

Obituary

In memoriam Knut Schmidt-Nielsen

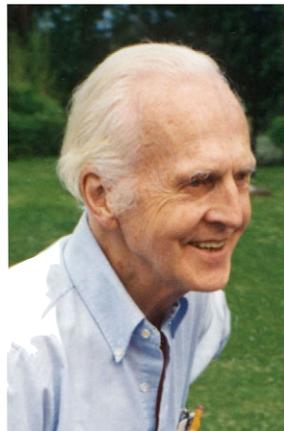
24 September 1915 – 25 January 2007

In the early hours of 25 January 2007, Knut Schmidt-Nielsen, James B. Duke Professor of Physiology Emeritus at Duke University, passed away peacefully in his home in Durham, North Carolina, at the age of 91. This tall, handsome Norse with his notoriously straight back and a great vital force had become frail over the past few years, but he remained alert to the very last, still enjoying a daily walk in the Duke Gardens with his caring wife Margareta. A giant of biology has left this world, a leading biologist who has broken new ground in many fields, a soft but powerful voice who was able to tell us like no other how animals work.

Have you ever wondered why your nose drips in winter? Knut Schmidt-Nielsen explained this to me one day in his notoriously lucid way. When we inhale cold dry air through the nostrils, the mucous membrane of the nasal conchae cools off while it releases water to humidify the air; when we exhale, the now water-saturated warm air cools off while flowing over the – still cooled – nasal conchae, and some of the water condenses onto the surface to be reabsorbed by the well-vascularized mucous membrane, but some excess water may eventually drip out of the nose. Of course, the motive for Knut's discovery of this mechanism of a nasal countercurrent heat exchanger in 1964 was more fundamental than this small inconvenience of human life. It derived from his broad quest into understanding how animals can survive in the desert, one problem being that there is no water to drink so that economy of water is vital to survive. In his book on *Desert Animals: Physiological Problems of Heat and Water*, written in 1962 and published in 1964, he “examined what we know about desert animals and how they manage to live in an environment of excessive temperatures and water shortage”. He explores in great detail how animals adapt to these extreme conditions and describes the research program that he has pursued throughout his life – examining how animals meet the challenges of their environment and how they adapt to life on dry land, or at sea. When I first met Knut in 1977 during our

scientific expedition to Kenya, led by his post-doctoral fellow and disciple C. Richard Taylor, he engaged in studying the nasal heat exchanger in camels and giraffes, not an easy undertaking as seen in Fig. 1, where Vaughn Langman, secured by a rope, tries to fit a thermocouple into the giraffe's nose while Dick Taylor operates the recorder and Knut directs the operation in the blazing African sun.

His autobiography, written in 1998, was aptly entitled *The Camel's Nose*, and in the preface Knut says “*The questions I have tried to answer have been very straightforward, perhaps even simple: Do marine birds drink seawater? How do camels in hot deserts manage for days without drinking water when humans could not survive without water for more than a day? How can kangaroo rats live in the desert without any water to drink? How can snails find water and food in the most barren deserts?... These are important questions. The answers not only tell us how animals overcome seemingly insurmountable obstacles... they also give us insight into general principles of life and survival.*” Knut's innate curiosity provoked interest beyond his lab in the myriad of specializations that allow animals to function in unique environments. He inspired followers to look at the natural world.



Knut Schmidt-Nielsen at the Conference on Comparative Physiology in June 1995.

The scientific investigator

His long career as a scientist started when he became a student in the laboratory of August Krogh in Copenhagen in 1937 – 70 years ago! August Krogh was a most creative comparative physiologist with broad perspective, one of the first to look into mechanisms of adaptation and the role of structure in determining functions. Through his imagination and wisdom, this great man influenced Knut's orientation in science, but also very close personal ties developed between them so that he became part of the Krogh family and, in 1939, married Krogh's daughter Bodil in his first marriage. For his first scientific project, Krogh suggested the comparative study



Fig. 1. Knut Schmidt-Nielsen in Kenya in 1977 measuring nasal temperature gradients in a giraffe, with Vaughn Langman holding the giraffe's head and C. Richard Taylor operating the recorder.

of osmoregulation in freshwater crayfish and in marine shore crabs that cannot survive in freshwater. It seems that, as so often, the first 'assigned' research project became determinant for the direction of future research. Still in Copenhagen, Knut asked his first independent scientific question that derived from this comparative osmoregulation study: how can marine birds survive without drinking freshwater? Twelve years later, when he had already found his interest in desert life, he wrote a paper, co-authored with Bodil Schmidt-Nielsen, entitled 'Do kangaroo rats thrive when drinking sea water?'. From these studies, there followed the discoveries on the importance of salt glands for osmoregulation and then the large series of studies on water balance mentioned above.

The scientific work of Knut Schmidt-Nielsen is broad and focussed on the question of *How Animals Work*, the title of a small but classic book published in 1972 as a result of a series of lectures given at Cambridge University. What solutions has nature found during evolution to solve difficult problems? Before tackling the water balance problem discussed above, he and his collaborators had addressed the question of how birds breathe and elucidating the mechanism by which air flows unidirectionally through the airways of the rigid bird lung. He postulated that birds flying at high altitude can achieve a high oxygen saturation of the blood due to a countercurrent system of

air and blood flow, similar to what is found in fish gills; later, this concept had to be modified to a crosscurrent flow of blood over the airway system. Another major field of work had to do with locomotion and its energetics, and here the challenge of understanding the effect of varying body size of animals became particularly prominent. *Scaling: Why Is Animal Size So Important?* is the title of Schmidt-Nielsen's last monograph published in 1984, a most lucid and scholarly essay, another classic of comparative biology where he discusses the consequences of varying body size on vital functions on the basis of experimental data interpreted by simple models. Around 1970, he had started a series of studies that tackled the problem of how body size affected O₂ consumption when animals were working, in contrast to the usual consideration of basal metabolic rate. These studies, in which C. Richard Taylor was involved, formed the basis for a broad project of assessing the functional limits of working animals, including the question of to what extent structural design of the organ system involved was a factor limiting performance, eventually leading to the concept of symmorphosis. This large international collaborative project started with the Kenya expedition in 1977, and Knut supported it with a keen interest as the mentor of several of the participants.

The leader of animal physiology

Knut Schmidt-Nielsen was one of the most prominent and most successful animal physiologists. Throughout his long scientific career, he addressed puzzling questions about how animals work by looking at how nature has solved these problems when enabling diverse animals to cope with varied functional stresses imposed by environment, specific niches or variations in body size. This research strategy has no doubt been stimulated by August Krogh, as seen above, or perhaps it was just reinforced by this great physiologist, because the very reason for the young Norwegian seeking to work with Krogh in Denmark was his interest in how animals work, kindled during his youth when he joined naturalists on their expeditions.

The *oeuvre* of Schmidt-Nielsen in comparative physiology is very broad, ranging from snails and birds to camels and giraffes, from desert tortoise to penguins, from osmoregulation and breathing to energy metabolism and thermoregulation. This achievement was possible because of the many post-doctoral fellows and students that have, over the decades, come to work with him. It is these disciples, successful comparative physiologists in all continents, that have carried on and further developed the research program in comparative physiology so inspiringly laid out by him. When asked by what main lessons Knut Schmidt-Nielsen had inspired him most, one of his later PhD students mentioned four virtues: curiosity, accuracy, simplicity and scope. That he was able to impart these virtues to his disciples made their success as independent researchers.

The promotor of comparative physiology

Besides this direct fostering of a new generation of comparative physiologists, Knut Schmidt-Nielsen has

influenced many more scientists through his writings, the original research papers as well as his books, which are masterpieces in the presentation of clear explanations of physiological principles and often provide simple answers to big scientific questions. He has written not only about what we know but also about what we do not as yet understand. And this has challenged many to find answers to how animals work. In addition to the monographs mentioned above, there is his large textbook on *Animal Physiology*, so lucidly written and so successful that it has appeared in five editions in English, the last one in 1997, and has been translated into several different languages.

In 1970, Knut Schmidt-Nielsen, together with C. Liana Bolis, Simon Maddrell and Richard D. Keynes, founded the International Conferences in Comparative Physiology, held under the auspices of the Interunion Commission for Comparative Physiology and set up by the International Unions of Physiological Sciences (IUPS) and of Pure and Applied Biophysics (IUPAB). They were convened every two years, mostly in Switzerland but with some exceptions, such as in 1980 when a conference on 'Comparative Physiology Perspectives' was organized in Denmark to honour Knut Schmidt-Nielsen on his 65th birthday. These conferences were indeed very successful, as they brought together biologists of varied orientations, and many collaborative projects across the disciplines have had their origin in these conferences; also, each one resulted in a carefully edited monograph, and in many of these Knut Schmidt-Nielsen's editorial skills were felt. The last of these conferences was held in 1995 in Ascona, Switzerland on the topic 'Principles of Animal Design' and was led and inspired by one of Knut's most prominent disciples, C. Richard Taylor, who had been chair of these conferences for many years and, unfortunately, died a few months after this conference. Under a new chair, the Interunion Commission changed the format of its activities so that these conferences were discontinued. But the royalties collected from the conference proceedings accrued and were recently turned over to IUPS as an endowment for 'Lectures on Emerging Topics in Comparative and Evolutionary Physiology' to be held at the quadriennial IUPS Congresses; these Lectures are to be called the 'Knut Schmidt-Nielsen Lecture', in recognition of his pioneering work and leading spirit in comparative physiology.

At the IUPS Congress in Budapest in 1980, Knut Schmidt-Nielsen was elected President of the International Union of Physiological Sciences, a function he fulfilled for two terms until 1986. Among the many initiatives he took, the one of

creating NIPS, the *News in Physiological Sciences*, had a resounding effect in promoting physiology. This new journal, jointly produced by the IUPS and the American Physiological Society, was intended to present frontier work in physiology in such a way as to be accessible and understandable by any physiology teacher anywhere in the world. Knut's idea was to help them to access advanced research results from fields other than their own specialty, thus counterbalancing the trend to ever narrower specialization that is associated with the need for focus in research. He took it on himself to be the founding editor of this journal, and I have seen how he worked on every manuscript received, even though it had been invited and even though the author was a most prominent scientist. But that made the success of this journal, which now continues under the simple title *Physiology*.

Rewards

With all this to his record, it is not surprising that Knut Schmidt-Nielsen has received many honours. He was a member of the US National Academy of Sciences, of the Royal Society of London and of the French Academy of Sciences, among many others. In 1992, he was awarded the most prestigious International Prize for Biology by the Emperor of Japan; to escort his wife Margareta to dinner with the Emperor and the Empress was one of the highlights in his late life, and his eyes would light up when he recounted these special experiences.

'Measuring a Life' is the title of the last chapter in Knut Schmidt-Nielsen's autobiography. His was indeed a life that cannot be measured with a yardstick, in that it is too rich and has too many facets, too many ramifications into branches that are still growing by the endeavours of his students and colleagues, and now their own students. For all of us who have had the privilege of knowing this gentlemanly colleague and have become his friend, we maintain a respectful memory of one who has indeed made rich contributions in his long life.

The author is Emeritus Professor of Anatomy at the University of Berne, and former President of the International Union of Physiological Sciences. He gratefully acknowledges the valuable contributions of Barbara A. Block and James H. Jones, former students of Knut Schmidt-Nielsen.

Ewald R. Weibel
University of Berne