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Preface

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A resume in science

Fifty years of life in the biological sciences — viewed from a physico-chemical point of observation — in the second half of the 20th century, have led to a powerful experience. From an era with slide-rules everything today is computer dominated. Great achievements were the products of great minds rather than the beautifully colored output of sometimes ill-defined, hard to justify simulations.

My teacher, Aharon Katchalsky, introduced me to Werner Kuhn and Peter Debye, pioneers in the understanding of polymers and electrolytes, which Aharon felt would lead to the study of charge-carrying polymers, polyelectrolytes, providing a basis for understanding the behavior of biological macromolecules. At Yale, in 1952, I met John Kirkwood and Lars Onsager who deepened my awe for reversible and irreversible thermodynamics and statistical mechanics pointed to the life-sciences. In my first Gordon Conference on Polymers in New London that year, I was privileged to lecture on Polyelectrolytes, under the *aegis* of Paul Flory, creator of modern polymer theory. In a visit to Boston George Scatchard deepened my insight into the behavior of protein solutions. At about that time the X-ray crystallographer Rosalind Franklin in London provided the information leading to the structure of the 'polyelectrolyte' DNA double-helix structure, Linus Pauling created the polypeptide α-helix and the β-sheet structures, Chris Anfinsen created the protein folding concept, Jacques Monod allostery, and Jeffries Wyman the rules for ligand binding to proteins and nucleic acids. I was privileged to be exposed to Felix Bloch's lecturing at the Weizmann Institute on the early stages of nuclear magnetic resonance and suggesting its application to chemistry and biology, to The Svedberg on the unique size and mass of biological macromolecules obtained by analytical ultracentrifugation, and to Otto Kratky on the merits of small-angle X-ray scattering for the determination of the size and shape of biological macromolecular particles and their complexes.

Unlike similar listings in 'Time' magazine the above list is far from complete. However, the scientists mentioned, who are slyly smiling watching us from 'heaven', are the giants who provided at least one of the shoulders on which the life sciences will rest at the start of the third millennium. I will, in the following provide a sampling of ongoing activities in selected areas of biophysics which have engaged my interest in scientific research.

I was born on 7 March, 1921, in Berlin, and went to elementary and high school in Czernowitz, then Roumania, where my father founded a textile factory in 1926. I came to Palestine in September 1939 to start my studies in chemistry at the Hebrew University in Jerusalem. World War II had just broken out. More details about

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my family and related stories can be found in my article — Never a Dull Moment, Peripatetics through the Gardens of Science and Life [1]. In 1941 I enlisted in the British Army and joined the 524 Palestinian Field Survey Company of the Royal Engineers. In Cairo, Egypt, I met my wife-to-be, Nutzi, who was also serving in the British Army, in the Palestinian ATS, and we were married on 18 September, 1943, in Cairo. In the summer of 1994 my unit was moved to Italy and in the summer of 1946 I was released from the army in Rehovot, Palestine. I could now return to the Hebrew University to continue my studies.

Aharon became my Master and PhD. thesis supervisor and introduced me to the intricacies of polyelectrolyte research, of which he was an initiator. In my work I describe [2] procedures for determining poly-methacrylic acid size and conformation by esterification and hydrolysis and viscosity studies with an increasing degree of ionization. In a joint paper with Werner Kuhn, B. Hargitay and Aharon [3] we demonstrated reversible dilation and contraction by changing the state of ionization of high polymer acid networks. With Aharon and Shneior Lifson an equation of swelling of polyelectrolyte gels was provided [4].

My studies were again interrupted in 1948 due to the outbreak of the Israeli War of Independence. I joined a unit called Hemed, the Army Unit of Science, by which we tried to create military defence equipment in beleaguered Jerusalem, using accessible materials and equipment. In the summer of 1948 I moved with Aharon to the Weizmann Institute of Science in Rehovot, where I remained throughout my scientific career, resuming my studies in 1949, following release from the Israeli army.

In February 1952 I completed my PhD. thesis and moved for 1 year of postdoctoral studies, on electrolyte conductance, to Yale University, New Haven, with Raymond Fuoss [5]. Ray had developed an equation for polyelectrolyte specific viscosity indicating increasing values with decreasing concentration, leading to fully extended chains at vanishing concentrations, a concept which I thought needed critical testing. On my way home to Israel in February of 1953 I stopped for 2 weeks in Strasbourg, France, in the laboratory of Charles Sadron, and performed experiments with Jean Pouyet [6] on the Couette low shear gradient viscometer, indicating that already at very low added electrolyte concentrations the viscosity anomaly characteristic of salt-free solution disappears.

Back at the Weizmann Institute I devoted my time to polyelectrolyte conductance measurements [7] and to the construction with Ephraim Frei and David Treves of a precise and versatile Couette viscometer with electrostatic restoring torque for the centipoise range [8,9]. In addition to work on synthetic polyelectrolytes [10], I could show that the viscosity of DNA is strongly shear-dependent and much higher molecular weights were obtained by extrapolating to vanishing rates of shear [11]. In collaboration with Uriel Littauer [12–14] we could show by added electrolyte and concentration-specific viscosity dependence that RNA, in distinction to DNA, is a single rather than a double chain macromolecule. With Ram Mohan [15] phase separation and specific interactions with ions, and later with Daniel Woodside [16] excluded volume properties, were demonstrated for polyvinylsulfonic acid salts.

In 1958 I went for a 2-year stay for research at the Mellon Institute in Pittsburgh, Pennsylvania, USA directed by Paul Flory. In a gratifying collaboration with Ed Casassa, in a series of publications summarized in 1964 [17] on the thermodynamic analysis of multicomponent solutions, we succeeded in providing basic equations on the definition of components in solutions containing charged macromolecular species, partial specific volumes and refractive index increments in multicomponent systems. These definitions provided reliable thermodynamic equations for light scattering and sedimentation of multicomponent systems [18], later to be extended to X-ray and neutron scattering [19,20].

Back in Rehovot I derived with Emil Reisler a precise equation for the refractive index of water as a function of temperature and pressure [21,22] which led Gerry Cohen to demonstrate that light scattered by water, deuterium oxide and other pure liquids [23] relates strictly to the Einstein piezo-optic model.

The study of multicomponent polyelectrolyte solutions was continued with Nobuhise Imai, Bill Carroll and Gerry [24–27]. An analysis for the determination of molecular weights by equilibrium sedimentation in density gradients was also given [28].

In 1965–1966 I spent a sabbatical year with Gary Felsenfeld in the Laboratory of Molecular Biology at the National Institutes of Health in Bethesda. The study of the temperature-dependent conformation and phase separation of polyriboadenylic acid (poly A) at neutral pH led to interesting results [29], showing that, if properly handled, biological macromolecules can be analyzed by the methods developed by Paul Flory for synthetic macromolecules. In the same year I could derive, in collaboration with Gordon Tomkins [30], the molecular weight of subunits, oligomeric and associated forms of bovine liver glutamate dehydrogenase, matters of intense dispute at that time. We demonstrated the hexamer structure of the native enzyme, in opposition to then current Monod symmetry considerations.

Back in Rehovot much of our work was devoted to DNA. Gerry [31] determined partial specific volumes, density and refractive index increments and solute–solvent interactions, which provided a strong basis for the interpretation of properties of DNA solutions, and were later summarized with other data in the Landolt–Börnstein Biophysics Series [32]. Aspects of light scattering and distribution of sizes of associated oligomers of glutamate dehydrogenase in solution were also analyzed with Emil [33], as well as the temperature and density dependence of the refractive index of pure liquids with Emil and with Allen Minton [34].

Important analyses with Emil [35] related to the interpretation of equilibrium sedimentation measurements of proteins in guanidine–HCl solutions, concerning the partial volumes, density increments and molecular weights of the subunits of rabbit muscle aldolase; a physical model for the structure of glutamate dehydrogenase was derived [36], the effect of toluene on the enzyme association was investigated [37], equilibrium and velocity sedimentation, light scattering studies and settling experiments with macroscopic models of the enzyme oligomer were performed with Emil and Jean [38]. Much of this and further work on bovine liver glutamate dehydrogenase was reviewed with Emil and with Bob Josephs [39,40].

Additional work related to dielectric dispersion properties of aqueous polyelectrolyte solutions with Baruch Sachs, Adrian Raziel and Aharon [41], the excluded volume study of potassium polystyrene sulfonate solutions with Adrian [42], poly-*para*-amino-styrene from poly-vinyl-benzoic acid by the Schmidt reaction in pure sulfuric acid with Dori Cwikel [43] based on an earlier study with Arieh Berger [44], photon correlation spectroscopy, total intensity light scattering with laser radiation and hydrodynamic studies of a well fractionated DNA sample with Doug Jolly [45], the flexibility of low molecular weight double-stranded DNA as a function of length, estimation of persistence lengths from light scattering, sedimentation and viscosity with Jamie Godfrey [46], bovine serum albumin in aqueous guanidine–HCl solutions, solute solvent interactions and comparison with other systems with Emil and Hezi Haik [47], scattering correction to the absorbance, wavelength dependence of the refractive index increment and the molecular weight of the bovine liver glutamate dehydrogenase oligomer and subunits with Bob, Emil and John Schellman [48], structural aspects of spectrin from human erythrocyte membranes with Tziki Kam, Bob and Walter Gratzer [49], solution scattering studies of dimeric and tetrameric spectrin with Michael Reich, Tziki, D. Worcester, E. Ungewickell and Walter [50].

The first physical study undertaken and published with Gerrit Voordouw, Tziki and Nina Borochov on uniquely sized DNA involved isolation and studies of the intact supercoiled, the open circular and the linear forms of ColE1-plasmid DNA [51]. Additional studies were undertaken on ColE1-plasmid DNA and its interactions with histones, sedimentation velocity studies of monodisperse complexes reconstituted with calf-thymus histones with Gerrit and Dorit Kalif [52] and binding of additional histones to chromatin core particles with Gerrit [53].

Further DNA studies with Nina and Tziki extend to the present period. Thus the dependence of DNA conformation on the concentration of

salt [54] and of laser light scattering on NaCl concentration [55], conformation of Li–DNA in solutions of LiCl [56], DNA flexing, folding and function [57], stiff (DNA) and flexible (NaPSS) polyelectrolyte chain expansion at very low salt concentrations [58] and polyelectrolyte excluded volume and expansion compared to non-ionic polymers [59].

Nucleosome structure and conformational changes with Jim McGhee and Gary [60] constituted a strong field of activity. Hydrodynamic studies of the interactions between nucleosome core particles and core histones with Gary [61], nucleosome core particle stability and conformational change, effect of temperature, particle and NaCl concentration with Juan Ausio and Dalia Seger [62], interaction of chromatin with NaCl and $MgCl_2$, solubility and binding studies, transition to and characterization of higher order structure with Juan, Nina and Dalia [63], nucleosome core particle structure and structural changes in solution with Otto Greulich, Juan, Dalia and Ellen Wachtel [64,65], transition of chromatin from the 10 nm lower to the 30 nm higher order structure, as followed by small angle X-ray scattering with Otto, Ellen, Juan and Dalia [66], the effect of positive supercoiling on DNA compaction by nucleosome cores with David Clark, Rodolfo Ghirlando and Gary [67]. The size and free spaces inside nucleosome core particles could be determined by fractal probing in solutions containing sugars differing in size [61,64].

An extensive field of study was based on the study of enzymes derived from bacteria living in extremely high salt, halobacteria, in the Dead Sea and in similar environments. Our studies included malate dehydrogenase from extremely halophilic bacteria from the Dead Sea, purification and some properties with Moshe Mevarech and Eberhard Neumann [68], purification and characterization of glutamate dehydrogenase from bacteria of the Dead Sea with Wolfgang Leicht and Moshe Werber [69], structure and activity of malate dehydrogenase from the extreme halophilic bacteria of the Dead Sea, conformation and interaction with water and salt between 5 and 1 M NaCl concentration with Shlomo Pundak [70], inactivation, dissociation and unfolding at NaCl concentrations below 2 M salt, salt concentration and temperature dependence of enzyme stability with Shlomo and Hamutal Aloni [71], a small angle X-ray scattering study of halophilic malate dehydrogenase with Michael and Tziki [72], solution structure of halophilic malate dehydro genase from small angle neutron and X-ray scattering and ultracentrifugation with Joe Zaccai and Ellen [73], denaturation of a halophilic enzyme monitored by small angle neutron scattering with Joe and G.J. Bunick [74], structure of halophilic malate dehydrogenase in multimolar KCl solutions from neutron scattering and ultracentrifugation with P. Calmettes and Joe [75], crystallization of halophilic malate dehydrogenase with Michael Harel, Menahem Shoham, Felix Frolow, Moshe Mevarech, Ada Yonath and Joel Sussman [76], the stabilization of a halophilic protein with Joe, Fabrice Cendrin, Hezi and Nina [77], isolation and characterization of the r-RNA gene clusters of the extreme halophilic archaebacterium *Haloarcula marismortui* with Moshe Mevarech, Sarah Hirsch-Twizer, Sarah Goldmann, Emanuel Yakobson and Pat Dennis [78], extracellular Ca-dependent inducible alkaline phosphatase from *H. marismortui* with Sarah, Katrin Hecht and Moshe Mevarech [79], cloning, sequencing and expression in *Escherichia coli* of the gene coding for malate dehydrogenase of *H. marismortui* with Fabrice Cendrin, Jadwiga Chroboczek, Joe and Moshe Mevarech [80], a biophysical study of halophilic malate dehydrogenase in solution, revised subunit structure and solvent interactions of native and recombinant enzyme with Francoise Bonnete, Christine Ebel and Joe [81]. The field of study of extreme halophiles was reviewed with Ellen including structural studies of halophilic proteins, ribosomes and organelles of bacteria adapted to extreme salt concentrations [82], halophilic proteins and the influence of solvent on protein stabilization with Joe [83], biochemical, structural and molecular genetic aspects of halophilism with Joe and Moshe Mevarech [84], life in unusual environments and progress in understanding the structure and function of enzymes from extreme halophilic bacteria [85]. In closing it should be stated that Orly Dym, Moshe Mevarech and Joel

[86] have now solved at medium resolution the X-ray crystallographic structure of malate dehydrogenase from *H. marismortui*, and Felix, Michal, Joel, Moshe Mevarech and Menahem [87] that of ferredoxin, so the stage now is set for reaching a complete understanding how adaptation to extreme salt concentrations proceeds in nature.

Theoretical and experimental aspects of studies undertaken have been reviewed in a number of publications not listed so far. Macromolecules in Research, Biology and Practice [88], Hydrodynamic and Thermodynamic DNA Studies [89], Biological Macromolecules and Polyelectrolytes in Solution [90], Polyelectrolytes Thirty Years Later [91], Thermodynamics and Structure of Biological Macromolecules [92], Protein and Nucleic Acid Hydration and Cosolvent Interactions, Establishment of Reliable Base-Line Values at high Cosolvent Concentrations [93], Ultracentrifugation, Light-, X-ray- and Neutron-Scattering of Peptides, Proteins and Nucleic acids in Solution [94]. A very recent paper entering the new millennium, Probing Protein-Sugar Interactions with Christine and Rodolfo [95], should be mentioned.

Science is a serious way of spending one's lifetime activities, however, lighter, human and social aspects should be mentioned in closing. In going through the various aspects of my work in the past half-century, I have not given a full list of all publications in my bibliography. I have tried to mention all adequate publications to cover all fields of work and to mention all co-workers with whom I have been engaged in joint work. I hope I have succeeded in this. I would also like to mention my 17 years of association with Biophysical Chemistry, first under the leadership of Michel Mandel, and then of Tony Watts who took over from Michel in a very satisfactory fashion. I have similarly been associated for 13 years with the *European Journal of Biochemistry* in reviewing papers submitted for publication. Membership at the European Molecular Biology Organisation (EMBO) has provided additional satisfaction and hard work in the Course Committee then guided by John Tooze. Membership on the Board and being Vice President of the International Union of Pure and Applied Biophysics (IUPAB) provided an additional window for world-wide interaction and led to a very successful International Biophysics Congress, organized with Israel Pecht in Jerusalem in 1987. Friendship with Walter Gratzer brought me close to *Trends In Biochemical Sciences* (*TIBS*) in its initial days and to *Nature*, enabling me to provide book reviews, comments and, unfortunately, obituaries as well. I will now provide a few examples from my bibliography pointing in this direction:

O Tempora, o Mores [96], God's Bonds [97], From A to Z, New Twists to an Old Helix [98], La Cage au DNA [99], Paul J. Flory, obituary [100], Polymers: The Origins and Growth of a Science, by Herbert Morawetz, book review [101], She Walked in the best Circles… [102], Life at the End of the Ribosome Tunnel [103], Par ma Foi, il y a plus de Quarante Ans que je fais de la Biophysique sans que j'en susse rien [104], Life in Unusual Circumstances, Clive Edwards, editor, book review [105], Biophysics of the Nineties: on the Road to Budapest with Maurizio Brunori [106], Dutch Scientists in and close to Biophysics [107].

I believe my early statement, Never a Dull Moment [1], to be indeed fully justified.

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