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DEDICATED TO

KEITH R. PORTER

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Manny Warman, Columbia University

*Keith Roberts Porter*  
*and the development of contemporary Cell Biology*

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By a unanimous and wise decision of the editorial board of *The Journal of Cell Biology*, this volume is dedicated to Keith Roberts Porter. The occasion is his 65th birthday, and the reason is his long list of contributions to the science of cell biology and his record of service to the community of cell biologists. Taken together, they are without equal.

The merit of the decision is that Keith Porter is honored while still very much alive and active. He may accept this expression of gratitude from his colleagues without being overwhelmed by memories of times long past; he may even enjoy it, after uttering a few sarcastic remarks about either the occasion or the editorial board. In keeping with his ideas about science and scientists, the dedicated volume is not a Festschrift, but a regular volume of *The Journal of Cell Biology*. His eulogy should come from the substance of the papers published in this volume, rather than from testimonial pieces.

#### THE MAGNIFICENT BEGINNINGS

The development of modern cell biology in the United States began in the middle 1940s, without the benefits or restrictions of a long and diversified tradition in cell research. To a very large extent, electron microscopy provided the quantal jump that marked the beginnings of a new era, and created — at least for a while — the impression of a sharp discontinuity with the past.

In those early times, electron microscopy was tried on a wide spectrum of biological specimens: from fragile and complex eukaryotic cells to such isolated, sturdy, macromolecular assemblies as collagen and myofibrils, and the scientific public of the period tended to assume that the solidity of the science produced was somehow connected with the sturdiness of the specimens examined. After a short look at a few of those tough macromolecular assemblies, Keith Porter set to work on the basic organization of eukaryotic cells, which was definitely the weakest area of the weak sector of the spectrum. It was a timely decision, for in only a few years the weak sector became an area of spectacular growth.

The new field had virtually no tradition; everybody working in it came from some other province in natural sciences. As a graduate student at Harvard and as a postdoctoral fellow at Princeton, Keith Porter had worked in experimental embryology, an area in which he had accomplished a real experimental feat: he had succeeded in producing hybrid embryos by fertilizing the enucleated eggs of one race of frogs with sperm from another race. But he left developmental biology soon after moving to The Rockefeller Institute for Medical Research in 1939, where he joined the department of pathology headed by James Murphy. There, he started working with Albert Claude on the fine structure of cultured animal cells, and succeeded in advancing this new line of investigation as far as it was possible with the electron microscopes of that period. The results of these studies turned out to be truly magnificent: among them was the discovery of the endoplasmic reticulum and the recognition of avian sarcoma virions in cultured fibroblasts. By now, the history of those early events is beclouded by legend and anecdotes (of the kind: Who said what to whom at a local pub after

a historical session at the electron microscope?). It should be clear, however, that those momentous findings were the result of close cooperation between Claude and Porter, with others (Ernest F. Fullam and Edward G. Pickels) in supporting roles, and that together they did much more than each of them could have done alone. Keith Porter continued to work in both directions long after Albert Claude's interests had moved to other problems. With Frances Kallman, he actually introduced the term "endoplasmic reticulum" into the literature, and with Helen P. Thompson, he used cultured tumor cells to visualize the virions of the murine mammary carcinoma.

#### THE ROCKEFELLER YEARS

It was about that time (1949) that Claude decided to return to his native Belgium, as there were great hopes that European science would be soon reborn from the ashes left by the war. Shortly after Claude's departure, James Murphy retired and Keith Porter became *de facto* head of the remaining group, reduced at that time to two persons only: him and me.<sup>1</sup> Keith Porter did not yet have the rank required by the local rules for the position of laboratory head, so Herbert Gasser, the director of the Institute, became officially our direct master. Gasser was an eminent neurophysiologist with a deep and genuine interest in morphology. Guided by foresight and interest, he decided to invest some of the resources of the Institute in biological electron microscopy, furnished the support and the equipment needed, and relied on Porter to provide the leadership for the activity of the new electron microscope laboratory.

That was in the early 1950s, at a time when preparative procedures for examining cells in tissues (rather than in cultures) were being developed rapidly in a few laboratories, including our own. These procedures depended heavily on further refinements<sup>2</sup> in microtomy, on which many attempts were being made; only a few proved successful. The outstanding example among the latter was the first version of the now-ubiquitous Porter-Blum microtome, designed by Keith Porter and Joseph Blum, the instrument maker of The Rockefeller Institute. With the new preparative procedures worked out reasonably well, the field of biological organization at the fine structure level was laid wide open for investigation. New findings were made in rapid succession and the population of the laboratory increased dramatically, with new trainees who ranged all the way from professors to students. In a few years, overcrowding in our small laboratory became critical; even desks installed in the corridor gave little relief. To that period belong Keith Porter's first study on striated muscle (with H. Stanley Bennett), his work on cilia (with Don W. Fawcett), the studies on protozoa (with Maria Rudzinska and Albert Sedar), on fibroblasts (with George Pappas), and the extension of the investigations on the endoplasmic reticulum to a variety of cell types (with Eichi Yamada, Raul Machado, and myself). One of the shining gems of the period was the discovery of the special

<sup>1</sup> I had joined Albert Claude's group at The Rockefeller Institute for Medical Research in 1946.

<sup>2</sup> Some significant refinements had been already introduced by Claude.

form taken by the endoplasmic reticulum in muscle cells. Porter's paper on the sarcoplasmic reticulum in amphibian muscle became a classic the day it was published.

#### AN OVERCROWDED BUT SPIRITED SCHOOL

After so many years, it is difficult to recapture in words the atmosphere of intense activity, remarkable achievements, great excitement, and unlimited optimism that prevailed in that laboratory, which otherwise looked like an unattractive dungeon sunk in the third basement of one of the old buildings of The Rockefeller Institute. Perhaps the list of cell biologists who either acquired there their full training or were given just a few finishing touches would better convey the ferment of that period. Michael Watson, John Luft, Don Fawcett, Sanford Palay, Russell Barnett, Walter Stoeckenius, Montrose Moses, Guido Majno, Marilyn Farquhar, Fritz Miller, Eichi Yamada, David Smith, Samuel Dales, Raul Machado, Howard Davies, Helen Deane, Roberto Sotelo, Gabriel Godman, George Pappas, Maria Rudzinska, Albert Sedar, Lucien Caro, Juan Vial, Carlo Bruni, Lee Peachey, David Luck, Peter Satir, Lewis Greene, and quite a few others were there at one time or another, working with either Keith Porter or me. At about the same time began the renewed interest of the laboratory in the biochemistry of cell fractions that brought Philip Siekevitz to our group.

Added to all this excitement was a pervading free spirit — often irreverent, but always helpful, because it acted as an antidote against imagined grandeur. Keith Porter was responsible for a good part of that spirit. Occasionally, he was the victim, but much more often he played the role of lord executioner, his preferred victims being carefully selected from among high officials. He showed great wit and intense interest in needling authority, and for this reason acquired the nickname "Herr Teufel," more in admiration than in dread. Perhaps someone should try to write a few tales from the third basement before all is forgotten.

#### A JOURNAL AND A SOCIETY

By the middle 1950s, it was clear that biological electron microscopy was going to be extremely productive and that it needed its own journal, because resistance against publishing papers on fine structure was increasing rapidly even in those journals that supposedly were animated by a broad and experimental spirit. It was our common belief — Keith Porter's and mine — that the future of the field depended to a very large extent on an integrated structural-functional approach to cell research, and that a new journal should try to attract and publish structural, as well as biochemical and biophysical, studies on cells and cell components. In addition to such basic considerations, practical problems made it desirable to cooperate, rather than compete, with other groups active in the field, primarily F. O. Schmidt's group at M.I.T. Keith Porter and H. Stanley Bennett took the initiative in discussing the issue with the administration of the Institute and with other interested parties. With Her-

bert Gasser's strong support, the discussions were brought to a favorable conclusion in the spring of 1954, and in 1955 the first issue of *The Journal of Biochemical and Biophysical Cytology* was published by The Rockefeller Institute. The list of the members of its first editorial board<sup>3</sup> gives a clear indication of the original intents of the Journal and of the constructive approach Keith Porter took in matters of scientific organization. Herr Teufel was not really joining the establishment; age and commitment were making him wiser.

In its second year of existence, the Journal published as a supplement an impressive volume: it presented the state of the field as it emerged from a symposium on biological electron microscopy organized by Porter and held at Arden House in Harriman, New York.

The publication of a journal that encouraged an integrated look at basic biological problems, the creation of many new biology laboratories throughout the country, and the change in orientation of some old research groups led, in the late 1950s, to a social regrouping in the basic biological sciences. Cell biology was becoming an attractive central field, a common ground for groups that had worked in complete isolation just a few years before. A new community was in the making. With the same remarkable sense of timing that led to the foundation of the *Journal of Biophysical and Biochemical Cytology*, Porter convened a group of cell biologists (some tested converts and some catechumens) at The Rockefeller Institute in the spring of 1960 and, with them as charter members, founded the *American Society for Cell Biology*. A few years later, he proposed that the name of the Journal be changed to *The Journal of Cell Biology* and that its editorial responsibilities be shared with the new Society. The proposal was accepted, and still governs the editorial policies of the Journal.

#### SUCCESS FOLLOWED BY PROBLEMS

After trying hard for about five years with very limited means, and after working harder for about ten more years with decent equipment, Porter made his laboratory a success at Rockefeller, but a success with all the mixed blessings that usually attend such a situation. He had been member and professor of The Rockefeller Institute for quite some time, officially and actually the head of the department; the laboratory had moved to new and (by comparison) spacious and elegant quarters in a new building; and — to compensate for those many years in the basement — it had a splendid view over the East River. Finally, everything seemed to be calm, stable, and serene; but we didn't count on deans, presidents, and *almae matres*. Any enterprising dean believes that a successful group must be split so that he can get one of the splinters, without thinking for a moment that some groups really deserve to be left alone. Also, and unfortunately, few scientists (properly imprinted in graduate school) resist the temptation to reeducate their alma mater. And so it came

<sup>3</sup> The editorial board included Richard S. Bear, H. Stanley Bennett, Albert L. Lehninger, George E. Palade, Keith R. Porter, Francis O. Schmitt, Franz Schrader, and Arnold M. Seligman.

about that, in 1961, Keith Porter left The Rockefeller University and moved to the Biological Laboratories of Harvard University with part of our former group. At the time of his departure, we unveiled his portrait, for which he provided, in the old style of the third basement, the inscription: "Our father who art at Harvard."

#### THE HARVARD YEARS

At Harvard, Porter returned to undergraduate teaching, in which he had been involved as a graduate student a number of years earlier.<sup>4</sup> He liked the experience, and the students gave his course high marks. The byproducts were two beautifully illustrated atlases entitled *An Introduction to the Fine Structure of Cells and Tissues* (with Mary A. Bonneville) and *Introduction to the Fine Structure of Plant Cells* (with Myron Ledbetter). The first has gone through a number of editions and has been translated into German, Italian, and French.

The research of Porter's new group concentrated on the sarcoplasmic reticulum and the T system (with Clara Franzini-Amstrong), on coated vesicles and their involvement in the uptake of specific proteins (with Thomas Roth), and, especially, on microtubules and their role in motility, cell division, and maintenance of cell shape (with Lewis Tilney, J. Richard McIntosh, and Ursula Goodenough-Johnson). From the period date a number of important findings concerning the fine structure of microtubules *in situ* (with Ledbetter) and the sensitivity of microtubules within living cells to cold and high pressure (with Tilney). Still at Harvard, Porter began to explore a very attractive system: the pigment cells (melano- and erythrophores) of fish scales, in which microtubules are heavily involved in the control of the distribution of pigment granules. Additional topics investigated on a more limited scale included particulate uptake and lipid absorption in the intestinal epithelium (with Robert Cardell), hepatocytes and hepatoma cells (with Carlo Bruni), and chromatolysis in neurons after transection of their axons (with Donald Price).

Although there was continuous progress in research, the rest of the picture at Harvard did not seem to be entirely to Porter's liking. I assume that, for a man interested in organizing and reforming on a large scale, the combination of cherished traditional formulae, high prestige, and limited resources (which seem to go together in great academic institutions) became discouraging after a while. *Almae matres* usually consider that education is essentially a unidirectional process, from the administration all the way down to students, without so much as a partial reversal in direction.

#### THE YEARS AT BOULDER

In the late 1960s (1968), Porter found the opportunity of organizing, on a scale commensurate with his talents and interests, a new laboratory at the University of Colorado in Boulder. The scope was broadened to cover develop-

<sup>4</sup> At Rockefeller, he had participated with the other members of the group in a graduate course in cell biology.



mental and molecular biology, as well as cellular biology, and the equipment has expanded to include scanning electron microscopes and, especially, a high-voltage (1,000 kV) electron microscope operated as a regional resource. Into the new machines were fed specimens of the kind used in the early beginnings: cultured cells examined *in toto* for the structural details of their surfaces or for the tridimensional aspects of their internal organization. Impressive variations in surface morphology as a function of cell transformation or phase in the cell's cycle were discovered, and another, finer reticulum seemed to appear in the cytoplasmic matrix within the meshes of the now old and respectable endoplasmic reticulum. But we are too close in time to the new findings to be able to assess their future intelligently.

#### AN INTERNATIONAL CONGRESS IN BOSTON

While Keith Porter was deeply involved in the organization of his Institute at Boulder, some people wondered if he had forgotten the community of cell biologists. All his past communal creations<sup>5</sup> were doing well, but there was no sign of any new spectacular development, and communities are demanding and impatient, besides being forgetful. At about that time, he proposed organizing the first international congress on cell biology, to be held in Boston in the year of the nation's bicentennial, with the American Society for Cell Biology acting as host.

The planning took two years, the officers of the Society had to be reeducated in temerity, the treasurer had to forget — with great reluctance — his conservative bent, and the local committee had to fight in defense of Bostonian propriety, but the congress finally took place. By indisputable consensus, it was a great scientific event and a memorable social occasion. The treasurer got all his money back, and Keith Porter appeared at the Congress Ball dressed like Benjamin Franklin, the American genius who knew how to needle authority in his own way.

#### INSTEAD OF A CONCLUSION

So it is fitting to honor Keith Porter for his science: an ever-closer look, by increasingly stronger and diversified means, at the organization of living systems. And it is also fitting to recognize his ability to dare, move, and organize on a large scale, and with a remarkable sense of timing, all kinds of activities, including this Journal and our Society.

This brief excursion through Keith Porter's career in science is incomplete, partial, arbitrarily limited to laboratories and universities, and thus dissected away from the context of his full life. Its style is unconventional to the point that it may appear irreverent to some readers. But the real intent is quite different: this short dedicatory paper is, in fact, humanized history written with great and due affection, for Keith Porter has been and still is our father — at least to many of us.

<sup>5</sup> They included the Tissue Culture Association founded in 1947.

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