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Knut Schmidt–Nielsen. 24 September 1915 — 25 January 2007

Steven Vogel

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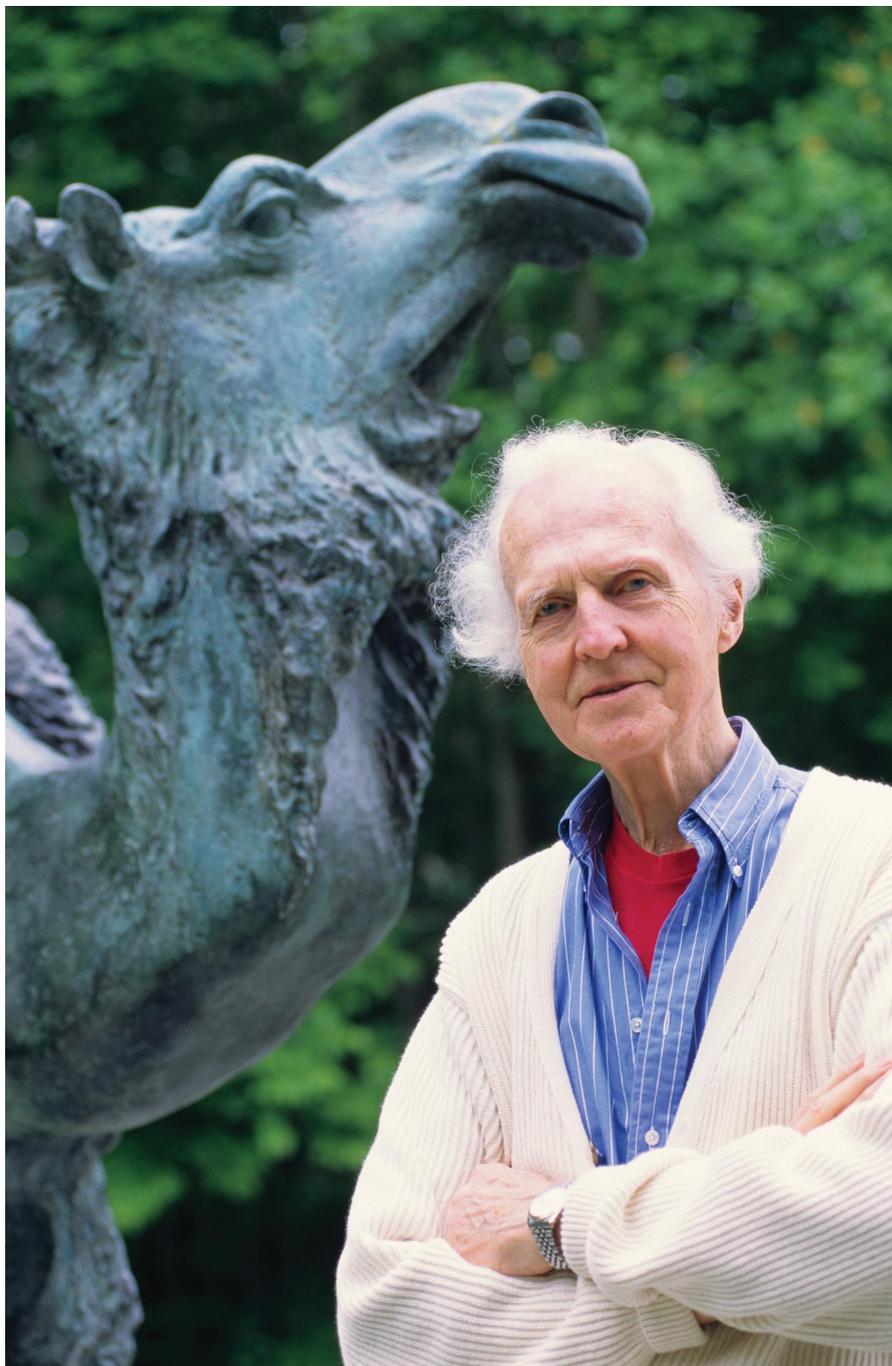
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KNUT SCHMIDT-NIELSEN
24 September 1915 — 25 January 2007



Kristen-Hilson

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BY STEVEN VOGEL

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Knut Schmidt-Nielsen, born in Trondheim, Norway, was the leading comparative physiologist of the second half of the twentieth century. He played a key role in the transformation of what, in the first half of the century, had been a well-regarded but essentially local approach to the subject begun by his mentor, August Krogh, into what is now an established, worldwide field. He was a pioneer in integrating field and laboratory measurements and in recognizing the intimate relationship between an animal's environment and its physiological adaptations. He greatly broadened and provided perhaps the best support for Krogh's notion that mechanisms could often be best illuminated by shrewd choice of experimental material, in particular by using animals in which a particular function met an especially strong challenge. He also drew attention to the way in which the pattern of variation of some feature or function varied with size—'scaling'—could be used as yet another tool for elucidating function. He began work that integrated animal locomotion and physiology, recognizing that locomotion typically represented an extreme challenge for physiological systems. More than any other person, he changed the way in which physiology is taught to undergraduates in the USA and elsewhere: from a human-oriented perspective derived from its origin in medicine to a comparative outlook compatible with the rest of biology.

EARLY LIFE

His Norwegian father, Sigval Schmidt-Nielsen, and grandfather, who were a biochemist and an engineer, respectively, both maintained a serious interest in natural history. Perhaps presciently, his grandfather, Olaf Schmidt-Nielsen, transferred flounder to fresh water, noting that they survived but failed to reproduce. His Swedish mother, Signe Sturzen-Becker, came from a literary family, although she herself was oriented towards physical science. Like his father, she had a doctoral degree, hers directed by Svante Arrhenius ForMemRS, 1903 Nobel laureate in chemistry, but she pursued no professional career.

Although his interest in science and natural history began early, Schmidt-Nielsen achieved no great academic distinction in either secondary school or in studying mining engineering at the Institute of Technology at Trondheim. Zoology, at the University of Oslo, went much better, on account both of the greater academic freedom it afforded and of the subject itself. In particular, he encountered physiology for the first time, specifically that of fishes, and during the summer of 1935 he first did fieldwork that extended beyond the simple collecting of specimens. Three subsequent summers produced information on feeding and growth of lake trout, published jointly with his father (1)*.

In 1937, toward the end of his degree programme at Oslo, on advice of an older friend, he contacted and then visited August Krogh FRS, in Copenhagen, in what proved to be a life-changing encounter. By that time Krogh held a secure place as one of the world's foremost physiologists. His Nobel Prize, in 1920, for work on capillary function might equally well have been awarded for earlier work showing that no active process helped gases pass across alveolar walls or for a variety of subsequent ground-breaking discoveries. The Zoophysiological Laboratory, which he directed, was a Mecca for physiologists, from graduate students to senior figures. Because Krogh agreed to accept Schmidt-Nielsen as a student, the 21-year-old Oslo undergraduate must have made a strong impression.

Krogh was at that point concerned with osmoregulation in aquatic animals, and he suggested that Schmidt-Nielsen look into regulation in crabs and crayfish; crabs, especially, vary widely in the range of salinities they can tolerate—a problem oddly similar to that which intrigued his grandfather. He shortly thereafter began keeping company with Krogh's youngest daughter, Bodil, and in effect became part of the Krogh household, making acquaintance with Niels Bohr ForMemRS, George de Hevesy (ForMemRS 1939) and other notable scientists who either lived in Copenhagen or spent time there. The Krogh laboratory itself must have been a stimulating place at that time, with such people as Hans Ussing (ForMemRS 1984), Erik Zeuthen and Kaj Linderström-Lang in their most productive years (Schmidt-Nielsen 1995). Copenhagen had an additional advantage for the physiologists because Bohr's physicists provided them with isotopes, initially deuterium, whose utility they immediately recognized (Krogh 1935).

However, the times were dauntingly turbulent. Schmidt-Nielsen, now married to Bodil Krogh, found himself in Norway when, in the spring of 1940, Germany occupied Denmark and Norway. He managed to get back to Denmark, where, reunited with Bodil, he spent the remainder of the war years. Conditions were difficult but the laboratory continued in operation; Denmark experienced a less harsh occupation, at least for the first few years, than other overrun countries. In the autumn of 1943, the scientific community of Copenhagen thinned out as the Jewish scientists, including those who had earlier left Germany, Austria and Hungary, fled to Sweden. Krogh himself went into hiding in 1944 when it became clear that he was about to be killed, and shortly thereafter he also found refuge in Sweden. Schmidt-Nielsen played a role in the Danish underground, helping to manufacture weapons in the machine shop of the laboratory. At the same time he worked on whale blubber, the digestion of fats, and the consequences of excessive oxalic acid in the human diet. His doctorate, awarded in 1946, concerned the absorption of fat in the intestine (2).

* Numbers in this form refer to the bibliography at the end of the text.

ACADEMIC CAREER

Shortly after the war, Schmidt-Nielsen renewed acquaintance with the other great Norwegian comparative physiologist, Per Scholander. Scholander had spent the war years in the USA, working for the military (Scholander 1990). Through Scholander he met Lawrence Irving, who offered both Knut and Bodil year-long research positions at Swarthmore College, a small but especially fine college in Swarthmore, Pennsylvania, and then arranged for them to spend an additional year at Stanford University. During this period, in collaboration with Irving and Scholander, he began investigating the physiological specializations of desert animals, work for which he probably remains best known, initially using kangaroo rats in the Arizona desert. A brief stint at the University of Oslo showed that conditions were still difficult in Europe, so Schmidt-Nielsen accepted a position at the medical school of the University of Cincinnati that had been advertised for a person with expertise in fat biochemistry. By this time Knut and Bodil had three children: Astrid, Mimi and Bent.

In 1952 Schmidt-Nielsen was appointed Professor of Physiology in the Department of Zoology at Duke University, which was to remain his academic home thereafter. At the time, Duke was best known for a diet clinic and parapsychology and was not regarded as in the top tier of American universities. Even so, Duke represented something of a cultural island in the least cosmopolitan and ethnically diverse part of the USA. Schmidt-Nielsen's elder daughter, Astrid, describes how one of her schoolteachers, announcing to the class the year's Nobel laureates, simply refused to believe that the grandfather of one of her pupils could possibly have received the prize. In addition, the appointment returned Schmidt-Nielsen to a non-medical institution, which he preferred, in a sense echoing Krogh, who had insisted that the Zoophysiological Laboratory be located in the Faculty of Science rather than the Faculty of Medicine. As a consequence, Duke's most famous physiologist did not reside in its Department of Physiology.

Shortly thereafter, he and Bodil, with the children as well as several scientific collaborators, spent a year in North Africa looking at the physiological mechanisms with which camels cope with their hot, dry, refugeless habitat. Back at Duke he returned to a related problem that had stymied him back in Norway, the way in which marine birds that eat such things as crustaceans manage a high-salt diet with access only to water of salinities beyond the capabilities of their kidneys—in effect, a marine desert. That led to investigations, some in southeast Asia, on marine reptiles and an unusual crab-eating marine frog, as well as to further work on camels, this time in central Australia. At the same time his marriage was breaking up and his personal life was deteriorating; the Schmidt-Nielsens would divorce in the 1960s, with Bodil accepting a faculty position at Case Western Reserve University, in Cleveland.

During the late 1950s and the two decades that followed, the Schmidt-Nielsen laboratory at Duke became a major centre of comparative physiology, sponsoring a large number of graduate students and distinguished postdoctoral visitors. Concomitantly, both the range of problems of concern and the facilities for addressing them increased. A new building, occupied in 1963, provided generous space; his configuration of that space had at least two notable features. He prevailed upon the designers to minimize the number of immovable furnishings, and he asked that an exterior door and one on a climate chamber be high enough to admit an adult camel. The first paid dividends; the latter was never used. At the same time, Schmidt-Nielsen, although eschewing formal administrative titles, played a major part in transforming the Zoology Department into one of the best in the country in fields well beyond his own.

Recognition, both formal and informal, gradually increased, stemming both from his scientific accomplishments and from his general articles and, especially, his books. He was elected to the National Academy of Sciences in 1963 and the Royal Society in 1985, as well as the analogous institutions of Norway, Denmark and France. Articles in *Scientific American* in 1953 (on the kangaroo rat) (4), in 1959 (one each on salt glands and camels) (7, 8), in 1971 (avian respiration) (15) and in 1981 (countercurrent systems) (18) drew still wider attention to the general significance of his work. He also wrote six books, each notably novel in approach and models of clear presentation, and including, finally, an autobiography. Honorary degrees and honours accumulated, culminating with the award, in 1992, of the International Prize for Biology (the Showa Prize) given by the Emperor of Japan.

Schmidt-Nielsen married Margareta Claesson in 1977, and the happiness of that marriage was obvious to all their friends and colleagues. The laboratory became less active during the 1980s and was terminated on his formal retirement in 1985. He remained busy, though, writing and playing what had become substantial roles in several scientific societies. He continued both to arrange the series of international conferences on comparative physiology that he and Liana Bolis initiated in 1972 and to edit the papers resulting from them. And he began a new journal, *News in Physiological Sciences* (renamed *Physiology* during 2004), dedicated to publishing general papers that would reduce the fragmentation of the field by providing accounts readable by any physiologist, a task that required—and received—tireless editorial work.

One should note that his interests and activities extended well beyond physiology. At different stages he did woodworking and pottery, both with an artistically talented eye. Graduate students and postdoctoral associates left with not only a more sophisticated outlook on science but also an equal improvement in their judgement of good wine. Each egg laid by the resident ostrich ('Pete', named after Scholander but later identified as a female) provided the impetus for a soufflé-party. A tall and imposing figure, he marched at formal university ceremonies in resplendent academic attire, thought locally to represent the University of Copenhagen but in reality his own design, realized by his animal caretaker who happened also to be a tailor.

COMPARATIVE PHYSIOLOGY

To see his scientific position in proper context, one has to explore the emergence of what has come to be called 'comparative physiology' during the twentieth century. The use of non-human animals in studies of function began much earlier, of course. William Harvey, in his famous book on circulation (Harvey 1628), exclaims, 'Had anatomists only been as conversant with the dissection of the lower animals as they are with that of the human body, the matters that have hitherto kept them in a perplexity of doubt would, in my opinion, have met them freed from every kind of difficulty.' Oddly, though, work on function—that is, physiology—had little place in traditional biology, even after Darwin's explicit recognition of the crucial role of the functional success of the organism in natural selection. Harvey was a physician, as was Claude Bernard, whose classic book on physiology bore the indicative title, *An introduction to the study of experimental medicine* (Bernard 1865). Similarly, most other major figures in the field were trained in or identified themselves with medicine rather than biology or zoology.

In the pre-Darwinian era even the anatomists, such as Aristotle and Marcello Malpighi, represented an anthropocentric tradition that transcended both time and nationality. And that tradition continued in physiology, with such major figures as Julius Mayer, Hermann von Helmholtz, Ernest Starling, J. S. Haldane, Jacques Loeb and Walter Cannon. Animal physiology produced no equivalent of Julius Sachs, the nineteenth-century father of the analogous area of botany. Nordenskiöld's magisterial *History of biology* (Nordenskiöld 1920) mentions physiology only parenthetically, and textbooks of zoology in wide use through the 1950s give it only minimal, and then human-oriented, attention.

Physicists speak of a 'Copenhagen school' of twentieth-century physics, the product and domain of Niels Bohr. One can equally well recognize a 'Copenhagen school of physiology', begun by Christian Bohr, the father of Niels, but defined as much by the work, the students and the associates of August Krogh, Bohr's student and head of the Laboratory of Zoophysiology—indeed, Krogh notes hearing casual use of the designation 'Copenhagen school' in a letter he wrote in the 1920s. Beyond specific discoveries, the laboratory had a consistently biological orientation, focusing on the general physiological problems of animals, with non-human material serving as far more than experimentally convenient surrogates for ourselves.

Bohr seems to have chosen the name 'zoophysiology' to define its approach. 'Comparative physiology' came later, perhaps because the outlook of the field bore little resemblance to comparative anatomy, a then well-established field with quite a different orientation. In the decades around the turn of the century the latter sought to reconstruct phylogenies by recognizing anatomical homologues. By contrast, in the physiology of Bohr and then Krogh, 'comparative' mainly represented a euphemism for 'biological'. The central idea consisted of studying a particular function in an animal in which the function is especially critical to survival. Its particular outlook was perhaps most clearly defined by Krogh, in a lecture for the American Physiological Society (Krogh 1929):

I have no doubt that there is quite a number of animals which are similarly 'created' for special physiological purposes, but I am afraid that most of them are unknown to the men for whom they were 'created', and we must apply to the zoologists to find them and lay our hands on them.

Because Bohr and Krogh, as well as Schmidt-Nielsen, had their roots in biology, mainly zoology, becoming this kind of physiologist took no great personal reorientation. Thus Krogh follows the statement above with a zoologist's credo: 'You will find in the lower animals mechanisms and adaptations of exquisite beauty and the most surprising character.' In retrospect, though, and even noting the word 'adaptations', the marriage of physiology and zoology remained oddly distant. Phylogenies, and indeed evolution in general, had no immediate role. One finds little evidence that the comparative physiologists looked to evolutionary convergence—shared, non-derived characters—as indicative of basic problems, constraints and mechanisms. A more literally 'comparative' physiology is only now emerging, many decades later. And despite the fact that its leading figures had early interests in natural history, the field remained quite laboratory-centred, although it seems unclear whether that was a matter of outlook or of resource limitations.

It was into the laboratory best representing this field in its full maturity, a field whose agenda had been declared but that we would regard as not yet fully explored, that Knut Schmidt-Nielsen stepped in the autumn of 1937.

BROADENING COMPARATIVE PHYSIOLOGY

Schmidt-Nielsen's early work was essentially conventional, that on fish ecology begun with his father and that under Krogh's aegis on osmoregulation in crustaceans and on the properties and absorption of fat in the intestine.

Science done in his recognizable personal style really began with the work on desert rodents, performed in the USA in the late 1940s. In particular, Krogh's science rarely if ever left the laboratory, with animals brought in and dealt with using his increasingly potent armamentarium of techniques. Field biology mainly involved describing, collecting, identifying, counting and occasionally weighing. Schmidt-Nielsen deftly combined field and laboratory measurements to show not just extreme cases of particular physiological adaptations but also the roles of such adaptations in the particular circumstances of the animals.

The rodent project began in the field, with what must have been severe problems of both access to material and adaptation of equipment for remote use. One now finds it difficult to imagine working with only a few kinds of transducer, without the option of telemetry, with mainly manometric and colorimetric read-outs, and, in particular, with virtually no electronics beyond simple voltmeters in a world without semiconductors. A miniature humidity-measuring device depended on a human hair; with a tiny temperature transducer and recorder, it was dragged into a burrow attached to the tail of a co-opted kangaroo rat. The project looked at both water balance and temperature regulation, obviously interrelated but usually the concern of different investigators. It rested on measurements, both within and outside burrows, of the conditions that animals actually encountered in nature. It continued with an evaluation of all factors involved in the match of inputs with outputs of both heat and water. And, back in the laboratory, it probed the underlying physiological mechanisms and their anatomical bases, in this case the special features of a kidney that excelled at water retention.

The results of this multi-level approach, one that drew much attention at the time, have now become common knowledge, unreferenced textbook matters. For the most part, desert rodents avoided major thermal problems by living in burrows and emerging only nocturnally. But they proved much more adept than expected at minimizing their need for water, with special devices on both input and output sides of the balance sheet. Under normal circumstances they needed neither drinking water nor even succulent vegetation. Seeds that had been stored in their burrows contained some moisture, and carbohydrate oxidation released so-called metabolic water. So dry seeds sufficed unless the seeds were unusually high in protein, forcing greater urea production and thus moist excretion. At the same time, occupying burrows with fairly high relative humidity reduced respiratory water loss. In addition, their kidneys could produce urine of such high salinity, that, if given (in the laboratory) a high-protein diet, they could slake their thirst with sea water (3).

Two episodes of fieldwork, in North Africa in 1953 and Australia in 1961, revealed a sharply contrasting set of adaptive devices in camels, the consummate large desert mammals. Although both their fur and low surface-to-volume ratio do reduce the problem, they cannot avoid the heat and respiratory dehydration of the midday sun and must have at least occasional access to drinking water. Camels, however, turned out to tolerate considerable elevation of body temperature during the day, confident in the knowledge that night and a cold sky for a radiative sink would follow. That permitted storing rather than offsetting some thermal input; moreover, the elevated temperature significantly decreased heat gain. In addition, they tolerated exceptional levels of dehydration and exceptionally great volume gains when water did become available (5).

An additional adaptive component became clear in the laboratory in the early 1960s. Per Scholander had earlier drawn attention to the ubiquity and diversity of biological countercurrent exchangers. All of these depended on intimate contact between two parallel sets of pipes, with permeable walls and with fluid in each set moving in a different direction. Schmidt-Nielsen showed that many mammals and birds used an analogous exchanger in their noses, although one with reciprocating flow in a single set of passageways. Passage walls stored heat from exhalation to warm subsequent inhalation; heat loss from inhalation cooled exhalations. In that way animals could conserve heat by exhaling air close to ambient rather than body temperature. Furthermore, because the moisture content of saturated air depends strongly on temperature, they could also reduce respiratory water loss by condensing water on exhalation and recovering it on inhalation (12).

Mammalian kidneys can produce urine with a greater salt concentration than that in their blood; desert rodents are merely extreme cases. No other vertebrate kidneys can do so, which presents an acute problem for non-mammalian marine vertebrates. Vertebrate bloods, as it happens, are less salty than sea water, so sea water cannot slake any non-mammalian vertebrate's thirst (and can slake that of only a few mammals). In effect, for vertebrates, the sea constitutes the largest desert of all. Worse, eating non-vertebrates, with internal fluids of seawater salinity, creates an additional demand for water. In the late 1950s Schmidt-Nielsen and his collaborators showed that both marine birds (figure 1) and reptiles have converted several kinds of pre-existing gland into hypertonic secretors (6, 9). The ability to drip highly saline solutions from these nasal glands permitted them to live in environments that lacked fresh water and to survive on diets of salty non-vertebrate food. Again, the work has taken its place as common knowledge with only rare reference to the seminal reports. Nor were nasal glands the only solution: Schmidt-Nielsen and his colleagues showed that the few amphibians tolerant of sea or brackish water retained urea (as sharks were known to do) to produce bloods of osmotic neutrality (11).

In about 1970, mainly in collaboration with the late C. Richard Taylor, then a postdoctoral fellow in the laboratory, work began on quite another subject, the cost of terrestrial locomotion. Rather than measuring metabolic rates on animals at rest or relying solely on cooperative humans, as had been usual, they managed to gather such data on a variety of animals moving on a variety of treadmills (14); Taylor then continued the work at Harvard. With Vance Tucker's concurrent metabolic measurements on flying birds in an adjoining laboratory and work (at Leeds University) of R. McNeill Alexander (FRS 1987) on the dynamics of legged locomotion and gait transitions, our understanding of the cost of transport advanced more in a decade than it had in the previous century. Schmidt-Nielsen and Taylor focused on how cost relative to body mass varied with body size, finding that cost dropped with increasing body size but with different rules from those for either flying or swimming. Whatever the size, legged locomotion proved more costly than either swimming, despite the work against a dense and viscous fluid in the latter, or even flying, despite the extra cost of merely staying aloft (16). Much present ecological interest in energetically optimal patterns of foraging and predation seems to trace to that work.

Nor were these the only concern of the Schmidt-Nielsen laboratory during its most active years. Less extensive but analogously eclectic investigations looked at such matters as the variation of capillary density and of gas transport parameters in the blood in mammals of different sizes, at dietarily induced diabetes in Egyptian sand rats, at cutaneous water loss in reptiles, at the influence of red blood cells on blood viscosity, at the unidirectional passage of



Figure 1. Knut Schmidt-Nielsen with a shorebird at a marine laboratory in Bar Harbor, Maine, during the 1950s.

air through avian lungs, and at the energetics of resonant panting in dogs. In addition, aspects of thermoregulation were studied in, among others, a monotreme (the echidna), ostriches, emus, rheas, bats, roadrunners, desert snails, African hunting dogs, penguins, hedgehogs and giraffes. Looking at such a variety of animals revealed both general patterns and a host of special challenges and specific adaptive devices.

BOOKS

Schmidt-Nielsen's influence on contemporary physiology rests at least as much on his books as on any investigations that he carried out or instigated. Besides serving as formal or informal editor for quite a few multi-authored volumes, he wrote six by himself, at least four of which broke new ground in content or approach.

His first, *Animal physiology*, first published in 1960 (10), was a short paperback intended to be used as one of a series from which instructors in American-style introductory courses in biology might assemble a package. In an engaging, jargon-free hundred pages, the basic

approach to physiology was transformed from the traditional human focus to one on general tasks that a successful set of physiological systems had to accomplish and how those tasks depended on an animal's place in nature. The book seems to have had a longer life than any other in the series, extending into a third edition, and it was translated into 11 languages. Perhaps more tellingly, within a few years all single-volume textbooks for introductory courses adopted some version of his approach.

With admirable clarity, *Desert animals: physiological problems of heat and water*, published in 1964 (13), summarized previous work and provided an integrated picture of adaptations to deal with problems of too much heat and too little water. Several aspects of the book strike the contemporary reader as noteworthy. Its content reflects the burgeoning interest in such problems in the decade that followed Schmidt-Nielsen's work on desert rodents and camels. At the same time it brings to bear a large amount of earlier work, largely in what would be considered natural history. And by defining the problems and exposing lacunae, it prefigures almost all subsequent work in the area; only the relationship between environmental physiology and locomotion strikes one as dated, and that more by omission than by commission.

In the 1970s Schmidt-Nielsen turned to another way in which comparative work could elucidate basic physiological mechanisms. Size and scaling had previously received some attention in his laboratory, with work on the relationship of the size of mammals to gas transport in their bloods and to the density of their capillaries. Quite a lot of data existed on size versus resting metabolic rates and on various anatomical proportions. Viewing scaling now as a specific subfield of comparative physiology, he organized a conference at Duke University in 1973, and another at Cambridge University two years later, the latter yielding a particularly valuable collection of papers (Pedley 1977). Out of this initiative also emerged his book *Scaling: why is animal size so important?*, published in 1984 (19), as well as one by his former student, the late William Calder (Calder 1984). Interest in scaling has only increased since then, coming to the attention of people working in ecology, plant physiology, and biomechanics. It must be noted, however, that problems have arisen—and later troubled Schmidt-Nielsen—from the overly confident conclusions drawn from scaling exponents by investigators with little sense of the experimental uncertainties endemic to all but anatomical data.

Perhaps Schmidt-Nielsen's most influential book will prove to be his textbook, *Animal physiology: adaptation and environment*, first published in 1975 (17) and going through four subsequent editions and translations into at least eight languages. As in its treatment in introductory courses, physiology had been, in effect, human physiology, and no clear distinction could be recognized between undergraduate textbooks for biologists and those intended for students in the various medical sciences. His textbook instigated an almost complete transformation from human to comparative physiology in these basic courses. Not only did it enjoy widespread use, but several successful alternatives taking its approach have appeared subsequently. In a sense, it provided a capstone for the amalgamation of physiology and zoology begun long ago by Bohr and Krogh.

Late in his career he wrote *The camel's nose: memoirs of a curious scientist* (20), an autobiography. It provides an engaging view of the questions posed by comparative physiologists and the ways in which they resolve them; no reader can fail to understand how the field can provide a lifetime of fascination. In the end, though, what makes it particularly noteworthy is less his analysis of his science than the extreme frankness with which he treats his personal life—the failure of his first marriage, the success of his second, his reaction to the sudden death of his daughter Mimi, and the period during which he underwent psychoanalysis.

That degree of revelation surprised friends and associates accustomed to his somewhat shy, formal and private personality. The intent seems to have been as obvious as it is important and unusual—to illustrate how even well-regarded scientists lead lives of at least normal emotional complexity.

PRINCIPAL HONOURS

- 1963 National Academy of Sciences USA, Member
- 1973 Royal Norwegian Academy of Sciences and Letters, Fellow
Royal Danish Academy, Fellow
- 1978 Académie des Sciences (France), Fellow
- 1979 Norwegian Academy of Science, Fellow
- 1985 The Royal Society, Fellow
MD (*honoris causa*), University of Lund (Sweden)
- 1992 International Prize for Biology (Showa Prize) (Japan)
- 1993 PhD (*honoris causa*), University of Trondheim (Norway)

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The frontispiece photograph was taken by Jim Wallace (© Duke Photography). Jonathan Kingdon created the sculpture in the picture; the full piece pairs a scientist, clearly Schmidt-Nielsen in mid-career, and this camel in its slightly supercilious posture, both at life size. (Online version in colour.)

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