in angles is significantly different. Interestingly, the difference between orientation with and without microtubules is comparable to the difference between cellulose synthase complexes moving on and between microtubules. So, the wider the microtubules are apart, the less do they influence cellulose microfibril orientation.

From images of vesicles to membrane regulation during cellulose production

Cellulose synthase complexes are inserted into the plasma membrane from the Golgi system, in an exocytosis event in which the Golgi vesicle membrane fuses with the plasma membrane.

In a movie we see three stages of behavior of cellulose synthase complex: erratic mobility, could be: the arrival of the Golgi structure at the plasma membrane; static localization, could be: the fusion of the membranes; and steady movement, that is: movement of the rosette through the membrane while depositing the cellulose microfibril.

Apart from exocytosis there is also endocytosis, removal of plasma membrane as vesicles back into the cell interior, by clathrin coated pits. There has to be internalization of plasma membrane during cell growth, since otherwise the plasma membrane would become wrinkled, because the vesicle is three-dimensional and the wall two-dimensional.

When plant cells are not turgid, the rosettes disappear from the plasma membrane, which I have shown in my PhD work. We speculated, imagined, that the rosettes fall apart, or are internalized or are not inserted anymore.

Recently, we could show that, Small cellulose synthase-Containing Compartments (SmaCCs) accumulate on shrinking microtubules in stress situations. Orientation and speed of movement of these SmaCCs differs from the movement of the cellulose synthase complexes, but is also not geared by motor molecules. The complexes sit on microtubules, and when the microtubules shrink the complexes move with their shrinking tips. From these tips they can be inserted into the plasma membrane, which in our imagination, provides a mechanism in which during stress condition, rain, wind, cold, heat, drought, the cellulose synthases are preserved such that they can come into action as soon as the stress is relieved, and start producing cellulose again.

From imaging cortical microtubules and cellulose microfibrils to imagining direction of cell elongation

Plants can be tall. How do we imagine that their cells grow? One of the paradigms in plant cell biology is that cell elongation takes place transverse to the direction of cellulose microfibrils, which themselves are organized in a transverse way by transverse cortical microtubules. 50 years ago, Paul Green predicted the existence of cytoplasmic structures before scientists had ever seen microtubules. About the properties of these cytoplasmic structures he predicted – the possession of a long axis and the ability to build cellulose microfibrils perpendicular to it –. This is not how this paper is often cited, and I urge young scientists to read the literature and not just cite from other publications.

In collaboration with our colleagues from Versailles we studied this in etiolated *Arabidopsis* hypocotyl cells, and as appeared this week in our congress, two other groups have the same results. Only the youngest cells have transverse orientations in all cell sides. In the other, still elongating cells, only the inner cell face has the transverse microtubules, lanes of cellulose synthase complexes and nascent cellulose microfibrils, but the radial cell faces have oblique orientations, and the outer cell face can have all different orientations. We show this in cells that have been opened to expose the outer wall with longitudinal, the sidewall with oblique, and the inner wall with transverse cellulose microfibrils. The imagination of the plant cell community was that transverse cellulose microfibrils inhibit cell swelling. We have to come up with new imaginations. Part of my imagination has always been that inhibiting wall stretching in a certain direction is a too simple idea and that we should take into account that determining in which cell sides new wall is deposited must play a role in the process of cell elongation. That, could be the main task of cortical microtubules.

From images from space experiments to imagination of the interaction between cortical microtubules and cellulose synthase complexes

We were selected to carry out an experiment in space, in the mission in which Dutch astronaut André Kuipers in 2004 carried out experiments in the ISS, the International Space Station. I will not talk about the money such an experiment costs, or the media hype it caused and also not about the hours of discussions I had with ESA to get equipment to do the right control experiment, a 1g centrifuge, and surely not about how the space lab at ESTEC in Noordwijk made an ordinary mistake, by which we, and all other cell biology groups involved, lost our results but were given the opportunity to fly again to the ISS. That second time we did get results that required lots of imagination.

Other researchers had already shown that protoplasts, plant cells from which the cell wall has been stripped of, do not develop in space, while on Earth they can grow into healthy plants. Since it had also been shown that microtubules *in vitro* do not organize well in space, our experiment dealt with our favorite polymers, microtubules and cellulose microfibrils.

We used tobacco BY-2 suspension cultured cells, that is, single cells with a cell wall, thus, a cell type in between protoplasts, without walls, and complete walled cells in a tissue. The cell containers, the 'Plunger Box Units', actually are small automatic test devices, small laboratories. The cells are growing well in nylon nets in the PBUs.

These walled cells were able to grow and divide normally at near weightlessness and their microtubules and cellulose microfibrils were organized as on Earth. Thus, when there is no gravity, the cell wall plays a role in organizing the microtubule array. Since there are more reports on cellulose microfibril orientation determining microtubule orientation, this gives speculation about the forces involved.

In electron micrographs we see cortical microtubules attached to the plasma membrane. Part of the rosette is below that membrane, which makes that rosettes and microtubules are in the same plane. Could the rosettes push the microtubules away in some instances, while mostly the microtubules restrict the movement orientation of the cellulose synthase complex? These forces depend on the attachment of the microtubules to the plasma membrane, and on the force of the movement of the rosettes, which should depend on the integrity and completeness of the rosette itself.

From images of actin cytoskeleton configuration to imagination of cell spaces that show specific transport behaviour

'Forces in cells' is still a not well-developed topic. In a project co-sponsored by the FOM Institute AMOLF, PhD student Agnieszka Esseling-Ozdoba injected artificial vesicles and latex beads into dividing plant cells. A speeded up movie of a dividing plant cell shows the formation of the cell plate, the new cell wall. A cartoon of a cell at cytokinesis shows the phragmoplast microtubules: two cylinders of microtubules transverse to the forming cell plate created by the fusion of Golgi vesicles.

Agnieszka imagined that not only size but also stiffness is a factor determining which structures can pass through the phragmoplast to the cell plate and which

ones cannot. That was her research question, which we studied in collaboration with the department of Physics and Colloid Chemistry of Wageningen University. We found that vesicles up to 150 nm in diameter could pass, but beads even as small as 20 nm in diameter did not reach the cell plate, and hung inside the phragmoplast. Thus, the phragmoplast cytoskeleton makes a cell space, where structures are sorted by size and stiffness. This phragmoplast contains microtubules as well as actin filaments. The ringlets of microtubules are positioned at the sides of the growing cell plate, but actin filaments are present in the whole area. Since the fluorescent synthetic vesicles move also through the phragmoplast area where there are only actin filaments and no microtubules, this research lets us imagine that at least later in phragmoplast development not the microtubules with their motors, as is generally thought, but the actin filaments with actin-related motor proteins transport the vesicles to the growing cell plate. This requires further research.

We see a comparable phenomenon in tip-growing cells. How do the Golgi bodies of which there are hundreds in a plant cell, reach the right side of the cell, where the vesicles have to be inserted into the plasma membrane? We studied this in the root hair, and the answer is: the actin cytoskeleton. In plant cells, the actin cytoskeleton is still more difficult to visualize reliably than the microtubule cytoskeleton and, therefore, the path from images to imagination and beyond is trickier. In a growing root hair the actin cytoskeleton in the subapex is finer than in the hair base. We imagine that this configuration of actin filaments keeps the larger organelles away from the cell tip where the vesicles have to insert, by giving a passageway for the vesicles, passive as a sieve, or active as a transport device, which is still an unknown. We called this configuration of the actin cytoskeleton fine F-actin.

From images of root hair deformation to imagination of root hair curling

Norbert de Ruijter could show that this fine F-actin increases when legume root hairs are treated with Nod factor produced by *Rhizobium* bacteria.

Nod factor is produced when the bacteria come into contact with legume roots, after which root hairs curl around the bacteria and bacteria enter the root nodules that the plant has made, in which bacteria start nitrogen fixation, a process crucial

for life on Earth. Scientists speculated that for root hair curling bacteria would be required.

My PhD student John Esseling tested his imagination that Nod factor alone could induce root hair curling by putting a drop of Nod factor onto the growth area of the root hair with an very fine pipette, technically challenging, but the type of experiment I like, since the answer would be YES, or NO or a NUMBER, here a percentage. The answer is: YES, always, when the drop with Nod factor was placed at the hair's hemisphere, the hair started curling towards the drop with Nod factor.

Seeing that something happens does not mean understanding it. How can the elongation direction shift? We imagine the following sequence of events. The first bacterium encountering the root hair tip produces Nod factor, which is immobilized in the cell wall – that is known-, and induces a local calcium ion increase – also known. Since during root hair elongation calcium ion is high at the tip, the region of high calcium shifts from the tip in the direction of the site where the bacterium attaches. Also fine F-actin increases, which delivers the Golgi vesicles to the plasma membrane for cell elongation. The bacteria multiply and therefore continually attach further to the growing hair tip. Eventually the curl entraps the colony of bacteria.

The importance of collaboration for correcting one's own scientific imaginations

Collaboration with scientists, especially of different disciplines, is important for fine-tuning one's own imaginations. I will only mention the collaboration that meant most to me. The collaboration with Bela Mulder gave us more than a possible theory about cell wall texture formation, cellulose production, and microtubule ordering, but gave Bela a professorship at Wageningen University and I became advisor bio-organization at the FOM institute AMOLF, a physics institute. This function has naturally finished, since many excellent physicists working on cell biological questions have been appointed the last years in this institute. I enjoyed the collaboration with Marileen Dogterom of AMOLF on microtubules. With Ton Bisseling of Wageningen University I collaborated on the topic of legume-Rhizobium interaction, part of which I just mentioned.

With Martien Cohen-Stuart and his group of Wageningen University we collaborated in the phragmoplast project. Collaboration with David Ehrhardt from Carnegie Institution at Stanford is still going on.

Based on the cell wall model, and other work, we received good money from the European Commission in the FP6 NEST Adventure program. We called our project CASPIC: Cellulose Architecture Systems biology for Plant Innovation Creation. In this project Bela Mulder and I collaborated with Ingo Burgert from Golm, Björn Sundberg and the company SweTree from Umeå, and especially with the group of Herman Höfte from INRA, Versailles. It was a successful project.

Application of basic research

Three months ago I was invited to present our work at a workshop on cell walls at Unilever, because they realize that knowledge about basic research is a prerequisite for application. One of the strengths of Wageningen University and Research Centre is the combination of basic research in the university with strategic and applied research in its institutes. Without basic research there is nothing to apply. The knowledge that is applied most in biology nowadays stems from the purely fundamental work on the structure of DNA, more than 50 years ago. The distinction is not between basic and applied, but between vague results and true facts. Only the latter should be published and will sooner or later be applicable, always! Of course, to be sooner applicable, the work should be on relevant topics. Unraveling the working of a cell is such a relevant topic.

Gender in the scientific workplace

In November last year in New York there was a play 'Photograph 51' by Josie Glausiusz, capturing the zeal and zest in the race to discover the structure of DNA. The play focuses on Rosalind Franklin, the physicist who in the laboratory of Maurice Wilkins actually did the experiments. When her best X-ray photograph 51 was shown to James Watson he recognized the helix that Franklin had seen too, as the missing piece in the puzzle for his and Frances Crick's model of the DNA double helix. As you may know: she did not receive the credits. In the play they ask: 'May she have triumphed if she was born at another time -or born a man?' I think to both questions the answer is: YES.

This brings me to the gender issue. When I was in the board of the LNVH, the network of female professors in the Netherlands, and mentioned the under-representation of women in the higher ranks of academia, the comment of one of the female PhD students was a question: 'So what?' To me the answer is clear: as a university, a company, or a country, you are not in the position to neglect 50% of the talent, the women. As many women as men start university education in the Netherlands, but their number decreases higher up the academic ladder, while that of men increases. Now that I leave, there remain only seven female chair holders in this university. Recent research of the LNVH and of McKinsey shows that it is a myth that there are not enough women willing to take on a demanding career: more women in middle management roles are focused on leading than their colleagues at entry level.

A tenure track system for Wageningen-UR

The best time in my work for me was the time as professor on a personal title with my own little group, independent, and with responsibilities only for people for whom I had acquired the money, sometimes together with them. I also enjoyed the time as chair, working together with the Plant Science Group professors on for instance restructuring our university management and financial system, which is the most transparent in the Netherlands now: the basis is: you can only spend the money that you generate yourself; an honest system, in itself favoring quality. Seems logical to anybody working outside a university.

The next step would be a complete tenure track system not based on topics but on people: if you have the capacities and want to work hard, Wageningen University and Research Centre has a place for you. This system from assistant to full professor in 12 years is expected to be more favorable for women, and 42% of the 64 trackers at this university are women. The slogan UP OR OUT to people such as Jacqueline Bloemhof, who received a tenure track position, does not feel scary: it's an opportunity, not a ratrace!

University education in modern molecular cell biology

The exercise of working on the cell wall model showed me the importance of a systems biology approach, in which laboratory, we say wet, experiments

are alternated with modeling. I was a member of a committee of NWO, the Netherlands Science foundation, to stimulate systems biology by distribution of research money. The money went to cancer institutes, not badly spent, and they had the best research proposals. If systems biology is the future of molecular cell biology, this should be reflected in the education system. Therefore: teach monodisciplinary, but with enough knowledge of the other discipline to collaborate multidisciplinary, and appreciate the few students who have talent for both experiments and modeling!

Thanks

Mr. Rector, it was an honor to work at this university. I acknowledge that much has been improved the last ten years under your guidance, first as director of the Plant Science Group, and now as Rector in the Executive Board of the whole organization. I find it satisfying to see how the laboratory of Plant Cell Biology further develops under the leadership of Marcel Janson. It was my task to prepare the group for a change from Plant Cytology, via Plant Cell Biology to Cell Physics. With the appointment of Marcel Janson I see this task as finished. Since the focus has changed, the name of the group should change as well. That is the main thing I added to this university: a laboratory where cell biology is being studied with the most modern approach. I thank everybody of the laboratory of Plant Cell Biology, who contributed to this endeavor, and wish them a great future. And I thank the NWO and EU programs that funded my research.

I thank the people with whom I collaborated in this and outside this university. That is a good thing of being a scientist. You are part of an international community, which is the city or village you actually live in. I found it great that the symposium of this morning was part of the Botanical Microscopy Meeting. Thank you Chris Hawes, and Victoria Lee of the Royal Microscopical Society, and scientists of this community of researchers who were together this week to discuss progress in our field, but especially I thank Tijs Ketelaar, who I have seen developing from MsC student to Assistant Professor.

Last but not least, I want to thank John, my children and my little grandchild Asha, for being caring when required and distracting when needed. When I

started to think about that cell wall model, John bought a flexible thread for me to visualize my thinking, my imagination. We talk about each other's work and that helps us to bring it at a higher level, and that will go on in the future.

How do I imagine the future

What am I going to do next? There is still an NWO committee to evaluate research proposals, there are invitations to talk at congresses and in universities, there are two courses in Beijing, China, to give. Last but not least, there are six PhD students who will defend their theses within one year from now, who I will continue to teach, together with the co-supervisors, the ins and outs of doing and reporting science:

Carolina Cifuentes, on cellulose *in vitro*, and its quantification in *Zinnia* cells *in vivo,*

Miriam Akkerman on cellulose synthase complexes, actin, Golgi and microfibrils,

Shipeng Li on EXO70, involved in exocytosis,

Jelmer Lindeboom on microtubules and cellulose synthase complexes,

Hannie van der Honing with her work on the role of the actin cytoskeleton in cell organization, and

Ying Zhang on SEC3a, an exocytosis protein, and on cellulose synthases in root hairs. She has shown that cellulose synthase complex insertion is highest at the side of the hair dome, consistent with the finding of Shaw and co-workers that this is the area of highest expansion.

And then. What is next? I want to start a new career in images, imagination, and insight. I will start working on this new project in May with a course in London: Practical guide to starting an art gallery. To the opening of the first exhibition of my gallery, called O-68, and located in Oranjestraat 68 in Velp, I invite all of you. Hopefully the opening will take place within one year from now.

Please follow me on linkedin:
http://nl.linkedin.com/pub/anne-mie-emons/28/26a/330

I thank you for your attention

Cell biologists make images of cell interiors, and movies of cell processes. Their research questions focus on cell function to gain insight in cell mechanisms. In the past 30 years cell biologists have seen many of their imaginations come true, from observing cell skeleton function in glass mini-containers, to filming enzymes in living cells producing cellulose microfibrils under experimental conditions. Their vision is that insight gained from basic research on cells will eventually be used in applications beneficial for mankind.

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