

In Memory of
Peter Läuger



Peter Luger

1934–1990

A man of towering intellect, utterly unassuming, a truly gentle man. This was Peter Luger. He died on September 13, in a mountaineering accident in the Andes of Venezuela. With him the biophysics community has lost a shining light and *The Journal of Membrane Biology*, a pillar.

Peter Luger was born in 1934 in Lorrach, a small German town in the Alemanic region north of Basel. There he spent his childhood and went to school, a humanistic gymnasium. In 1953 he began his studies of chemistry, physics and mathematics at the University of Basel, just a few miles from his hometown. After a short spell at the University of Hamburg, he returned to Basel to do graduate work under Werner Kuhn, and obtained his Ph.D. in physical chemistry in 1961. He stayed on at Basel University for seven years, first as a Research Assistant, then as Privat Dozent, and in 1968, while serving after Kuhn's death as acting department head, he was called to the chair of biophysics at the newly founded University of Konstanz.

In Konstanz, Peter Luger started his work on biomembrane transport for which he became so justly famous. The roots go back to the Basel period, to his inquiries into the physical chemistry of permeation of ion-exchange membranes. But it was at Konstanz where his biological interest really took off. There a new biology department was in the making. It was to be cast in an unconventional mold; biochemistry and biophysics, rather than the traditional zoology and botany lore, were to be its backbone. To this undertaking, Peter brought the biophysics bedrock. In no time a group of young men flocked to him who were trained in physics and were eager to direct their efforts towards a new frontier.

Thus started the Konstanz School of biomembranes, with Peter as guide and attractor. His imaginative work using artificial lipid bilayers in aqueous

phase as model systems for biological membranes soon attracted world-wide attention. He began with an exact physical characterization of these membrane systems and then zeroed in on the mechanisms of ion transport.

Like few, he knew how to plumb the depths of things and see the quantitative relations. Others before him had tried to come to grips with the question of how ions permeate cell membranes, and through their efforts the field towards the end of the 1960s had reached a stage where the transport in a membrane channel could be described as a series of thermally activated processes in which the ion moves from one binding site to another across energy barriers. Those descriptions essentially amounted to static pictures which clashed with what just then was emerging from protein physics: that protein structures are dynamic. X-ray diffraction, NMR and optical measurements had revealed that protein molecules in thermal equilibrium can adopt many conformations and that the attendant internal motions occur over a wide spectrum of time, picosecond to seconds. The biophysical endeavors with proteins and biomembranes had developed separately and their paths had rarely crossed. But by the end of the 60s the common ground was plain to see, and it became possible to envision a channel made of protein whose energy profile varies in a time-dependent manner. And so, Peter attacked the knotty problem of multistate channels whose conformational transitions are electrostatically coupled to the ion movement within the channels. His early training had put him in trim for that. He worked out a series of solutions for ion translocations, which became the beacon that lit the way to a unified concept of membrane transport. Two formerly distinct things, ion carrier and ion channel, became essentially one: both entities were transmembrane pro-

teins with multiple conformational states, proteins that differ only in the extent of the conformational changes engendering the ion translocations.

With the unified channel-carrier concept in tow, Peter Luger was ready by the turn of the decade for his next step of synthesis: the drawing of the ion pump into the concept. He showed how an ion channel with multiple conformational states can become a pump when its energy profile is modified in a time-dependent way by extrinsic energy: the absorption of light, a change of redox state or the phosphorylation of an amino acid alters the channel's affinity for the permeant and, at the same time, sets the height of the energy barriers. This way an ion may be released to one side of the membrane, while another ion is taken up from the opposite side during the transition back to the original channel state.

The experiments attending this theoretical work led him and his colleagues to explore the light-driven bacteriorhodopsin- and the Na, K-ATPase ion pumps. These are pumps that translocate net charge across the cell membrane, and their activity depends on the transmembrane electric field. The Konstanz School ingeniously exploited these properties to peer into the transport operations through measurements of membrane currents taken on whole cells or on isolated membrane preparations, and through measurements of transient charge movements in response to sudden perturbations of the electric field. Those experiments were guided by coherent theory or, at least, a theory as coherent as the young biophysics would afford. Inevitably theory will outrun experiment, and Peter's was no exception, but he never let the testing fall too far behind. His conceptions have weathered well.

He had a special knack of penetrating beneath the outward form of things to see the workings from within. His analyses of channels and pumps attest to that, but perhaps nothing illustrates this better than the model for the rotating bacterial flagellum he thought out in passing, as it were, in the mid 70s, in between studies of channels and carriers. I will dwell on it because this work of his is little known (*Nature*, 1977, 268:368). Here in the flagellar mechanism was a movement generated not directly by ATP but by a transmembrane gradient of hydrogen ions—a problem worthy of his mettle: how to generate a torque with an ion flow. His model is an elegant electrochemical turbine: the H^+ flux through a membrane channel drives the flagellar rotor, a double-wheel structure with ion-binding spokes intersecting at an angle; the 10^{-1} -V H^+ transmembrane gradient dropping radially as the rotor generates a centrifugal force exerting a 10^{-19} -J torque.

Peter Luger made it easy to follow his trains of



thought. His lectures were meticulously prepared and his writings, crystal clear. His discussions were always tolerant and gentle, even those with the occasional combative opponent. Where the adversary used vigor, he would use rigor; when the adversary breathed fire and fury, he breathed order and logic. Scientific disputes, we all know, can be as adrenalin-consuming as any squabble, but there is something satisfying about them: no bully can very well argue with a theorem; information and logic will always carry the day.

In his last years Peter Luger worked on a book on ion pumps. I had the pleasure to see it develop from outline to piecemeal chapters to magnum opus. He finished it just before his death. It offers us a sweep of his fertile mind. ("Electrogenic Ion Pumps" will be published next year by John Wiley & Sons.) On September 9, the Sunday before his death, he delivered a lecture on "The Kinetic Basis of Voltage Sensitivity," at a symposium of the Society of General Physiologists at Woods Hole. It was a masterful presentation—his final lecture.

I met Peter Luger at one of the Titisee Conferences. I drew then, as is my habit, the caricature which is reproduced on this page. It shows him in professorial pose as he was giving his talk. But to

anyone who knows him it will be obvious that then I did not really know him. The cartoon shows nothing of that warmth and kindness that suffused his entire being, which became apparent once one got to know him and got him to drop his reserve. The photograph on page 104, taken by one of his students, captured a little of this kindheartedness. Peter was reserved, even shy, yet to his colleagues and students he was always available in his little office, ready to share from the depth and breadth of his knowledge. No anteroom nor guarding secretary was there to impede access; he himself had devised too many stratagems for jumping energy barriers to know better than that.

He served on the editorial board of this journal since 1972, nearly since its founding, and on the boards of *Biochimica Biophysica Acta* and the *European Journal of Biophysics*. He was advisor to the Deutsche Forschungsgesellschaft, several Max-Planck institutes, and a member of the Council of the International Union of Pure and Applied Biophysics. In 1990 he was elected to the newly formed Academia Europaea. The Max-Planck Society had offered him an institute in Frankfurt some time ago. He opted to stay at the university he had helped to forge and to be close to the Alps he loved.

Peter cherished nature. He was particularly fond of hiking in the mountains. As often as he could, he would go up the Alps on the Swiss side not far from where he lived. There he charged his batteries, we

might say, and after a weekend he would come back invigorated and tanned, with a manuscript under his arm, a new equation in his head, or a flower sketch in his notebook. He was no mean amateur botanist. In the hikes we took together he knew every bush and tree. This love of nature drew him, on that September day, to the mountain from which he did not return.

The gap he has left is immense—in this journal, in his university, in the ranks of scientists. It is a loss I hardly trust myself to speak of, for apart from ties of a professional nature, there had developed between us over thirteen years, a close friendship and affection. We were *Geistesbruder*. Nor can I better describe him than by saying that, perhaps of all men I have known, he came closest to the mold and ideal of scientist and human being, which every mentor would like to see his student aspire to.

His career has been cut short in midrun while still in the full tide of powers and promise. Yet, knowing how he was, I think Peter here would say that he was lucky—lucky to have been given the grace to obtain a slightly deeper glimpse into the secrets of nature and to earn the recognition of his peers.

Werner R. Loewenstein