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Born in the coastal village of Luarca in the Asturias province of northern Spain, Ochoa enrolled as a medical student at the University of Madrid in 1946. There were few if any graduate studies in the biomedical sciences either in Spain or elsewhere in Europe at the time, and the medical curriculum was the only recourse. Upon completing his medical courses and with no inclination toward clinical practice, he directly sought opportunities for experimental work. Social and political turbulence and a state of war in Spain, Germany, and the United Kingdom drove him from one refuge to another. Buffeted by all these events, he was unwavering in his devotion to science. He always remained on course in the face of all kinds of adversities, experimental and societal. His conviction that hard work would be rewarded sustained him during the most difficult hours and permeated the atmosphere around him. Upon completion of his medical thesis, he set out for Germany to spend the next 2 years in the laboratory of Otto Meyerhof first in Berlin and then in Heidelberg. Meyerhof was renowned for his work on the energetics of muscle contraction for which he had been awarded, along with A. Hill, the Nobel Prize in Physiology or Medicine in 1922. This time he explored the action of cozymase, later known as DPN diphosphopyridine nucleotide and currently as NAD nicotinamide adenine dinucleotide. Meyerhof, with his status under attack by German racial laws, wrote A. After that he was able to join Rudolph A. Peters in the biochemistry laboratory of Oxford University where, in studies of thiamin pyrophosphate in pyruvate metabolism, he was lured by oxidative aerobic phosphorylation. The obligate coupling of phosphorylation to the oxidation of pyruvic acid was observed by Ochoa and at the same time by Herman Kalckar in Copenhagen and by Vladimir A. Belitzer in the Soviet Union; Ochoa later estimated the number of phosphates fixed per oxygen atom consumed P: O ratio to be near three. Once again, the state of war in the United Kingdom enveloped all research activity and drove Ochoa, an alien, to accept in an invitation to St. Louis to join the laboratory of Carl and Gerty Cori. In explorations of phosphorylation in disrupted liver tissue, he found a curiosity, inorganic pyrophosphate P<sub>i</sub>. Because its source and fate were so vague, the finding was never published. I failed then but did discover the source of P<sub>i</sub> several years later when it emerged as the entity released from nucleoside triphosphates in the synthesis of coenzymes, nucleic acids, and also proteins, fatty acids, and key metabolic intermediates. After 1 year in St. Louis, Ochoa was offered a position as Research Associate in the Department of Medicine in the New York University School of Medicine, where he would remain for 32 years until retirement in 1978. With the least favorable facilities, Ochoa embarked on the discovery and characterization of the enzymes that he hoped would explain how cells derive virtually all their chemical energy. His confidence was based on the success in earlier decades in resolving and reconstituting alcoholic fermentation and glycolysis. The expectation was that discrete, isolatable enzymes would be identified as responsible for aerobic phosphorylation. The tricarboxylic acid cycle had just been proposed by Hans Krebs to explain how pyruvate was metabolized to carbon dioxide and water. Key intermediates in the cycle were the tricarboxylic acids citrate and isocitrate, the enzymology of which Ochoa believed would help clarify aerobic phosphorylation. I wanted to learn the enzymology and the new biochemistry I had not been taught in medical school 8 years earlier. With the war concluded and with nutritional science in its twilight and bored with the feeding and bleeding of rats for 3 years, I was able to persuade the Director of the National Institutes of Health to let me spend some months away learning about the new and exciting world of enzymes. I was very fortunate that Ochoa was willing to take me, a complete novice in all aspects of biochemistry. Earlier, he had been summarily evicted from space in the Psychiatry Department in the Bellevue Hospital of the Medical School; upon returning from a concert one Sunday afternoon, he found his desk and equipment moved out into the hall. When I arrived, his group consisted of a graduate student Alan Mehler and two technical assistants. Initially appointed as a Research Associate in Medicine and in as an assistant professor at the advanced age of 40, his stature in science was recognized the

next year with the offer of a full professorship and chairmanship of the Department of Pharmacology. His reluctance to accept this promotion and associated responsibilities was characteristic of his indifference to academic titles and authority. Will the research work not suffer if I become a department chairman? Shannon, later the Director of the National Institutes of Health. It was only in that Ochoa moved back across First Avenue to assume the vacated chairmanship of the Department of Biochemistry. Patterned along the lines of the instrument devised by Otto Warburg in Germany, it was the highly effective successor to the laborious and insensitive respirometric assays of metabolic reactions that had been relied upon for several decades. It remained and died of old age. Those early months in , learning the rudiments of dynamic biochemistry, enzyme fractionation, and spectrophotometry, were the most exciting in my life. I was awed by enzymes and fell instantly in love with them. I have since had love affairs with many enzymes none as enduring as with DNA polymerase , but I have never met a dull or disappointing one. The day I came into the Ochoa laboratory after Christmas in several pig hearts fresh from the slaughterhouse awaited me. My project was to separate aconitase an activity that converts citrate in two stages to isocitrate into its two presumed component enzymes. Starting with a water extract of the ground-up heart muscle, I tried over the next months, using ammonium sulfate fractionation and other maneuvers, but failed to separate aconitase into two discrete enzymes. Some years later when aconitase was purified to homogeneity by others, it was found to be a single polypeptide. As events proved, the separated enzymes of the citric acid cycle could account for the oxidative reactions but not for the bulk of the energy captured by aerobic phosphorylation. Unlike the energetic couplings in alcohol fermentation and glycolysis, intact mitochondria were later discovered by others to be the means used in generating a proton motive force that results in the ultimate coupling of ATP synthesis to oxidative steps in the cycle. Marianne Grunberg-Manago, a postdoctoral fellow, while exploring possible mechanisms of aerobic phosphorylation, observed an activity in a bacterial extract that exchanged  $[^{32}\text{P}]\text{Pi}$  into ADP. Equation 1 Equation 2The initial hope that this enzyme, named polynucleotide phosphorylase, might be responsible for the biosynthesis of ribonucleic acid RNA was dispelled by the lack of a requirement for a DNA template to direct the assembly of a specific RNA message, the indiscriminate assembly of a polymer of any one or a mixture of nucleoside diphosphates, and finally the discovery of true RNA polymerases, which copy DNA templates with great specificity using nucleoside triphosphates rather than diphosphates. The role of polynucleotide phosphorylase in the bacteria in which it has been found is the disposal of RNA with salvage of its precious nucleotides. Although polynucleotide phosphorylase was disappointing for its lack of a biosynthetic role, it was the first enzyme that could make RNA-like chains and proved to be of great value in deciphering the genetic code. Heppel employed polynucleotide phosphorylase to synthesize a variety of RNA-like polymers, which were then used to identify many of the nucleotide triplets that encode the amino acids in the synthesis of proteins. Ochoa could reasonably have shared the Nobel Prize with R. He had become a United States citizen, a devoted New Yorker, and a true internationalist in spirit. Nevertheless, he persuaded me, despite my own strong aversion to Franco, to go to Spain in his stead and arranged an attractive itinerary with receptions by his intimate friends and relatives. My late wife, Sylvy, and our three sons Ken, 9; Tom, 11; and Roger, 12 were given the most affectionate welcome and expression of kinship in our opposition to their fascist government. It took place in December Nearing the end of the year in his laboratory, my most formative year in science, I was about to leave for the Cori laboratory in St. With Mehler, we had discovered and partially purified the malic enzyme that catalyzed the reaction: Now we were completing a very large scale preparation starting with several hundred pigeon livers. We had only to fill in some details in a paper we had already prepared for publication. Late one night, Ochoa and I were dissolving the final enzyme fraction, which had been collected in many glass centrifuge bottles. I had just poured the dissolved contents of the last bottle into a measuring cylinder that contained the entire enzyme fraction. Then I brushed against and overturned one of the empty, wobbly bottles on the crowded bench. That bottle knocked over another and the domino effect reached the cylinder with the enzyme. It fell over and all of the precious material spilled on the floor. It was gone forever. Ochoa tried to be reassuring, but I remained terribly upset. By the time I got home by subway train an hour later, Ochoa had called several times because he was so worried about my safety. The next morning back in the laboratory I glanced at the supernatant fluid beyond the last fraction. I might have

discarded it because in our trial procedures it had been inactive. I collected the solid material, dissolved it, and assayed it for activity. This fraction had the bulk of the enzyme activity and was severalfold purer than the best of our previous preparations. Rather than suffusing a blinding intelligence, Ochoa taught me that with an ethic of unremitting experimental work, good things eventually happen. I believed they would for me as they had for him. Fascinated by every aspect of biochemistry and involved in all, his work ranged from muscle contraction and photosynthesis to vitamins and virus replication. He delved into the intricacies of the synthesis and breakdown of carbohydrates, lipids, nucleic acids, and proteins and played a major role in the drama of the genetic code. A courtly, charming, El Greco-like figure, intensely competitive and ambitious, he was eager to describe his latest findings, absorb those of others, and at times even appeared to intrude in all domains with little concern. To celebrate his 70th birthday in , Ochoa chose as guests the scientists he most respected worldwide. Symposia and celebratory dinners, starting in Barcelona, were followed by a visit with Salvador Dali in his museum in his hometown in Figueras and culminated in a gala of events in Madrid. It was a party, the likes of which has not been seen in scientific circles before or since. Throughout his career, Severo had the constant and loyal support of his wife, Carmen. While in New York, they were the most gracious hosts in their modest apartment to an uninterrupted parade of students, postdoctoral fellows, visiting scientists, and colleagues. They especially enjoyed music, fine food, travel, and good company. With no children and attachments to his beloved New York weakened by the loss of most of his contemporaries in science, he and Carmen finally returned to Madrid in Her death shortly thereafter was a loss from which he never recovered despite the adoration of devoted family, friends, and students. To the legion of postdoctoral fellows, students, and sabbatical guests who came to him from every corner of the world and left to become leaders in science and to the Spanish nation, Severo Ochoa will live on in their memory as a great teacher and an inspiration for the pursuit of science. Barker, Herman Kalckar, Efraim Racker, Harland Wood, and so many others of my colleagues and students who have also been my teachers.

### 2: Severo Ochoa ( of Reglas y consejos sobre investigaci3n cientific)

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