AUGUST KROGH*

NOVEMBER 15, 1874 — SEPTEMBER 13, 1949

P. BRANDT REHBERG

Schack August Steenberg Krogh was born in Grenaa, Jutland. His ancestors had emigrated from Holstein and Schleswig, where his father's family had settled as small farmers three hundred years earlier. Krogh's father was a brewer, though he had been trained as a shipbuilder. Ships and the sea were some of Krogh's unceasing interests.

Krogh, who was the oldest of six brothers and sisters, had already been taught to read and write by his mother at the age of five. Soon after his sixth birthday she wrote in a letter: "August reads almost too fluently, as he frequently out of sheer eagerness omits the signs. We have begun with German, geography and arithmetic. Next fall, if it please God, I shall hand him over to the secondary school in an adequate state; then he himself must take care of his education." Krogh's aversion to official punctuation remained characteristic of him; he put the punctuation marks as it pleased him. After the summer vacation, at the age of six, he was sent to a small secondary school. According to his own opinion, however, going to school did not markedly influence his development. Outside school he cultivated his early awakened interest in nature. At an early age he was interested in animals and for hours he would follow the behavior of insects and spiders. Likewise, with the help of Rostrup's *Flora,* he botanized eagerly in the surroundings of Grenaa. At the age of twelve he had read from beginning to end the large popular Danish encyclopedia available at that time. At this early age he also tried his hand at experimenting, performing—though not always successfully—the chemical and physical experiments he had read about. He had to content himself with the limited material within his reach in the small country town, and he himself assumed that this fact helped to develop his later remarkable ingenuity in improvising apparatus from the few and primitive things at his disposal. As a rule, Krogh's apparatus was inexpensive, and he maintained his economizing attitude even after large funds had been put under his control. Also he exhibited by this time a thorough or rather an exaggerated economy with paper; later in his life he used the tiniest possible scraps of paper, a habit which made it seldom easy for others to decipher his writing.

---

* From the Zoophysiological Laboratory, The University of Copenhagen. This appreciation of Professor Krogh first appeared in Danish in the Year Book of the University of Copenhagen. At the request of the Editors, Professor Rehberg very kindly prepared an English translation for this *Journal.*

In 1889, when in his fifteenth year, he became a voluntary disciple in the navy. It was his intention to be a naval officer, partly because he could not advance in school until he was sixteen years old and eligible for the preliminary examinations. However, after an expedition with the inspection boat *Hauch* he renounced this plan, passed the preliminary, and later, in 1893, the final examination at Aarhus cathedral school. Krogh hesitated: should he study physics or choose zoology in which he had taken an interest through his older friend, the zoologist William Sørensen (who spent many holidays in Grenaa and with whom Krogh used to scour the fields)? He passed the university "prelims" and then wrote an extensive outline of his plans. With this he persuaded his father to give him permission to study zoology. At this juncture Krogh was fortunate: William Sørensen, who was ahead of his time in comprehending the general significance of physiology for zoology, suggested that Krogh should attend Christian Bohr's lectures for medical students. Krogh followed Sørensen's advice—a step which turned out to have a decisive influence on his future. After the very first lecture he understood that here was his proper field and, in 1899 when he received his master's degree, he was appointed assistant at Christian Bohr's laboratory of medical physiology at the University of Copenhagen.

However, prior to this appointment, Krogh had begun to devote himself to zoophysiological problems. As a student he investigated the hydrostatic mechanism of *Corethra* larvae, a peculiar type of mosquito larvae which, by means of completely closed air sacs acting as a swim bladder, is able to regulate its buoyancy in water in the same manner as fishes. Krogh did not solve the mystery of their curious organs, but for use in these studies he worked out a method for the microscopic analysis of small air bubbles which, however, was not published until 1911.[1] It is typical of Krogh's first publications that they are based on an understanding of physics which was rarely found in biological circles at that time. He wrote about the significance of turgescence for plants, hydrostatic conditions in the animal kingdom, gases in sea water, and sap rising in plants—frequently in the form of a criticism of the interpretations of other scientists whom he showed were lacking the necessary knowledge of physics. This ability to apply physical knowledge to biological domains remained typical of Krogh's work, which was always distinguished by a brilliant intuitive perception of physical conditions, especially in microscopic dimensions. In contrast, when he was forced to use chemistry in his work, one had the impression that his chemical knowledge was acquired knowledge.

Krogh's ability to find the cause of discrepancies in other investigators' results was well developed at that time and always played an important part in his scientific studies. Many years later, he himself explained his

[1] On the hydrostatic mechanism of the Corethra larva with an account of methods of microscopical gas analysis. Skand. Arch. Physiol., 1911, *25,* 183.

view in the following way: "When experimental results are found to be in conflict with those of an earlier investigator the matter is often taken too easily and disposed of, for instance by pointing out a possible source of error in the experiments of the predecessor, but without inquiring whether the error, if present, would be quantitatively sufficient to explain the discrepancy. I think that disagreement with former results should never be taken easily, but every effort should be made to find the true explanation. This can be done in many more cases than it is actually done; and as a rule it can be done more easily than by anybody else by the man 'on the spot' who is already familiar with essential details, but it may require a great deal of imagination and very often it will require supplementary experiments."[3]

The time spent in Christian Bohr's laboratory became of utmost importance to Krogh through the insight he gained there into the significance of quantitative work and the necessity of proving whether a theory is quantitatively sufficient. Quantitative work was especially attractive to him, the more so when the existing technique was unsatisfactory and accuracy was paramount. This principle, together with physical intuition, was to be typical of much of his work.

Another ability, also of great importance for Krogh, was his capacity for "visual thinking," as he called it. He was able to see before him the image of an apparatus, projected into space; he could preserve this image, improve it, and get it to move. He made use of this ability when he constructed an apparatus, when he scrutinized the descriptions of other investigators' experiments, and when he reflected upon the way in which an organ functions. Krogh never made a drawing before having seen in this way the apparatus ready before him; if he drew at too early a stage he felt hampered. In a paper on "visual thinking" he described this habit of thought which he assumed to be the background of all his other abilities.[8] In this paper he also mentioned that his brain frequently worked unconsciously and he perceived many ideas during sleep. His memory was queerly specialized: animals, plants, and apparatuses were remembered directly while he, for example, was unable to recall special pages in a book or faces. On the other hand, he retained by heart—but purely intellectually—the quotations and verses which enchanted him, while he was unable to recollect chemical formulae.

Another special gift should be mentioned here, namely, that of observation. He was able to detect minute details, for example, in a microscopic picture of living tissue or in a complicated experimental arrangement. Thus, during his study of the capillaries, he worked with much lower

[3] The progress of physiology. Am. J. Physiol., 1929, *90,* 243; also in Science, 1929, *70,* 200.

[8] Visual thinking. An autobiographical note. Organon, Warsaw, 1938, *2,* 87.

microscopic magnifications than any of his numerous collaborators, but time and again he surprised them by describing the details he could observe at low magnification.

Krogh's first extensive work, his thesis in 1903 on skin and lung respiration of the frog, appeared as a synthesis of his own zoological interests and Christian Bohr's principles of respiration physiology.[4] Here he showed that oxygen metabolism occurs primarily through the thin lung walls with their short diffusion path, while the more easily diffusible carbon dioxide escapes essentially through the skin. The dissertation shows strikingly Krogh's sense for quantitative viewpoints.

Krogh's investigation which was first to gain international renown is a good example of his typical abilities. The Imperial Academy of the Sciences of Vienna had offered a prize for investigations into the participation of free nitrogen in respiratory metabolism. This task required scrupulous accuracy and for a long time Krogh was concerned with it in his thoughts. Finally he arrived at the conclusion that it would be necessary to control the temperature in the respiration apparatus more accurately than usual. Therefore, the whole apparatus should be immersed in water, a procedure which would be feasible only if it were very small. Consequently, Krogh constructed a small apparatus, and it appeared that the results of previous investigators were erroneous because of faulty temperature control. In this investigation his unique capacity for designing apparatus, his critical sense, and his ability to work quantitatively were already fully developed. Krogh demonstrated that nitrogen does not participate in the respiratory metabolism, and he won the offered prize.[5] This treatise is an impressive example of his working method, which he later applied to his long series of investigations into respiratory physiology.

In his doctoral thesis Krogh pointed out that the respiration of toad's skin can be assumed to be due exclusively to diffusion, while, on the other hand, he wholly supported Bohr's views on lung respiration, stating that it occurs predominantly by means of secretory processes and is regulated by the nervous system. However, in the years to come, he became more familiar with respiratory processes and he came to realize that neither in his own works nor in those of other scientists could a valid proof of this view be found. With the methods available, no answer could be given to the serious controversial question of whether the gas exchange in the lungs takes place by a passive or an active process. New apparatus yielding much greater accuracy had to be constructed. The most important one was Krogh's microtonometer with its associated micro gas analysis ap-

[4] *Frøernes Hud- og Lungerespiration.* København, Gyldendalske Boghandel, 1903, 114 pp.

[5] Experimental researches on the expiration of free nitrogen from the body. Skand. Arch. Physiol., 1906, *18,* 364.

paratus.[6] The microtonometer requires an air bubble of only *ca.* 10 mm.,[3] and, therefore, the equilibrium between air tension in the blood and in the bubble is reached rapidly. By means of this apparatus a small air bubble can be analyzed with sufficient accuracy, and its composition can be compared with the air in the lung alveolus.

Through numerous experiments and a steady pursuit of possible sources of error Krogh finally arrived at the conviction that Bohr was wrong: gas exchange is due to diffusion. This conclusion brought Krogh into a precarious situation. He was Bohr's assistant and at the same time his intimate co-worker. He even had the largest share in designing the apparatus used in the work published in collaboration with Bohr and Hasselbalch on the connection between carbon dioxide tension and oxygen binding of the blood.[7] Therefore he hesitated a long time before publishing his results on the gas exchange in the lungs. However, in 1910, the famous seven papers on "The mechanism of gas-exchange" appeared.[8–14] Before exposing the decisive material in the last paper he lowered the rapier before his old tutor with the following words: "I shall be obliged in the following pages to combat the views of my teacher Prof. Bohr on certain essential points and also to criticise a few of his experimental results. I wish here not only to acknowledge the debt of gratitude which I, personally, owe to him, but also to emphasize the fact, patent to everybody who is familiar with the problems here discussed, that the real progress, made during the last twenty years in the knowledge of the processes in the lungs, is mainly due to his labours and to that refinement of methods, which he has introduced. The theory of the lung as a gland has justified its existence and done excellent service in bringing forward facts, which will survive any theoretical construction, which has been or shall hereafter be put upon them."[14] But then he continues his criticism and gives a review of his own results of tension measurements. The result of these investigations, which has ever since formed the basis of our knowledge concerning the uptake of

---

[6] On microanalysis of gases. Skand. Arch. Physiol., 1908, *20*, 279.

[7] Bohr, Christian, Hasselbalch, K. A., and Krogh, August: Ueber einen biologischer Beziehung wichtigen Einfluss, den die Kohlensäurespannung des Blutes auf dessen Sauerstoffbindung übt. Skand. Arch. Physiol., 1904, *16*, 402.

[8] Krogh, August and Krogh, Marie: On the tension of gases in the arterial blood. Skand. Arch. Physiol., 1910, *23*, 179.

[9] Krogh, August and Krogh, Marie: On the oxygen metabolism of the blood. Skand. Arch. Physiol., 1910, *23*, 193.

[10] Krogh, August and Krogh, Marie: On the mechanism of the gas exchange in the lungs of the tortoise. Skand. Arch. Physiol., 1910, *23*, 200.

[11] Krogh, August and Krogh, Marie: On the combination of haemoglobin with mixtures of oxygen and carbonic oxide. Skand. Arch. Physiol., 1910, *23*, 217.

[12] Krogh, August and Krogh, Marie: Some experiments on the invasion of oxygen and carbonic oxide into water. Skand. Arch. Physiol., 1910, *23*, 224.

[13] Krogh, August and Krogh, Marie: On the rate of diffusion of carbonic oxide into the lungs of man. Skand. Arch. Physiol., 1910, *23*, 236.

[14] Krogh, August and Krogh, Marie: On the mechanism of the gas exchange in the lungs. Skand. Arch. Physiol., 1910, *23*, 248.

oxygen in the lungs, was summarized by Krogh himself as follows: "The absorption of oxygen and the elimination of carbon dioxide in the lungs takes place by diffusion and by diffusion alone. There is no trustworthy evidence of any regulation of this process on the part of the organism."[14] For some time the advocates of the secretion theory tried to contest Krogh's views, but every check of his results, even when carried out under the most unfavorable conditions, corroborated his findings and served to emphasize the correctness of his statement that the partial pressure of oxygen was always higher in the alveolar air than in the blood; therefore, conditions were favorable for diffusion.

In collaboration with Marie Krogh (he had been married in 1905) Krogh subsequently investigated whether this diffusion was sufficiently large to explain the uptake of oxygen. In her thesis,[15] Marie Krogh applied the method of determining the diffusion constant of the lungs, which had been worked out in collaboration with August Krogh, and she was able to state conclusively that diffusion is sufficient to explain the oxygen uptake. The new view on the gas exchange in the lungs brought forward a series of new problems, and many questions had to be reconsidered and treated on the basis of the recent observations.

In the following years Krogh published numerous papers in a great variety of fields, including the circulation through the lungs, and the significance of the venous fluid for the minute volume of the heart. These investigations were performed at times in collaboration with Marie Krogh, at times with Johs. Lindhard, the medical doctor who later was appointed professor in the theory of gymnastics. Through many years Krogh kept up an extremely fruitful collaboration with both scientists. Like Krogh, Lindhard was very critical and he claimed equally high accuracy in his experiments. He was not endowed with the same imagination as Krogh, but their collaboration was exemplary and resulted in a series of extremely important papers.

Marie Krogh's contribution to the development of certain sides of Krogh's work cannot be estimated highly enough. Throughout his career Krogh worked on two fronts, as a comparative physiologist dealing with a series of zoophysiological problems, and as a specialist in human physiology concerned with a number of physiological problems of paramount significance for medical science. Marie Krogh, who was a physician, no doubt recognized more clearly than did Krogh himself the medical implications of his work and she certainly played an important part in the choice of his subjects during the years when problems of human physiology prevailed over zoophysiological ones.

Krogh left Bohr's laboratory in 1908. In the same year, he was appointed

---

[15] *Luftdiffusionen gennem menneskets lunger.* København, Jensen & Kjeldskov, 1914, 123 pp., illus.

lecturer in zoophysiology, although without a laboratory, until in 1910 the "old laboratory," as his pupils called it, was first established. Krogh came to work under modest conditions; the laboratory was installed at the place where his official residence was supposed to be, while he himself moved to a flat in the garret. Nevertheless, the laboratory was equipped according to Krogh's liking, and one could find there many of the laboratory refinements which later reappeared in the new laboratory at Juliane Maries Vej and from there made their way into numerous laboratories all over the world.

During the time before the laboratory was established, Krogh and his wife took the opportunity of making an expedition to the Isle of Disko where they performed a series of studies on the metabolism and diet of Eskimos.[16] This was indeed a task which put a person to the test; but Krogh carried through his experiments even under the most difficult climatic conditions.

After the establishment of the "old laboratory" Krogh continued his work on human physiology. In collaboration with Lindhard, he started a series of investigations on the physiology of exercise, which became models for numerous studies of this type throughout the world and formed the basis for a Scandinavian school within this branch of science. This school can be characterized by such names as Emanuel Hansen, Erik Hohwü Christensen, Marius Nielsen, and Erling Asmussen. Their work was so distinguished that, in 1931, the Health Organization of the League of Nations entrusted the group with the task of performing a model investigation into problems of the physiology of exercise. This task was attacked by a "team" of young scientists, one of the first and typical examples of teamwork which later became so popular; the result was a number of important papers.[17]

In the first investigations on the physiology of exercise during the period 1910-1920, numerous methods for the determination of circulation and respiration were developed. Thus, for example, the minute volume of the heart at work was studied in detail.[18] During these years, Krogh's eminent skill as a designer of apparatus came to its full development; instruments of greatest importance, such as the "tilting spirometer,"[18] the electromagnetic bicycle ergometer,[19] and an apparatus for gas analysis with an accuracy of 1/1000% were designed.[20] By means of these instruments the

[16] A study of the diet and metabolism of Eskimos undertaken in 1908 on an expedition to Greenland. Medd. om Grønland, 1913, *51,* 1.

[17] See Krogh, August: Liste over August Kroghs publikationer. Vid. Medd. Nat. For., 1948-49, *3,* xvii.

[18] Krogh, August and Lindhard, Johannes: Measurements of the blood flow through the lungs of man. Skand. Arch. Physiol., 1912, *27,* 100.

[19] Krogh, August: A bicycle ergometer and respiration apparatus for the experimental study of muscular work. Skand. Arch. Physiol., 1913, *30,* 375.

[20] Krogh, August: A gas analysis apparatus accurate to 0.001% mainly designed for respiratory exchange work. Biochem. J., Lond., 1920, *14,* 267.

influence of food on the efficiency of muscular work was demonstrated,[21] and it was found that in the beginning of muscular work the organism develops an oxygen deficiency which is not compensated for until the conclusion of the work.[22] At the same time, Krogh studied circulation and clearly recognized the importance of the venous flow back to the heart. Finally, he developed, in collaboration with Lindhard, the N_2O-method for the determination of the heart's minute volume.[23]

In connection with these investigations Krogh was automatically led to problems concerning the oxygen supply of the tissue. At the start of physical exercise, a considerable improvement of the blood distribution in the working muscles must occur; otherwise, the better utilization of the oxygen content of the blood cannot be explained. Very early Krogh actually arrived at the conclusion that during rest a large number of muscle capillaries are closed and that they open during work.[24] The problem was now to prove this assumption. Quite new devices had to be applied: microscopic observation of living tissue, injection methods, and histological methods. After intense work, again and again checking and rejecting the methods, Krogh succeeded in showing that his conclusion was correct.[25] In the course of 1918-1919 his results were published in scientific journals and immediately aroused greatest attention. Surprisingly soon the great significance of Krogh's observations was understood and by 1920 he was awarded the Nobel prize in medicine and physiology. It has been objected that prior to Krogh other investigators had observed that the capillaries can be contracted. This is correct, and Krogh himself stressed this fact as he gradually became acquainted with the older literature. Furthermore, contemporary scientists were studying the capillaries—Steinach, Richards, Dale, Ebbecke—but none of them had visualized so clearly the problem as a whole nor understood its importance for the circulation and a large number of other physiological processes. For many years, Krogh therefore directed almost all his strength and the working capacity of his collaborators toward the study of the capillaries.

Even before Krogh had been awarded the Nobel prize, foreign scientists had found their way to his laboratory in Copenhagen. As early as 1915 the first one, the Swedish physiologist G. Liljestrand, had come in order

---

[21] Krogh, August and Lindhard, Johannes, with the collaboration of Liljestrand, Göran and Gad-Andresen, Knud: The relative value of fat and carbohydrate as sources of muscular energy. With appendices on the correlation between standard metabolism and the respiratory quotient during rest and work. Biochem. J., Lond., 1920, *14*, 290.

[22] Krogh, August and Lindhard, Johannes: The changes in respiration at the transition from work to rest. J. Physiol., Lond., 1919-20, *53*, 431.

[23] *Op. cit.* (see note 18).

[24] The supply of oxygen to the tissues and the regulation of the capillary circulation. J. Physiol., Lond., 1918-19, *52*, 456.

[25] Studies on the capillariomotor mechanism. I. The reaction to stimuli and the innervation of the blood vessels in the tongue of the frog. J. Physiol., Lond., 1919-20, *53*, 399.

to participate in the investigations of the physiology of exercise—but now scholars arrived from all over the world, especially from the United States of America. There was no lack of problems. Was the observed regulation of the number of open capillaries in the tissue a chemical, a hormonal, or a nervous one? In what way could the capillaries with their mono-layer epithelial walls contract? The young Danish physician, Bj. Vimtrup, was able to show that the frog's capillaries are provided with special muscle cells, the so-called Rouget cells, which can contract the capillaries.[26] Many years later, Beecher, an American co-worker, demonstrated that an epithelial mechanism is also present in mammals, and that, as it was emphasized by other investigators, the capillaries can be closed by swelling of the cell nuclei.[27]

Krogh and his co-workers demonstrated that the opening and closing of the capillaries is effected both by nerves and hormones. As early as 1922, Krogh was able to publish a review of his own studies and the results of other investigators on capillary physiology.[28] This was not his first monograph. In 1916 he had been invited to write a monograph on *The respiratory exchange of animals and man.*[29] Due to its exhaustive treatment of the subject it was immediately acknowledged as the classical textbook in this field. In his new monograph on capillaries we find the same comprehension of his own observations and careful treatment of other scientists' results. These two books are, however, very different. We cannot help noticing that *The anatomy and physiology of capillaries* was written much more freely, much more *con amore.* On almost every page new problems and viewpoints are presented. The respiration monograph is a handbook in which knowledge of that time is compiled and digested; the monograph on capillaries, on the other hand, can be read like a novel. No wonder, therefore, that this book has inspired numerous investigators. It appeared in three editions, and still more editions could have appeared if Krogh had not proceeded to new tasks and felt that his contact with the current literature in this field was no longer sufficient to justify the responsibility for a new issue. Few books have exerted their influence within such varied fields. Drinker's lymph investigations, Mygind's investigations into Ménière's disease, the present author's kidney work—just to mention a few of them—have been inspired in one way or another by Krogh's capillary

---

[26] Vimtrup, Bj.: Beiträge zur Anatomie der Capillaren. I. Über contractile Elemente in der Gefäszwand der Blutcapillaren. Zeitschrift für Anatomie und Entwicklungsgeschichte, 1922, *65,* 150; II. Beiträge zur Anatomie der Capillaren Weitere Untersuchungen über contractile Elemente in der Gefäszwand der Blutcapillaren. *Ibid.,* 1923, *68,* 469.

[27] Beecher, H. K.: The independent control of the capillary circulation in a mammal. Skand. Arch. Phys., 1936, *73,* 1.

[28] *The anatomy and physiology of capillaries.* New Haven, Yale University Press, 1922, 276 pp.

[29] *The respiratory exchange of animals and man.* London, Longmans, Green, 1916, 173 pp.

studies. Moreover, scarcely any medical man in research work can escape the influence of Krogh's viewpoints.

Krogh wrote his papers and books in the English language which he mastered to perfection. When I was once asked to find a typical example of modern scientific English, I consulted a British scientist. "Take one of Krogh's chapters," was his answer. Krogh published but very few papers in Danish, and sometimes he was criticized for it; a Danish scientist should write in his native language, he was told. Krogh answered that one serves both one's country and science better by writing in a way suited to make one's works known in wider circles.

Krogh gained the attention of the scientific world through *The anatomy and physiology of capillaries,* and we can plainly speak of a Krogh school in the U.S.A. In order to illustrate Krogh's influence on American physiology it may be mentioned that eight professors on the present staff of Harvard University—among them Drinker, Landis, Churchill, and Beecher—studied with Krogh. The gratitude of American physiologists to Krogh was also manifested by their wish to deliver, in addition to the President's commemorative oration, a special American homage in tribute to Krogh at the recent Physiological Congress in Copenhagen.

In the years immediately after 1920, the capillary studies were continued, especially by investigating the formation of edema[30] and the innervation of the capillaries.[31] Simultaneously, however, Krogh started out on numerous new tasks. During his stay in the U.S.A. in 1922, where he delivered the Silliman lectures on his work on capillaries,[32] Krogh took the opportunity of acquainting himself with the preparation of newly discovered insulin. On his return to Denmark he organized, in collaboration with Hagedorn, the Danish production of insulin. For many years Krogh had been in contact with *Løvens kemiske Fabrikker.* He succeeded in convincing the proprietor that insulin should be manufactured without profit to private persons. The result was the foundation of two institutions, Nordisk Insulin Laboratory and Nordisk Insulin Fond, for many years presided over by Krogh. Both institutions are of great importance for Scandinavian science. Moreover, it has been possible to produce insulin at a much lower price than elsewhere. Krogh also studied the scientific problems involved in insulin treatment, such as its influence upon respiratory metabolism.[33] His main

---

[30] Krogh, August and Harrop, G. A.: Quelques remarques sur les stases et les oedèmes. C. rend. Soc. biol., 1921, *84,* 325.

[31] Krogh, August, Harrop, G. A., and Rehberg, P. B.: Studies on the physiology of capillaries. III. The innervation of the blood vessels in the hind legs of the frog. J. Physiol., Lond., 1922, *56,* 179.

[32] *Op. cit.* (see note 28).

[33] Krogh, August and Rehberg, P. B.: The influence of insulin on metabolic processes. Page 91 in volume in honour of I. P. Pavlov's 75th birthday, Leningrad, 1925.

interest, however, he devoted together with Hemmingsen to the problem of the standardization of insulin.[34]

A few years later the Rockefeller Foundation announced their willingness to help improve Krogh's working conditions. At that time, the old laboratory was crowded with guests from abroad. Thus, at one time, C. K. Drinker, A. N. Richards, E. D. Churchill, and several others were at the laboratory; many guests had to be refused. In the course of negotiations with the Rockefeller Foundation an arrangement was made according to which not only Krogh's institute, but five different laboratories were placed in the new stately laboratory building at Juliane Maries Vej. Krogh put his heart and soul into the building of the new institute. Every single room was drawn with all its details and a plan was made for every single wall. He surveyed the trees in the neighborhood and calculated their shadows at various seasons of the year. Many new improvements were devised, and the building, which was ready at the end of 1928, is largely stamped with Krogh's effort and differs in many respects from other institutes. Naturally this applies mainly to Krogh's own department which during the following years—and, by the way, even today—is visited by many people who are about to build their own institute. As an example of an unusual idea of Krogh's it may be mentioned that he made an attempt at building especially dust-free rooms and store rooms in the laboratory. He was not completely successful because of poor materials, but later this ideal was achieved, for example, in the new University Library. It is a specialty of the Zoophysiological Laboratory (the new name of the department) that in all rooms the furnishings and equipment can easily be moved and re-collected in another way.

Scholars from all over the world came to work in the new laboratory, and many young Danish scientists were informally appointed to the staff. In the first years, the investigations of the physiology of exercise mentioned above were performed, and Krogh continued to work out new methods—for example, one for the determination of the total osmotic pressure of the blood.[35] Moreover, he constructed a marvellous balance which is able to register the weight of a human with an accuracy of *ca.* 2 gm., even while the test person rides a bicycle ergometer suspended on the balance.[36]

There is one more problem in the field of human physiology which Krogh succeeded in treating, namely, heat regulation in man, especially the physi-

---

[34] Krogh, August and Hemmingsen, A. M.: The assay of insulin by the convulsive-dose method on white mice. Publications of the League of Nations III. Health, 1926, III, *7,* 40.

[35] Covián, Fr. Grande and Krogh, August: The change in osmotic pressure and total concentration of the blood in man during and after muscular work. Skand. Arch. Physiol., 1935, *71,* 251.

[36] Krogh, August and Trolle, Carsten: A balance for the determination of insensible perspiration in man and its use. Skand. Arch. Physiol., 1936, *73,* 159.

ological problems of heating houses. His activity in this field was concentrated in the House Heating Commission which, shortly before the war, was established by the Academy for the Technical Sciences with Krogh as president. He took an active part in the planning of both the technical and the scientific investigations. Similarly, in this case his ingenious ability as a constructor of apparatus was of decisive influence for experimental methodology. In this connection it is worth mentioning his microclimatograph which consists of a wrist watch with the clockwork reconstructed so that it can register temperature and humidity on a smoked glass plate.[37] The apparatus has proved useful in many other investigations and is especially applicable to ecological studies. The physiological part of the investigations was entrusted to Marius Nielsen and Lorentz Pedersen, the physiological results being published together with the technical ones in an extensive series of publications in 1947-48;[38] and even after this time Krogh was interested in these problems and new experiments were started shortly before his death.

As it appears from this review of Krogh's work on human physiology, his research studies covered a large number of fields—respiration, metabolism, circulation, insulin, and heat regulation—but he made still further excursions to other domains, though abandoning them rapidly. It is through the above mentioned work that he gained his great name and fame among scientists. And yet this is but one side of his scientific activity.

His achievements as a zoophysiologist are equally extensive and significant, and his work within this realm was continued throughout the years, from his first papers on hydrostatic mechanics[39] to the last ones on the production of heat in insects.[40] Krogh never lost his interest in zoophysiology—on the contrary, this was perhaps what attracted him most. Thus, in a speech to the Congress in Boston in 1929 he stated: "You will find in the lower animals mechanisms and adaptations of exquisite beauty and the most surprising character, and I think nothing can be more fascinating than the senses and instincts of insects as revealed by the modern investigations."[41] Thus he actually refrained from work on zoophysiological problems only at times when practical work forced him to do so, for example during his insulin period; otherwise one could be quite sure that he was engaged in one or another zoophysiological study.

---

[37] A micro-climate recorder. Ecology, 1940, *21,* 275.

[38] Boligopvarmningsudvalgets Meddelelser: Nos. 2, 3, 1947 and Nos. 4, 5, 6, 7, 9, 10, 11, 1948.

[39] Om Turgescens Betydning for Plantelegmets Fasthed og Spalteaabningernes Mekanik. Biol. Selsk. Forh. i Vinterhalvaaret, 1900-1901, p. 4; Om hydrostatiske Forhold i Dyreriget, *Ibid.,* p. 14.

[40] Determination of temperature and heat production in insects. Zeitschr. vergl. Physiol., 1948, *31,* 274.

[41] Krogh, August: The progress of physiology. Science, 1929, *70,* 203; also in Am. J. Physiol., 1929, *90,* 247.

Also in his zoophysiological work a definite trend can be followed through the years. As mentioned before, when a student he started on his investigations into the hydrostatic mechanism of *Corethra* larvae, and this problem was resumed many years later. Likewise the problem of the respiration of insects was taken up again, applying the improved methods of air analysis.[42] His micro air analysis apparatus, designed for the investigation of gas tension in blood, had opened the possibility of studying the respiration of the trachea, an investigation which had not been feasible before.[43] Krogh demonstrated the great significance of diffusion for the respiration of insects and its rôle as a restricting factor. Somewhat later he constructed his micro-respiration apparatus which makes a determination of the metabolism of single insects possible. Krogh used the method to investigate the influence of temperature on the metabolism of insects. This work led him to similar studies in other animals and, furthermore, to the discovery that the metabolism increases with temperature according to a Van't Hoff curve. The influence of temperature on metabolism and respiration is dealt with in *The respiratory exchange of animals and man,*[44] which contains a multitude of material from the fields of comparative physiology. Inserted among the other papers appears an investigation, in collaboration with Schmit-Jensen, on the cellulose fermentation in the paunch of ruminants[45] and, in addition, one, in collaboration with I. Leitch, on the hemoglobin of fishes,[46] which was shown to be adapted to the oxygen tension of the environment.

After the strenuous period of work on the capillaries and insulin and the ensuing intermission in his zoophysiological activities, Krogh turned to the problem of metabolism in the sea. Is it possible, as stated by Pütter, that certain aquatic animals can live on dissolved material? For a number of years Krogh, in collaboration with Spärck, conducted studies on the biology of oysters.[47] This series of investigations, the results of which have

---

[42] *The comparative physiology of respiratory mechanisms.* Philadelphia, The University of Pennsylvania Press, 1941, vii, 172 pp.

[43] On the composition of the air in the tracheal system of some insects. Skand. Arch. Physiol., 1913, *29,* 29.

Studien über Tracheenrespiration II. Ueber Gasdiffusion in den Tracheen. Pflügers Arch., 1920, *179,* 95.

Studien über Tracheenrespiration III. Die Kombination von mechanischen Ventilation mit Gasdiffusion nach Versuchen an Dytiscuslarven. Pflügers Arch., 1920, *179,* 113.

[44] See note 29.

[45] Krogh, August and Schmit-Jensen, H. O.: The fermentation of cellulose in the paunch of the ox and its significance in metabolism experiments. Biochem. J., Lond., 1920, *14,* 686.

[46] Krogh, August and Leitch, I. The respiratory function of the blood in fishes. J. Physiol., Lond., 1919, *52,* 288.

[47] Gaarder, Torbjørn and Spärck, R.: Biochemical and biological investigations of the variations in the productivity of the West Norwegian oyster pools. Conseil pour l'Exploration de la Mer. Rapports et Proces-Verbaux 1931, *75,* 47; also *Hydrograpisch-biochemische Untersuchungen in norwegischen Austern-Pollen.* Bergens Museums Aarbok, Naturvidenskabelig rekke, 1932, No. 1, 144 pp.

been published by other scientists (in the first place by Gaarder and Spärck), was performed in a West Norwegian pond rented by the laboratory; here, Norwegian and Danish scientists investigated the conditions for the propagation of oysters. Krogh took a lively part in the discussions and planning of these experiments which lasted many years and were very costly; but despite their high expense the costs of these experiments were covered by the sale of oyster breedings. On the whole, Krogh was always successful in conjuring the funds required for the intensive work at the laboratory, to which the State contributed only a very modest sum. The remaining part was raised from outside funds or in some other way, for example by running the laboratory workshop on a purely commercial basis. All apparatus designed in the laboratory, and this means primarily by Krogh himself, was built in the workshop and sold without profit for the designer, the total income being the laboratory's. Thus, the basal metabolism apparatus constructed by Krogh on the basis of the "tilting spirometer" was sold by the hundreds to hospitals and doctors. The income of the laboratory in the course of years amounted to a figure of six digits.

The investigations on metabolism in the sea, which had now started, required new methods. Again Krogh was the man to develop them: methods for the quantitative determination of the chemical composition of the plankton[48] as well as for the study of the quantity of dissolved nutrient substances in water.[49]

It may be noted that at a much earlier date, Krogh had been interested in oceanographic investigations. During his first stay in Greenland (1902), he measured carbon dioxide in sea water[50] and established our knowledge of the equilibrium between the carbon dioxide content of the air and sea water,[51] which is so important as a regulating factor for the carbon dioxide content of the air. With the help of his precision air analysis apparatus Krogh also analyzed the composition of the atmosphere and he stated the extreme constancy of the latter.[52] At the same time he demonstrated how small the changes were even in a city of the size of Copenhagen.[53]

In connection with the work on the diet of aquatic animals, which finally refuted Pütter's theory of the significance of dissolved substances, Krogh started working on the problem of the osmoregulation of aquatic animals. To these studies, where investigations into the permeability of the skin

[48] Eine Mikromethode für die organische Verbrennungs-analyse, besonders von geløsten Substanzen. Biochem. Zschr., 1930, *221,* 247.
[49] Krogh, August and Keys, Ancel: Methods for the determination of dissolved organic carbon and nitrogen in sea water. Biol. Bull., 1934, *67,* 132.
[50] On the tension of carbonic acid in natural waters and especially in the sea. Medd. om Grønland, 1904, *26,* 331.
[51] The abnormal CO_2 percentage in the air in Greenland and the general relations between atmospheric and oceanic carbonic acid. *Ibid.,* 1904, *26,* 407.
[52] The composition of the atmosphere. An account of preliminary investigations and a programme. K.D. Vid. Selsk. Fys. Medd., 1919, *1,* 12.
[53] See note 52.

play an important part, Krogh applied as early as 1935 the nowadays extensively used isotopes, stressing their enormous applicability in biology.[54] In the years to come the osmoregulatory studies were continued and, in 1939, Krogh summarized our knowledge in this sphere in a monograph on *Osmotic regulation in aquatic animals*[55] which, like the lectures on capillaries, immediately became the classic book in this field and a source from which many investigators have received inspiration.

About a year later Krogh accomplished the publication of another monograph on *The comparative physiology of respiratory mechanisms,*[56] reviewing all the knowledge gained in this domain in the course of the twenty-five years which had elapsed since the publication of his first monograph on almost the same subject.[57] This book and the viewpoints expressed in it will certainly become a gold-mine for zoophysiologists.

Again and again Krogh resumed problems which had caught his attention during one period or the other. Since his very youth he had been interested in the flight of birds and insects; throughout the years he repeatedly discussed the possibilities of studying more thoroughly the mechanism and energy balance of animal flight, examining the various ways of attacking these problems. As late as 1945, after his retirement from the professorship and after having moved to his private laboratory, he found opportunity for resuming study of this question. Again his imagination and his ability as an experimenter were unique. Investigations on the flight of grasshoppers were performed partly by means of a grasshopper merry-go-round carrying 32 grasshoppers, partly with single animals in an air tunnel. When published by his co-worker Weis-Fogh, these studies will undoubtedly prove to be basic for our knowledge in this domain.

As already mentioned, Krogh's very first work was a contribution to the sap tension in plants.[58] In his later years he came back to related problems investigating, in collaboration with the Swedish plant physiologist, Hans Burström, the flow of the sap of trees in relation to the development of the buds.[59] These investigations were performed during his forced emigration towards the end of the war, when it was found safest for him to settle in Sweden.

Krogh's scientific production embraces numerous fields, many more than are mentioned here, and almost three hundred papers are included in his bibliography. Here I wish to refer to the lists of his publications found both in the Communications of the Academy for the Technical Sci-

---

[54] The use of isotopes in biological research. Orvosi Hétilap, Budapest, 1935.

[55] Krogh, August: *Osmotic regulation in aquatic animals.* Cambridge, Cambridge University Press, 1939, 242 pp.

[56] *Op. cit.* (see note 42).

[57] *Op. cit.* (see note 29).

[58] *Op. cit.* (see note 39).

[59] Krogh, August and Burström, Hans: The biochemistry of the development of buds in trees and the bleeding sap. K. D. Vid. Selsk., Biol. Medd., 1946, *20,* 2.

ences,[60] and in the *Vidensk. Medd. fra Dansk naturhistorisk Forening, København.*[61] Krogh's significance in science is not limited to his scientific production. He has been an important guide for other scientists, mostly Danes, but also numerous foreigners who came for his advice concerning problems which frequently were outside his scientific domain. But even if a subject was ever so remote from his thoughts, Krogh was always ready to listen to his visitor; as soon as his interest was caught he was able to give advice and the interviewer did well to follow his suggestions. If, on the other hand, a young scientist approached him to have a problem suggested, he came in vain.

For many years it was easy to come and talk with Krogh on scientific matters; nobody was refused an interview. In later years, however, Krogh found it necessary to economize his time—so many things were left for him to do—and therefore he asked visitors to look for advice elsewhere. But if one was admitted, an "interview" with him took a very typical course. First, Krogh asked the visitor to talk about his problem. In the beginning he sat listening with his head somewhat bowed to the side and a scrutinizing glance in his eyes. Then he asked a single question, more questions, and somewhat later, maybe some hours later, he would start speaking, and if his interest had actually been awakened he was generous with his time. He then gave his advice, whether to continue or to stop, whether there was a practicable way to go, and where it led. Not all who came understood that it was a good thing to follow his advice; maybe some actually did not want to learn, but would rather have had their own ideas confirmed, while others may have assumed that Krogh did not understand their problem as profoundly as they did themselves. Therefore they went away angry because he had not approved of their ideas. Many of them certainly regretted that they had not listened to him and relinquished a plan. Krogh's intuitive judgment of whether a goal could be reached in a given way was fabulous even in fields remote from his thoughts. This capability was also of enormous value to his own work. Beyond doubt, there are few scientists who initiated so many diverse problems and yet were able successfully to complete so many.

Also, for young scientists at the laboratory Krogh was an outstanding teacher not only of the experimental procedure to attack a problem, but, of course, primarily in making them comprehend the interrelationship of the problems as a whole. Nobody who worked at his side for even a short time could help being influenced by his way of working. Krogh was opposed to the simple collecting of scientific facts: "Facts are necessary, of course, but unless fertilized by ideas, correlated with other facts, illuminated by

---

[60] Fortegnelse over August Krogh's publikationer, revideret af dr. phil. Axel M. Hemmingensen. Meddelelser fra Akademiet for de tekniske videnskaber., 1949, No. *1*, 39.

[61] *Op. cit.* (see note 17).

thought, I consider them as material only for science . . . Too many experiments and observations are being made and published and too little thought is bestowed upon them," he once said in a speech,[62] and it was this doctrine he taught the young generation.

On the other hand, Krogh was always very reluctant to encourage a young man to become a scientist. He did not advocate such decisions, he rather warned against such a career. It was his view that the requirements for a degree in zoophysiology should be such that only the highly interested and capable candidates could pass. He had the great pleasure to see his children and children-in-law develop notable scientific abilities. Not many scientists receive on their seventieth anniversary a volume dedicated to them which contains seven scientific papers written by four children and three sons-in-law and with a preface by a daughter-in-law.[63]

On his fiftieth birthday his pupils published a fine book in his honour —a tribute paid as a rule to a scientist of a more advanced age.[64] If they had waited until his sixtieth birthday, an edition of one volume would not have been sufficient.

Krogh's lectures were brilliant, perhaps not so much for their form as for their content. He made great effort to be up to date in the whole field, and all new discoveries and viewpoints were included in his lectures. It was intellectually gratifying to attend his examinations, but for many candidates they certainly were too difficult; it was hard for many of them to grasp the elementary aspects. On the other hand, Krogh was an unsurpassed teacher for advanced students and hardly any one of them left his lectures without realizing that he had been in touch with an outstanding scientist.

As the years went by, Krogh became tired of the great burden of preparing the lectures and, from 1934, he was given dispensation from his teaching load. He then gave only a few series of lectures on special topics (osmoregulation, comparative respiratory physiology, etc.) From then on, he had little contact with the students, most of whom knew him only as the author of the well-known textbook.[65] This book was the result of another of Krogh's activities. When in 1903 new regulations were issued for high school teaching, it was decided that the treatment of man in the natural history classes should be based on physiological rather than anatomi-

---

[62] Krogh, August: The progress of physiology. Science, 1929, *70,* 203; also in Am. J. Physiol., 1929, *90,* 248.

[63] Krogh, August. Dr. phil., Dr. jur., Dr. med., Dr. sc. Til hans 70 Aars Fødselsdag 15 November 1944 (Udg. af August Kroghs Børn og Svigerbørn). (Red. af Knut Schmidt-Nielsen) 76S. ill. og 3 Tvlr. 4°. 44. Privattryk. Ikke i Bogh.

[64] *Physiological papers, dedicated to Prof. August Krogh.* R. Ege, H. C. Hagedorn, *et al.,* Eds. Copenhagen, Levin and Munksgaard, 1926; London, Wm. Heinemann Ltd., 1926, xvi, 375 pp.

[65] *Kortfattet Laerebog i menneskets Fysiologi (for Gymnasiets mat.—naturv. Linie).* København, Gyldendal, First ed., 1908; Second-tenth eds., 1912-1946. Ninth and tenth eds. in collaboration with Prof. P. Brandt Rehberg. 130 pp.

cal views. In 1908, Krogh's *Text book on the physiology of man* was published for the first time. In its way this book is just as excellent as Krogh's scientific publications. In about a hundred pages the physiology of man is reviewed in such a way as to be read to everybody's profit by people of widely varying backgrounds. The more one knows to start with, the more one finds in this book. It is both easy and extremely difficult, because it contains so much information for a reader who tries to penetrate the depths of the sentences. For forty years this book has been the only Danish school book on this subject and it has appeared in eleven editions. Although the character of the book is preserved and the contents changed only slightly, every new edition meant hard work, and by replacing a few words he could frequently express quite new viewpoints. Undoubtedly because of this book, general knowledge of physiology for many years was greater among students in Denmark than in other countries, although by now the difference may have disappeared.

Krogh felt closely attached to high school teachers and he understood the significance of keeping the teachers *à jour* with the progress in physiology. He achieved this partly by lecturing and partly by publishing papers in the popular periodical *Naturens Verden*. In these articles he often went outside his own field and dealt, for example, with brain physiology, especially with Pavlov's conditioned reflexes, and with sense physiology—two domains which he never entered in his own research but in which he always was vitally interested. On the whole, his biological interests were very wide; thus, for example, he was an expert on Danish flora. Moreover, his old love of the sea induced him to spend a lot of time during the summer vacations in a small jolly-boat on the Isefjord, studying animal life.

Krogh was extremely industrious. He started work in his laboratory early in the morning and the cleaning personnel were not allowed to enter his rooms before 9 o'clock. From 9 to 10 o'clock he paused, then he continued and as a rule did not stop before late in the evening. Once when an interviewer asked about his hobby, he answered, "My work."

Despite this enormous diligence which almost grew in the course of time, he nevertheless had the leisure to take an interest in the problems of the day. He read a great deal, preferably British and American literature. I remember that his library at the time I first met him included a large number of books dealing with naval history and the complete works of Kipling and other British authors. He knew his Kipling so well that he was able to send quoted passages with the statement of the first use of their words to the *Oxford Dictionary*. He liked to read aloud from Kipling, and many of his friends keep a pleasant remembrance of a party of children and friends gathered in front of the fireplace while one of Kipling's stories was read for them. Krogh was also vividly interested in history and archaeology and, not least, in the history of science and its development. In collaboration with V. Maar he translated and published Steno's *Preliminary communication of a treatise on solid bodies which are naturally embedded in other solid bodies.*[66] He has written repeatedly about Steno, and his very last literary work is an essay on Steno in the book *Prominent Danish personalities.*[67]

A peculiar feature of his mind was his attitude towards music. Not only was he lacking in an ear for music—he simply disliked music, which he considered a kind of disturbing noise causing him almost physical discomfort.

Krogh's attitude towards other people was frequently determined by a first impression or by one or another reaction of the person in question. From this impression Krogh formed his picture. This might appear arbitrary and subjective, but as a rule he turned out to be right even though he himself would not deny that he possibly could be unjust. To him things were either black or white. If he was your friend, he was it completely and usually forever; was he your enemy, he very rarely changed his mind. If he had reason for mistrust he was through with the man. To him applied William Sørensen's motto, "In the last instance everything depends on the character." Something of this attitude was also to be found in his scientific criticism. He could be violent in scientific controversies, which he considered almost useful for science, since they appeared to him to be a necessary link in the comprehension of truth. But, in a speech given in Boston in 1929, he says apologetically: "We may fondly imagine that we are impartial seekers after truth, but with a few exceptions, to which I know that I do not belong, we are influenced and sometimes strongly by our personal bias and we give our best thoughts to those ideas which we have to defend."[68]

It was the same uncompromising attitude which resulted in his passionately discussed resignation from the Royal Danish Academy of which he had been a member since 1916. He had given numerous lectures in the Academy and he had been a keen participant in the sessions for many years. The reason for his resignation was that he failed to induce the Academy to take a more active attitude concerning the economic support of science, and he thought that in the long run his action would prove useful. "At least it has shown the authorities that if they want to do something positive public opinion will be behind them," he wrote in a letter to an American friend.

---

[66] Steno, Nicolaus: *Foreløbig meddelelse til en afhandling Om faste legemer, der findes naturlig indlejrede i andre faste legemer.* I oversaettelse ved August Krogh og Vilhelm Maar. Med indledning og noter. København, Gyldendal, 1902, 106 pp.

[67] Niels Steensen 1638-1686. Store danske Personligheder, Berlingske Forlag, Kbhvn., 1949, p. 44.

[68] The progress of physiology. Science, 1929, *70,* 203; also in Am. J. Physiol., 1929, *90,* 248.

Krogh did not attach much importance to formal honours and refused to accept decorations. On the other hand, he was very appreciative of tributes of respect from his colleagues, for example, membership of numerous foreign societies and the six honorary degrees which he was awarded in the course of time.

His affiliation with Copenhagen University meant very much to him. Admittedly, he was not interested in sharing the University's administrative duties; according to his own view, he had only two obligations: to teach and to do research, the latter above all. Therefore he refused the deanship, nevertheless taking an active part in discussions of the faculty concerning the teaching program or the problems of promoting scientific work; in these fields his opinion frequently was of decisive influence.

Danish science has suffered a great loss in the death of August Krogh. His working ability was practically unimpaired until his final illness, and until his last day he was vividly interested in a great variety of problems.[60] If he had been allowed to live, many new discoveries would certainly have come to light.

[60] His last paper, which was actually published after his death, was: Reminiscences of work on capillary circulation. Isis, 1950, *41,* 14.