NATIONAL ACADEMY OF SCIENCES

PER SCHOLANDER

1905—1980

A Biographical Memoir by
KNUT SCHMIDT-NIELSEN

Biographical Memoir

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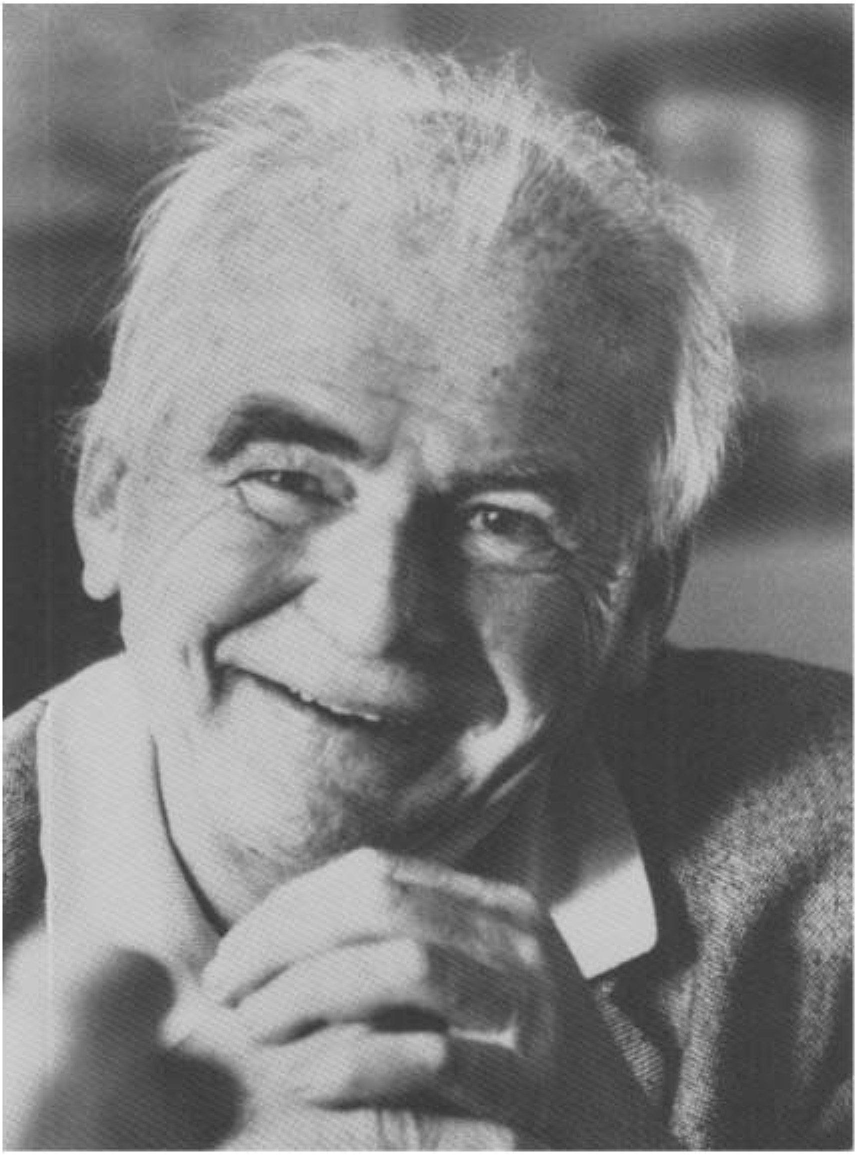

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PER FREDRIK THORKELSSON SCHOLANDER

November 29, 1905–June 13, 1980

BY KNUT SCHMIDT-NIELSEN

THE MOST IMPRESSIVE ASPECT of Scholander's scientific life is his versatility as a biologist and his ability to make significant contributions in a broad range of fields. He was first of all a physiologist, but his work always signified a fresh approach to broader biological problems and principles. He had an ability to ask the right questions, to conceive of simple experiments and design the necessary equipment, to utilize novel approaches, and to present simple and logical answers to important questions. As a person he was warm and enthusiastic, generous and kind, and utterly unconcerned with the hassles of form and bureaucracy.

Scholander was born in Sweden and grew up in a family of talent and culture. His father was an engineer; his mother, Norwegian born, was an accomplished professional pianist; his grandfather was a prominent architect, as well as a writer and musician, and a professor at the Royal Academy of Arts. Scholander has related that, as a small boy, he crawled underneath his mother's Steinway grand piano when she practiced, smothered by the waves of emotion in the music. He himself became an accomplished violinist, which I first discovered when late one night I found him playing in the laboratory to a record that omitted the first violin.

Because of the divorce of his parents, Scholander moved to Norway, where in 1924 he matriculated at the Faculty of Medicine of the University of Oslo (then Christiania). At that time medical students started with Latin, philosophy, chemistry, and physics, whereupon followed years of preclinical work in anatomy, physiology, and so on. Although Scholander was terribly bored by much of this, he continued his medical studies and completed his medical education in 1932, within the normal time span. Scholander has described how his textbooks were always full of marginal notes about explanations he did not believe, but his grades did not reflect his brilliance. There was a rumor among the university students—probably untrue—that he completed his final medical examinations with the unique distinction of having obtained the lowest grades ever given a passing student.

Scholander's years as a medical student became significant in a very different and unexpected way. Walking home from the University one day, bored with tedious coursework, he picked some lichens off the trees along the street. At home he found a flora for lower plants and soon had the lichens identified. He continued collecting, and when his flora proved inadequate, he sought further help from the professor of botany, Bernt Lynge. Lynge recognized the unusual talents of the young student, who rapidly became an outstanding lichen specialist. Lynge himself, because of severe arthritis, was unable to go to Greenland and offered Scholander the opportunity to take his place as a botanist on several arctic expeditions. As a result, Scholander spent three summers (1930–1932) in Greenland and Spitzbergen. His contributions to lichenology, particularly his revision of the family Umbilicariaceae (1934b), placed him among the world's foremost lichenologists at that time.

The young physician—who was never to practice medicine—had become a botanist. He was approached by the professor of systematic botany, Jens Holmboe, who suggested that he should present himself for a doctorate in botany, and in 1934 he was awarded the Dr. Philos. by the University of Oslo. It might be expected that his dissertation would deal with lichens, but this would be uncharacteristic for Scholander—he was awarded the doctorate based on a monograph of the vascular plants of Spitzbergen (1934a).

During the arctic expeditions, Scholander had been intrigued by the many seals, polar bears, and diving birds he saw. He clearly saw that many important questions needed answers, such as "How do diving seals get enough oxygen?" and "Why don't they get divers' disease as humans do after descending to similar depths?" He obtained working space in the basement of the University Physiological Institute, and with the aid of the professor of anatomy, the geneticist Otto Mohr, he was awarded a small university research fellowship that enabled him to pursue his interests in physiology. He developed new methods for the continuous recording of the respiratory metabolism of diving animals, and one of his publications (1937b) caught the attention of the distinguished Danish physiologist August Krogh, who immediately understood Scholander's genius for design of experimental apparatus. At that time I was a student in Copenhagen, and when Scholander came to give a lecture on his studies of diving animals, I sat there completely spellbound by his brilliant presentation and the simple and logical answers he provided to questions that long had puzzled physiologists who contemplated the mysteries of diving physiology.

The most characteristic differences between a diving seal and a human are strikingly simple. First, when a seal begins a dive, it exhales and dives with a minimal volume of air in the lungs. It may seem counterproductive to dive with little air in the lungs, but it greatly reduces the amount of nitrogen taken up by the blood and the tissues during the dive. This seems to be the key factor in how seals and whales avoid divers' disease, or the bends, which is so tragically well known from humans who ascend after dives to great depths. The oxygen-carrying capacity of the blood, however, is much greater in the seal than in humans. Its blood volume is relatively larger, and both blood and muscles contain much larger amounts of hemoglobin, and thus hold more oxygen, than in mammals in general. A seal's most characteristic response to an experimental dive is to slow the heart down to a few beats per minute; the blood is diverted to the most vital organs, notably the central nervous system and the eyes. The muscles, which are able to function anaerobically through the formation of lactic acid, receive no blood and thus acquire an oxygen debt that is repaid when oxygen is again available at the termination of the dive. These important results were summarized in a monograph (1940a) that remains the foundation for what we understand today of the physiology of diving animals.

At about the same time, Laurence Irving at Swarthmore College had also done distinguished work on diving physiology, and August Krogh arranged for a Rockefeller fellowship for Scholander to continue his studies of diving physiology at Swarthmore. Scholander, however, was still in Norway when the Second World War broke out, and the Rockefeller Foundation cancelled all fellowship awards. When Krogh was informed about this, he sent an urgent telegram to Scholander that he should immediately leave for the USA, and Scholander obtained space on the last ship that left Norway for the USA. Once landed, he of course received the cancelled fellowship, and the studies of diving animals were continued in collaboration with Irving.

However, as the United States became involved in the Second World War, Laurence Irving went to the Air Force, and Scholander followed him there. Both Irving and Scholander made substantial scientific and practical contributions during their military service. Scholander became involved in the testing of military equipment and survival gear. He developed simple and reliable field methods; for example, he studied the conditions under which field stoves caused carbon monoxide poisoning in tents and snow houses, he tried sleeping bags under blizzard conditions, and tested covered life rafts during storms in the Aleutian Islands.

During this time he also arranged a quick and unauthorized rescue mission to an airplane that had crashed at the tip of the Alaskan peninsula. One survivor had been seen, but rescue teams had failed to reach the site over land and Scholander's camp commander had vetoed parachute jumps. Going in by plane would be insubordination, but Scholander found a young pilot who, risking his career, volunteered. Another medical doctor and a priest joined them, and the three, who had never jumped before, came down successfully, although with some difficulty. They found that two men had perished, but three survivors were taken care of by the M.D. while Scholander took on the cooking, greatly helped by the plane's cargo of sacramental wine for Passover, or "Hangover" as Scholander called it. Eventually the survivors and the rescuers were taken out by a bush plane from Anchorage.

I have later heard that Scholander, as a result of the successful Aleutian rescue, was to be courtmartialed for insubordination. As the case slowly moved through the military channels, it became known to Detlev Bronk, who was angered by the bureaucratic stupidity of punishing one of the most effective scientists in the Air Force. By some unknown intervention, the case was aborted at the highest level in Washington.

After the years of military work, Irving and Scholander, with support from the Navy, established a research laboratory at Point Barrow, Alaska. Among the most important results were measurements of the metabolic heat production and the insulation needed for warmblooded animals, mammals and birds, to keep warm in the arctic climate. It turned out that larger animals, such as foxes and eskimo dogs, could sleep at temperatures as low as −30 or −40°C without any increase in heat production. Smaller animals, however, started to shiver at temperatures well above freezing, and they needed increased heat production to stay warm and maintain a normal body core temperature of 37°C. The information was in agreement with the simple physical laws of heat exchange, and the studies clearly showed that below a certain temperature, the lower critical temperature, the metabolic rate increased linearly with the decrease in temperature. This model for the responses of warmblooded animals to low temperatures has remained the model for virtually all later studies of this nature (1950c,d,e).

The arctic work included studies of coldblooded animals and of plants, and also the tolerance of various organisms to freezing. Scholander devised a simple and elegant method for determining the amount of body water in a mosquito larva that was actually frozen to ice inside the intact animal. He showed that these, when they were thawed out, were still alive and unharmed after more than 80 percent of their body water had been frozen to ice (1953e).

Scholander's many ingenious methods for the analysis of minute samples of gas became very helpful in an unexpected area. He noticed that gas bubbles tended to develop under ice, and also that a chunk of ice chopped from a glacier gave off bubbles of gas when put into a drink to cool it. Scholander determined that ice is virtually impermeable to gases; he froze thin sheets of ice, 0.1 mm thick, and floated them on cold mercury. He introduced small volumes of gases under the ice and attempted to measure changes in their composition. He was never able to detect any penetration, and concluded that ice at −10°C is at least 70,000 to 80,000 times more impermeable to gases than a layer of water. This made him wonder whether the air trapped deep in the Greenland glaciers contains a permanent record of the composition of the atmosphere in earlier periods (1956b,e; 1958c,g; 1960c; 1961c; 1962g).

After the two years of work at Barrow, Scholander left the Arctic Research Laboratory. A. Baird Hastings, professor of biological chemistry at Harvard University, was a person who fully understood Scholander's genius, and he offered him a position as research fellow. During two years in Hastings' laboratory, Scholander developed a series of elegant micromethods for blood and gas analysis, and started applying these to solving some of the intriguing problems of how gases are secreted into the swimbladder of fish. Depending on the depth at which a fish is found, the gases in the swimbladder are under high pressure. Gases that are dissolved in the surrounding seawater are at partial pressures close to those in the atmosphere, and they are secreted into the swimbladder against pressures that in deep sea fish may amount to several hundred atmospheres. The micromethods Scholander had developed were ideal for these studies. He now demonstrated that not only oxygen, but also nitrogen, is secreted against tremendous concentration gradients. That this is possible for oxygen, a relatively reactive gas, was perhaps not surprising, but how could nitrogen, a presumably totally inert gas, also be secreted actively against such concentration gradients? The answer to both puzzles lay in the unusual vascular supply to the swimbladder and in physical principles that, once they were understood, were simple to explain. The blood supply to the swimbladder forms a counter-current system that is an essential part of the secretion mechanism (1954a,b).

The swimbladder studies were continued during the three years of Scholander's association with the Woods Hole

Oceanographic Institution as a physiologist (1952–1955). The result was a series of papers that now form the foundation for our understanding of swimbladder function (1955g, 1958f, and others).

In 1955 Scholander was called to the University of Oslo as professor and director of a new Institute of Zoophysiology. His three years in Oslo were very active. He continued studies of the adaptation of humans to cold and answered questions of how primitive humans can keep warm in cold climates. Eskimoes, Lapps, and Australian aborigines were compared with Norwegian students. The latter slept outdoors at temperatures around 0°C, naked in a single-blanket sleeping bag. For an unacclimatized person this is intensely uncomfortable and it is impossible to sleep, but after five or six days of acclimatization the students had no trouble. The most notable change in their physiology was a substantial increase in metabolic heat production. (The motivation of the students to go through with these uncomfortable experiments seemed to be related to their being granted permission to hunt reindeer.)

When the Australian aborigines were studied, it was found that they could sleep through a cold night with a normal metabolic rate. The difference was that the aborigines permitted the temperatures of the legs to drop to around 10°C. In other words, they had adapted by permitting their peripheral temperatures to drop instead of increasing their metabolic rate. This, of course, is a more economical approach; keeping the legs warm requires a substantial increase in metabolic heat production.

After three highly productive years in Norway, Scholander was brought to the Scripps Institution of Oceanography through the efforts of its director, the oceanographer Roger Revelle, and he remained there until the end of his life. With tremendous enthusiasm he took up one problem after another. Among these were some important problems of plant physiology. The question of how water can be brought to the top of the tallest trees had always intrigued him, and studies that he had initiated while he was at Woods Hole and in Oslo were continued (1957a, 1958b, 1961d). The fact that suction, in combination with the cohesion of water, can explain the ascent of the sap led to later studies of osmotic phenomena in other plants, and eventually to the development of the solvent tension theory of osmosis. Important in this connection was a series of studies of mangroves and their salt balance and the question of how they manage with their roots in seawater. These studies started on the Cape York Peninsula in northern Australia (1962h) and continued for several years (1965a,c; 1966a; 1968b).

The solvent tension theory of osmosis was founded on Scholander's experience in plant physiology. A series of elegant experiments, in part carried out in collaboration with H. T. Hammel, also of Scripps, provided easily comprehended support for Scholander's theories (1971c,e). The theories were severely criticized by several physical chemists, who based their arguments on classical thermodynamic arguments. Scholander's ingenious experiments remained unchallenged; only their interpretation could be disputed. Although Scholander's view is simple and intuitive, it is undoubtedly more convenient to adhere to the traditional way of thinking about osmotic phenomena. I can only regret that I do not have the competence to evaluate the controversy and give proper perspective to the significance of Scholander's contributions in this field.

A most important development during Scholander's many years at the Scripps Institution was the design and building of the research vessel *Alpha Helix.* During his many field expeditions, Scholander had understood the importance of bringing adequate equipment into the field, where the important physiological problems are evident. He conceived of a laboratory ship that should be able to take a group of a dozen or so scientists to any area of the world. The ship should be equipped with modern laboratories and an excellent machine shop. This was based on Scholander's own experience; he was a skilled machinist and this had helped him during his many successes in designing new methods and equipment. He saw the absolute necessity of always having at his disposal a good machine shop that could solve problems as they arise under field conditions.

Support for building the ship was obtained from the National Science Foundation, and in 1966 the ship started on its first cruise, the Billabong Expedition to the Great Barrier Reef. A National Advisory Board, initially chaired by Baird Hastings, evaluated applications for use of the ship. Over the fourteen years the ship remained in service as a floating physiological laboratory, expeditions went to Australia, the South Seas, the Amazon, the Antarctic, the Galapagos, the Bering Sea, and other sites. Several hundred scientists from all over the world have participated actively in these expeditions, and the records of Scripps Institution show that the work on the *Alpha Helix* has resulted in a total of 547 publications in recognized scientific journals—an impressive record for the relatively modest funds invested in the *Alpha Helix.*

Not only through the *Alpha Helix,* but throughout his life, Scholander became a seminal figure for physiologists who were concerned with the problems that animals and plants encounter in nature. He was an immensely enthusiastic person, a true naturalist who perceived interesting scientific problems wherever he moved. He led a restless and highly productive life. A large number of scientists, now active and recognized around the world, have been associated with Scholander and have been influenced by his stimulating and dynamic personality. In 1951 he married the daughter of Laurence Irving, Susan, who remained his devoted companion the remainder of his life.

Throughout his productive life, Scholander retained the ability to open up new fields of investigation. He was not only a brilliant scientist, but also an enthusiastic and charming person, engaging, warm, and generous. His way of managing the increasing constraints imposed by the bureaucracy of university life and government support of science was merely to ignore them. As an example of his charming and untraditional personality, I wish to relate his study of wave-riding dolphins. Many of us have seen dolphins or porpoises that playfully ride along just in front of the bow wave of a ship, motionless and effortlessly remaining in place. This, of course, aroused Scholander's curiosity. It belongs to the story that the free ride of the dolphins had been the subject of theoretical analysis by fluid dynamicists, but Scholander thought that the theory, to use his own words, "missed the boat." When on board a Norwegian sealing vessel, he rigged up a simple device—with a streamlined vane attached to a spring to measure the forces in the bow wave—and he found that these might indeed explain how a dolphin gets the needed forward thrust to remain in the wave (1959a,d). Characteristically, Scholander concluded his paper with these words: "This, I believe, is the way dolphins ride the bow wave, and if it is not, they should try."

Scholander died in his home in La Jolla, California, on June 13, 1980. He was seventy-four years old. Ten days earlier he had broken his hip in a fall in his laboratory, but after a brief hospital stay he was home again and enthusiastically planning for the summer's activities, which included a trip to Europe. A sudden collapse ended his long and productive life.

THE MATERIAL I HAVE USED to prepare this biography has been assembled with the help of Susan Irving Scholander and the present director of the Physiological Research Laboratory at Scripps

Institution of Oceanography, Dr. Fred N. White. Archival material has been made available to me by Elizabeth N. Shor, also of Scripps Institution of Oceanography. My own familiarity with P. F. Scholander's life comes from my admiration for his scientific contributions and from many years' close friendship. Other good friends have helped me by reading my manuscript.

HONORS AND DISTINCTIONS

EDUCATION

M.D., University of Oslo, 1932
Dr. Philos. (Botany), University of Oslo, 1934

PROFESSIONAL APPOINTMENTS

1932–1934	Instructor of Anatomy, University of Oslo
1932–1939	Research Fellow in Physiology, University of Oslo
1939–1941	Rockefeller Fellow
1939–1943	Research Associate, Department of Zoology, Swarthmore College
1943–1946	U.S. Air Force. Commissioned as Captain, 1943; Major, 1946
1946–1949	Research Biologist, Swarthmore College
1949–1951	Research Fellow, Department of Biological Chemistry, Harvard Medical School
1952–1955	Physiologist, Woods Hole Oceanographic Institution
1955–1958	Professor of Zoophysiology, University of Oslo, and Director of Institute of Zoophysiology
1958–1973	Professor of Physiology, Scripps Institution of Oceanography, University of California, San Diego
1963–1970	Director, Physiological Research Laboratory, University of California, San Diego
1973–1980	Emeritus Professor, Scripps Institution of Oceanography, University of California, San Diego

HONORS AND AWARDS

Rockefeller Fellow, 1939–1941
Soldiers' Medal for Valor (for Aleutian rescue), 1945
Legion of Merit (for pilot ejection seat), 1946
Norwegian Academy of Sciences, 1955
American Academy of Arts & Sciences, 1959
National Academy of Sciences, 1961
American Philosophical Society, 1962
Cosmos Club, 1964
John Simon Guggenheim Fellow, 1969–1970
Doctor of Science, University of Alaska, 1973
Royal Swedish Academy of Sciences, 1974
Doctor of Science, Uppsala University, 1977
Fridtjof Nansen Prize, Oslo, 1979

BIBLIOGRAPHY

This list is based on one compiled by Susan Irving Scholander in 1964 and is updated with information received from Scripps Institution of Oceanography. It includes items published in books and journals, but not reports to government agencies and grant-giving foundations.

1932

With B. Lynge. Lichens from N.E. Greenland. Skr. Svalb. Ishavet, no. 41. 120 pp.

1933

a. Notes on *Peltigera erumpens* (*Tayl.*) Vain. s. l. Nyt Mag. Naturv., 73:21–54.

b. With J. Devold. Flowering plants and ferns of Southeast Greenland. Skr. Svalb. Ishavet, no. 56. 220 pp.

1934

a. Vascular plants from northern Svalbard. Skr. Svalb. Ishavet, no. 62. 155 pp.

b. On the apothecia in the lichen family Umbilicariaceae. Nyt Mag. Naturv., 75:1–41.

1937

a. With Eilif Dahl and B. Lynge. Lichens from Southeast Greenland. Skr. Svalb. Ishavet, no. 70. 90 pp.

b. New graphic methods for the recording of the respiratory gaseous exchange. Skr. Nor. Vidensk. Akad. Oslo, no. 3. 73 pp.

1938

a. A modified manometric blood gas apparatus. Scand. Arch. Physiol., 78:145–48.

b. New method for the determination of the blood volume in animals. Scand. Arch. Physiol., 78:189–96.

c. With W. Bjerknes. Method for continual airbreathing in closed-circuit apparatus. Scand. Arch. Physiol., 79:164–68.

1940

a. Experimental investigations on the respiratory function in diving mammals and birds. Hvalråd. Skr., no. 22. 131 pp.

b. On the respiratory adjustment to prolonged diving in the seal. Am. J. Physiol., 129:456–57.
c. With L. Irving and S. W. Grinnell. Respiratory metabolism of the porpoise. Science, 91:455.
d. With L. Irving and S. W. Grinnell. Experimental studies on the physiology of diving mammals. Science, 92:483.

1941

a. With L. Irving and S. W. Grinnell. The respiration of the porpoise, *Tursiops truncatus*. J. Cell. Comp. Physiol., 17:145–68.
b. With L. Irving. Experimental investigations on the respiration and diving of the Florida manatee. J. Cell. Comp. Physiol., 17:169–91.
c. With L. Irving and S. W. Grinnell. The depression of metabolism during diving. Am. J. Med. Sci., 202:915–16.
d. With L. Irving and S. W. Grinnell. Significance of the heart rate to the diving ability of seals. J. Cell. Comp. Physiol., 18:283–97.

1942

a. Method for the determination of the gas content of tissue. J. Biol. Chem., 142:427–30.
b. With L. Irving and S. W. Grinnell. Aerobic and anaerobic changes in seal muscles during diving. J. Biol. Chem., 142:431–40.
c. With L. Irving and S. W. Grinnell. The regulation of arterial blood pressure in the seal during diving. Am. J. Physiol., 135:557–66.
d. With L. Irving and S. W. Grinnell. On the temperature and metabolism of the seal during diving. J. Cell. Comp. Physiol., 19:67–78.
e. With S. W. Grinnell and L. Irving. Experiments on the relation between blood flow and heart rate in the diving seal. J. Cell. Comp. Physiol., 19:341–50.
f. Microburette. Science, 95:177–78.
g. Analyzer for one ml of respiratory gas. Rev. Sci. Instrum., 13:27–31.
h. Volumetric microrespirometers. Rev. Sci. Instrum., 13:32–33.
i. A micro-gas-analyzer. Rev. Sci. Instrum., 13:264–66.

j. With G. A. Edwards. Volumetric microrespirometer for aquatic organisms. Rev. Sci. Instrum., 13:292–95.

k. Analyzer for quick estimation of respiratory gases. J. Biol. Chem., 146:159–62.

l. Microgasometric determination of nitrogen in blood and saliva. Rev. Sci. Instrum., 13:362–64.

m. With G. A. Edwards. Nitrogen clearance from the blood and saliva by oxygen breathing. Am. J. Physiol., 137:715–16.

n. With L. Irving and G. A. Edwards. Experiments on carbon monoxide poisoning in tents and snow houses. J. Ind. Hyg., 24:213–17.

o. With F. J. W. Roughton. A simple microgasometric method of estimating carbon monoxide in blood. J. Ind. Hyg., 24:218–21.

p. With L. Irving and S. W. Grinnell. Experimental studies of the respiration of sloths. J. Cell. Comp. Physiol., 20:189–210.

1943

a. With L. Irving and S. W. Grinnell. Respiration of the armadillo with possible implications as to its burrowing. J. Cell. Comp. Physiol., 21:53–63.

b. With L. Irving and G. A. Edwards. Factors producing carbon monoxide from camp stoves. J. Ind. Hyg., 25:132–36.

c. With G. A. Edwards and L. Irving. Improved micrometer burette. J. Biol. Chem., 148:495–500.

d. With F. J. W. Roughton. Micro gasometric estimation of the blood gases. I. Oxygen. J. Biol. Chem., 148:541–50.

e. With F. J. W. Roughton. Micro gasometric estimation of the blood gases. II. Carbon monoxide. J. Biol. Chem., 148:551–63.

f. With G. A. Edwards and F. J. W. Roughton. Micro gasometric estimation of the blood gases. III. Nitrogen. J. Biol. Chem., 148:565–71.

g. With F. J. W. Roughton. Micro gasometric estimation of the blood gases. IV. Carbon dioxide. J. Biol. Chem., 148:573–80.

h. With N. Haugaard and L. Irving. A volumetric respirometer for aquatic animals. Rev. Sci. Instrum., 14:48–51.

1947

a. With L. Irving and O. Hebel. Apparatus for complete recording of respiratory exchange in man. Fed. Proc. Fed. Am. Soc. Exp. Biol., 6:134–35.

b. Accurate analysis of respiratory gases in 0.5 cubic centimeter samples. Fed. Proc. Fed. Am. Soc. Exp. Biol., 6:197–98.
c. Analyser for accurate estimation of respiratory gases in one-half cubic centimer samples. J. Biol. Chem., 167:235–50.
d. Simple syringe burette. Science, 105:581.
e. With S. C. Flemister and L. Irving. Microgasometric estimation of the blood gases. V. Combined carbon dioxide and oxygen. J. Biol. Chem., 169:173–81.
f. With H. J. Evans. Microanalysis of fractions of a cubic millimeter of gas. J. Biol. Chem., 169:551–60.
g. With L. Irving. Micro blood gas analysis in fractions of a cubic millimeter of blood. J. Biol. Chem., 169:561–69.

1949

Volumetric respirometer for aquatic animals. Rev. Sci. Instrum., 20:885–87.

1950

a. Volumetric plastic micro respirometer. Rev. Sci. Instrum., 21:378–80.
b. With H. Niemeyer and C. L. Claff. Simple calibrator for Warburg respirometers. Science, 112:437–38.
c. With V. Walters, R. Hock, and L. Irving. Body insulation of some arctic tropical mammals and birds. Biol. Bull. Woods Hole, Mass., 99:225–36.
d. With R. Hock, V. Walters, and L. Irving. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. Woods Hole, Mass., 99:237–58.
e. With R. Hock, V. Walters, and L. Irving. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. Woods Hole, Mass., 99:259–71.

1951

a. Nitrogen tension in the swimbladder of marine fishes in relation to the depth. Fed. Proc. Fed. Am. Soc. Exp. Biol., 10:121.
b. With C. L. Claff, C. T. Teng, and V. Walters. Nitrogen tension in the swimbladder of marine fishes in relation to the depth. Biol. Bull. Woods Hole, Mass., 101:178–93.
c. With H. Erikson and L. Irving. Apparatus for complete volu-

metric recording of the respiratory gaseous exchange in man. Scand. J. Clin. Lab. Invest., 3:228–33.

1952

a. With C. L. Claff, J. R. Andrews, and D. F. Wallach. Microvolumetric respirometry. J. Gen. Physiol., 35:375–95.
b. With C. L. Claff and S. L. Sveinsson. Oxygen consumption during the cleavage of single cells. Fed. Proc. Fed. Am. Soc. Exp. Biol., 11:141.
c. With C. L. Claff and S. L. Sveinsson. Respiratory studies of single cells. I. Methods. Biol. Bull. Woods Hole, Mass., 102:157–77.
d. With C. L. Claff and S. L. Sveinsson. Respiratory studies of single cells. II. Observations on the oxygen consumption in single protozoans. Biol. Bull. Woods Hole, Mass., 102:178–84.
e. With C. L. Claff, S. L. Sveinsson, and Susan I. Scholander. Respiratory studies of single cells. III. Oxygen consumption during cell division. Biol. Bull. Woods Hole, Mass., 102:185–99.
f. With J. H. Kinoshita and J. P. Bunker. The use of the volumetric respirometer in the determination of plasma carbon dioxide. J. Lab. Clin. Med., 40:156–60.
g. With J. Wyman, Jr., G. A. Edwards, and L. Irving. On the stability of gas bubbles in sea water. J. Mar. Res., 11:47–62.
h. With W. Flagg, V. Walters, and L. Irving. Respiration in some arctic and tropical lichens in relation to temperature. Am. J. Bot., 39:707–13.
i. With R. J. Hock, H. Erikson, W. Flagg, and L. Irving. Composition of the ground-level atmosphere at Point Barrow, Alaska. J. Met., 9:441–42.

1953

a. With W. Flagg, V. Walters, and L. Irving. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool., 26:67–92.
b. With L. van Dam. Composition of the swimbladder gas in deep sea fishes. Biol. Bull. Woods Hole, Mass., 104:75–86.
c. With L. van Dam. Concentration of hemoglobin in the blood of deep sea fishes. J. Cell. Comp. Physiol., 41:522–24.
d. Studies on the physiology of frozen plants and animals in the Arctic. Abstracts Communications, 19th Int. Physiol. Congr., pp. 741–42.

e. With W. Flagg, R. J. Hock, and L. Irving. Studies on the physiology of frozen plants and animals in the Arctic. J. Cell. Comp. Physiol., 42, suppl. 1. 56 pp.

1954

a. With L. van Dam. Secretion of gases against high pressures in the swimbladder of deep sea fishes. I. Oxygen dissociation in blood. Biol. Bull. Woods Hole, Mass., 107:247–59.
b. Secretion of gases against high pressures in the swimbladder of deep sea fishes. II. The rete mirabile. Biol. Bull. Woods Hole, Mass., 107:260–77.

1955

a. With L. van Dam and Susan I. Scholander. Gas exchange in the roots of mangroves. Am. J. Bot., 42:92–98.
b. Evolution of climatic adaptation in homeotherms. Evolution, 9:15–26.
c. With W. E. Love and J. W. Kanwisher. The rise of sap in tall grapevines. Plant Physiol., 30:93–104.
d. With L. van Dam, C. L. Claff, and J. W. Kanwisher. Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull. Woods Hole, Mass., 109:328–34.
e. With W. E. Schevill. Counter-current vascular heat exchange in the fins of whales. J. Appl. Physiol., 8:279–82.
f. Hydrostatic pressure in coconuts. Plant Physiol., 30:560–61.
g. With L. van Dam and T. Enns. Secretion of inert gases and oxygen by the swimbladder of fishes. Biol. Bull. Woods Hole, Mass., 109:338–39.
h. With Alan C. Burton and Otto G. Edholm. Man in a cold environment. Physiological and pathological effects of exposure to low temperatures. Scand. J. Clin. Lab. Invest., 7:349.

1956

a. With L. van Dam and T. Enns. Nitrogen secretion in the swimbladder of whitefish. Science, 123:59–60.
b. With J. W. Kanwisher and D. C. Nutt. Gases in icebergs. Science, 123:104–5.
c. With H. Erikson, J. Krog, and K. Lange Andersen. The critical temperature in naked man. Acta Physiol. Scand., 37:35–39.
d. Climatic rules. Evolution, 10:339–40.

e. With L. K. Coachman and E. Hemmingsen. Gas enclosures in a temperate glacier. Tellus, 8:415–23.

f. With L. van Dam and T. Enns. The source of oxygen secreted into the swimbladder of cod. J. Cell. Comp. Physiol., 48:517–22.

g. Observations on the gas gland in living fish. J. Cell. Comp. Physiol., 48:523–28.

h. With L. van Dam. Micro gasometric determination of oxygen in fish blood. J. Cell. Comp. Physiol., 48:529–32.

1957

a. With Berthe Ruud and H. Leivestad. The rise of sap in a tropical liana. Plant Physiol., 32:1–6.

b. With L. van Dam. The concentration of hemoglobin in some cold water arctic fishes. J. Cell. Comp. Physiol., 49:1–4.

c. With L. van Dam, J. W. Kanwisher, H. T. Hammel, and M. S. Gordon. Supercooling and osmoregulation in arctic fish. J. Cell. Comp. Physiol., 49:5–24.

d. With K. Lange Andersen, J. Krog, F. Vogt Lorentzen, and J. Steen. Critical temperature in Lapps. J. Appl. Physiol., 10:231–34.

e. With H. T. Hammel, K. Lange Andersen, and Y. Løyning. Metabolic acclimation to cold in man. Fed. Proc. Fed. Am. Soc. Exp. Biol., 16:114–15.

f. "The wonderful net." Sci. Am., 196(4):96–107.

g. With J. Krog. Countercurrent heat exchange and vascular bundles in sloths. J. Appl. Physiol., 10:405–11.

h. With H. Leivestad and H. Andersen. Physiological response to air exposure in codfish. Science, 126:505.

i. Oxygen dissociation curves in fish blood. Acta Physiol. Scand., 41:340–44.

j. With H. T. Andersen and H. Leivestad. "Air diving" in fishes. Acta Physiol. Scand., 42, suppl. 145:6–7.

k. With H. T. Hammel, K. Lange Andersen, and Y. Løyning. Metabolic acclimation to cold in man. Acta Physiol. Scand., 42, suppl. 145:63–64.

l. With J. Krog. Counter current vascular heat exchange, with special reference to the arteriovenous bundles in sloths. Acta Physiol. Scand., 42, suppl. 145:89–90.

m. With G. Sundnes. Gas secretion in fishes lacking "rete mirabile." Acta Physiol. Scand., 42, suppl. 145:125–26.

1958

a. With H. T. Hammel, K. Lange Andersen, and Y. Løyning. Metabolic acclimation to cold in man. J. Appl. Physiol., 12:1–8.
b. The rise of sap in lianas. In: *The Physiology of Forest Trees,* ed. Kenneth V. Thimann, pp. 3–17. New York: Ronald Press.
c. With L. K. Coachman, E. Hemmingsen, T. Enns, and H. de Vries. Gases in glaciers. Science, 127:1288–89.
d. With H. Jensen. Bag spirometer. Scand. J. Clin. Lab. Invest., 10:225–26.
e. With H. T. Hammel, J. S. Hart, D. H. LeMessurier, and J. Steen. Cold adaptation in Australian aborigines. J. Appl. Physiol., 13:211–18.
f. With G. Sundnes and T. Enns. Gas secretion in fishes lacking rete mirabile. J. Exp. Biol., 35:671–76.
g. With L. K. Coachman and T. Enns. Gas loss from a temperate glacier. Tellus, 10:493–95.
h. Counter current exchange. A principle in biology. Hvalråd. Skr., no. 44. 24 pp.
i. Studies on man exposed to cold. Fed. Proc. Fed. Am. Soc. Exp. Biol., 17:1054–57.
j. With H. Leivestad and G. Sundnes. Cycling in the oxygen consumption of cleaving eggs. Exp. Cell. Res., 15:505–11.
k. With O. Iversen. New design of volumetric respirometer. Scand. J. Clin. Lab. Invest., 10:429–31.

1959

a. Wave-riding dolphins: How do they do it? Science, 129:1085–87.
b. Experimental studies on asphyxia in animals. In: *Oxygen Supply to the Human Foetus,* ed. James Walker and A. C. Turnbull, pp. 267–74. Oxford: Blackwell Scientific Publications.
c. Supercooling and freezing in poikilotherms. In: *Simposios Conferencias, 21st Congr. Int. Ciencias Fisiol.,* Buenos Aires, pp. 77–81.
d. Wave-riding dolphins. Science, 130:1658.

1960

a. Oxygen transport through hemoglobin solutions. Science, 131:585–90.
b. Oxygen diffusion. Science, 132:368.
c. With D. C. Nutt. Bubble pressure in Greenland icebergs. J. Glaciol., 3:671–78.
d. With E. Hemmingsen. Specific transport of oxygen through hemoglobin solutions. Science, 132:1379–81.
e. Man in cold environment. Discussion. Fed. Proc. Fed. Am. Soc. Exp. Biol., 19, suppl. 5:8–10, 11–12.

1961

a. With H. T. Hammel, D. H. LeMessurier, E. Hemmingsen, and W. Garey. Circulatory adjustment in pearl divers. Fed. Proc. Fed. Am. Soc. Exp. Biol., 20:103.
b. With D. C. Nutt and L. K. Coachman. Dissolved nitrogen in West Greenland waters. J. Mar. Res., 10:6–11.
c. With E. A. Hemmingsen, L. K. Coachman, and D. C. Nutt. Composition of gas bubbles in Greenland icebergs. J. Glaciol., 3:813–22.
d. With E. Hemmingsen and W. Garey. Cohesive lift of sap in the rattan vine. Science, 134:1835–38.

1962

a. With M. S. Gordon and B. H. Amdur. Freezing resistance in some northern fishes. Biol. Bull. Woods Hole, Mass., 122:52–62.
b. With H. T. Hammel, D. H. LeMessurier, E. Hemmingsen, and W. Garey. Circulatory adjustment in pearl divers. J. Appl. Physiol., 17:184–90.
c. With C. R. Olsen and D. D. Fanestil. Some effects of breath holding and apneic underwater diving on cardiac rhythm in man. J. Appl. Physiol., 17:461–66.
d. With Edda Bradstreet. Microdetermination of lactic acid in blood and tissues. J. Lab. Clin. Med., 60:164–66.
e. With Edda Bradstreet and W. F. Garey. Lactic acid response in the grunion. Comp. Biochem. Physiol., 6:201–3.
f. With R. W. Elsner and E. Hemmingsen. The work of maintaining flotation in sea water. Physiologist, 5:136.

g. With W. Dansgaard, D. C. Nutt, H. de Vries, L. K. Coachman, and E. Hemmingsen. Radio-carbon age and oxygen-18 content of Greenland icebergs. Medd. Grönl., 165(1). 26 pp.

h. With H. T. Hammel, E. Hemmingsen, and W. Garey. Salt balance in mangroves. Plant Physiol., 37:722–29.

i. With C. R. Olsen and D. D. Fanestil. Some effects of apneic underwater diving on blood gases, lactate, and pressure in man. J. Appl. Physiol., 17:938–42.

j. Physiological adaption to diving in animals and man. Harvey Lect., 57:93–110.

1963

a. With R. W. Elsner and W. F. Garey. Selective ischemia in diving man. Am. Heart J., 65:571–72.

b. The master switch of life. Sci. Am., 209(6):92–106.

1964

a. Animals in aquatic environments: Diving mammals and birds. In: *Handbook of Physiology. Sect. 4: Adaptation to the Environment*, ed. D. B. Dill, pp. 729–39. Bethesda, Md.: American Physiological Society.

b. With T. Enns. Oxygen transport by hemoglobin collision. Fed. Proc. Fed. Am. Soc. Exp. Biol., 23:468.

c. With H. T. Hammel, E. A. Hemmingsen, and Edda D. Bradstreet. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Natl. Acad. Sci., USA, 52:119–25.

d. With R. W. Elsner, A. B. Craig, E. G. Dimond, L. Irving, M. Pilson, K. Johansen, and Edda Bradstreet. A venous blood oxygen reservoir in the diving elephant seal. Physiologist, 7:124.

e. From the frozen forest to tropical mangroves. In: *Program Abstracts, Pt. 2, Proc. Alaska Sci. Conf.*, p. 38. Washington, D.C.: American Association for the Advancement of Science.

1965

a. With H. T. Hammel, Edda D. Bradstreet, and E. A. Hemmingsen. Sap pressure in vascular plants. Science, 148:339–46.

b. With T. Enns and E. D. Bradstreet. Effect of hydrostatic pressure on gases dissolved in water. J. Phys. Chem., 69:389–91.

c. With H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. Sap pressure in plants. Science, 149:920–21.
d. Tension gradients accompanying accelerated oxygen transport in a membrane. Science, 149:876–77.
e. Reverse osmosis and sap pressure in vascular plants. Science, 150:384.
f. With R. Elsner. Circulatory adaptations to diving in animals and man. In: *Physiology of Breath-Hold Diving and the Ama of Japan*, pp. 281–94. Washington, D.C.: National Academy of Sciences Publ. 131.

1966

a. With E. D. Bradstreet, H. T. Hammel, and E. A. Hemmingsen. Sap concentrations in halophytes and some other plants. Plant Physiol., 41:529–32.
b. The role of solvent pressure in osmotic systems. Proc. Natl. Acad. Sci. USA, 55:1407–14.

1967

a. Osmotic mechanism and negative pressure. Science, 156:67–69.
b. Negative pressure in plants and osmotic mechanism. Science, 156:541.
c. Osmotic pressure. Science, 158:1212.
d. With T. Enns and E. Douglas. Role of the swimbladder rete of fish in secretion of inert gas and oxygen. Adv. Biol. Med. Phys., 2:231–44.

1968

a. With R. W. Elsner. A comparative view of cardiovascular defense against acute asphyxia. Proc. 2nd Int. Symp. Emergency Resuscitation, Oslo. Acta Anaesthesiol. Scand., suppl. 29:15–33.
b. How mangroves desalinate seawater. Physiol. Plant, 21:251–61.
c. With A. R. Hargens and S. L. Miller. Negative pressure in the interstitial fluid of animals. Science, 161:321–28.
d. With R. S. Bandurski and E. Bradstreet. Metabolic changes in the mud-skipper during asphyxia or exercise. Comp. Biochem. Physiol., 24:271–74.

e. With M. de Oliveira Perez. Sap tension in flooded trees and bushes of the Amazon. Plant Physiol., 43:1870–73.

1969

a. With L. Irving, E. A. Hemmingsen, and E. Bradstreet. Ultraviolet absorption in the cornea of arctic and alpine animals. In: *The Biologic Effects of Ultraviolet Radiation,* ed. F. Urbach, pp. 469–71. London: Pergamon Press.
b. With S. B. Stromme and J. E. Maggert. Interstitial fluid pressure in terrestrial and semiterrestrial animals. J. Appl. Physiol., 27:123–26.
c. With A. R. Hargens. Stretch mounting for osmotic membranes. Microvasc. Res., 1:417–19.

1971

a. State of water in osmotic processes. Microvasc. Res., 3:215–32.
b. Imbibition and osmosis in plants. In: *Topics in the Study of Life: The Bio Source Book,* ed. Amy Kramer, pp. 138–47. New York: Harper & Row.
c. With M. Perez. Experiments on osmosis with magnetic fluid. Proc. Natl. Acad. Sci. USA, 68:1093–94.
d. With J. E. Maggert. Supercooling and ice propagation in blood from arctic fishes. Cryobiology, 8:371–74.
e. With M. Perez. Effect of gravity on osmotic equilibria. Proc. Natl. Acad. Sci. USA, 68:1569–71.

1972

a. With M. Perez. Molecular buoyancy and osmotic equilibrium. Proc. Natl. Acad. Sci. USA, 69:301–2.
b. Tensile water. Am. Sci., 60:584–90.

1973

With H. T. Hammel. Thermal motion and forced migration of colloidal particles generate hydrostatic pressure in solvent. Proc. Natl. Acad. Sci. USA, 70:124–28.

1975

Water states and water gates in osmotic processes, and the inoperative concept of molfraction of water. J. Exp. Zool., 194:241–48.

1976

With H. T. Hammel. *Osmosis and Tensile Solvent.* Berlin: Springer Verlag.

1978

a. Rhapsody in science. Annu. Rev. Physiol., 40:1–17.
b. Water under tension, its fundamental role in capillarity, osmosis and colligative properties. In: *Frontiers of Human Knowledge,* Skrifter rörande Uppsala universitet, C:38, Acta Univ. Ups. Nova Acta Regiae Soc. Sci. Ups. Ser. VC, pp. 297–308.
c. With A. R. Hargens and W. L. Orris. Positive tissue fluid pressure in the feet of antarctic birds. Microvasc. Res., 15:239–44.