

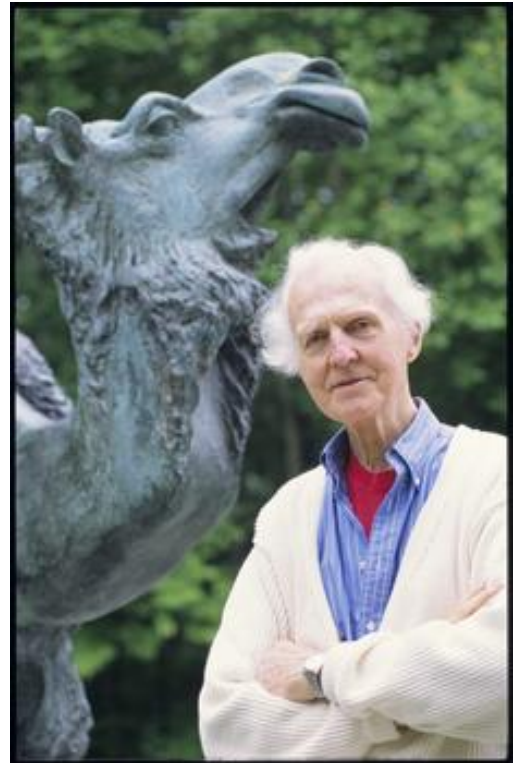


Comparative Biology Loses Another Giant: The Passing of Professor Knut Schmidt-Nielsen (1915-2007)

On January 26, 2007, the comparative physiologist Knut Schmidt-Nielsen died at his home, surrounded by family, in Durham, North Carolina at age 91. He represented indeed stood with few others as a paradigmatic figure of what we can recognize as the classic era in the development, expansion, and recognition of his field, comparative physiology. His achievements did not go unrecognized—he received numerous honorary degrees and national academy memberships and was awarded the first International Prize in Biology by the Emperor of Japan.

Comparative physiology traces its roots in large measure to a laboratory in Copenhagen, Denmark, one begun by Christian Bohr (father of the famous physicist Niels Bohr) and brought to its peak by August Krogh, Nobel Laureate. The physicists recognize a so-called Copenhagen School, centering on Niels Bohr; physiologists might well recognize a parallel-in time as well as place—a school begun by the earlier Bohr. So well accepted is its approach to the subject that one easily forgets that before it came along, "comparative" as a designation referred to work, mainly anatomical, that inferred ancestry and lineages from studies of extant organisms. Function was largely ignored; it was a nuisance that, by driving convergence, complicated analyses. Krogh took comparative work as a way to recognize the basics of function, a way to sort out the general from the accidental and epiphenomenological adaptation, and he pioneered the use of the diversity of nature in studies of function. He suggested, as well, that looking at extreme cases of physiological function and adaptation might have special value for elucidating functional principles, in revealing nature's inner secrets—but neither he nor his associates pursued the matter extensively.

That latter agenda largely remained for his successors and has continued to this day, initiated in particular by Knut Schmidt-Nielsen, his close friend and Norwegian compatriot Per Scholander. Schmidt-Nielsen received his doctorate under Bohr's sponsorship and spent the war years in occupied Denmark. He came to the United States in 1946 and spent several years at the invitation of Lawrence Irving at Swarthmore College, where he began exploring the water balance of kangaroo rats. He then moved to Stanford University and the University of Cincinnati; he joined the Zoology Department at Duke University in 1952, where he remained until well beyond his formal retirement in 1995. At the time neither that department nor the university could be considered first-rate; the subsequent success of the department and the legacy of physiology at the Duke Medical School—reflects not just his presence but his high standards and considerable efforts with respect to all of its areas and activities.



While his laboratory at Duke remained modest in both size and expenditures, its output was quite remarkable in both diversity and significance, a result, in part, of his remarkably broad curiosity about how animals work. To work done there we can trace our appreciation of the special value for understanding temperature regulation and water balance of studies on the physiology of desert animals, from camels to snails. Counter-current exchange mechanisms, first recognized by Scholander, took on additional roles and arrangements—such as the reciprocating flow exchangers widespread among nasal passages. Salt glands in marine birds and reptiles put to functional purpose the mock turtle's tears. Students studied the cost of penguin migrations in Antarctica and thermogenesis in the heads of marlin and swordfish. The way birds achieved unidirectional flow through high-efficiency lungs despite alternating inhalations and exhalations was largely elucidated there. The use of scaling exponents to deduce function was pressed forward with Schmidt-Nielsen's written and organizational urgings in the 1970s. (It must be put on record that he was not persuaded by recent explanations of the significance of the body-mass vs. metabolic rate scaling exponent of 0.75, recognizing its limitations of both input data and applicability.) He enjoyed collaborations, even ones of daunting complexity, and much of his best work took advantage of his ability not just to inspire, but to organize.

Schmidt-Nielsen's legacy remains as much as anything in the clarity with which he explained physiological principles. The increased recognition of the value of a comparative approach to physiology traces as much to his books and semi-popular articles as to the direct output of his laboratory and the subsequent work of his students. One finds it hard to imagine that he long worried about his mastery of English, but then understands his intolerance of poor writing by native speakers. He had a special talent—or, more likely, fastidiousness and tirelessness—for focusing on central issues and for direct, unambiguous prose. His first book, *Animal Physiology* (1960) was a small paperback in a series designed for first-year biology students. It sold in enormous number, probably more than any of the other titles, eventually going into a third edition and multiple translations. It represents comparative physiology as we now know it when undergraduates had easy access to nothing else of the sort. *Desert Animals* (1964), a larger work, put that area of physiology on the map. And *Scaling* (1984) does the same for another area—defining the issues and catalyzing a renaissance of work that continues today.

In 1975, Schmidt-Nielsen produced another book entitled *Animal Physiology*, this one a full-fledged textbook for an undergraduate course. Few senior figures in any field invest valuable mid-career effort in textbook writing, but he had in mind a particular mission. Now in its fifth edition, the book has effectively reset the canon for such courses and has become the standard for college courses around the globe. Previous textbooks were almost indistinguishable from books on medical or human physiology. His book and more recent textbooks by others are truly comparative in the sense that traces to Krogh, as they use diversity to illuminate principles rather than to infer ancestry or to catalog nature's range.

He leaves us as well an extraordinarily frank autobiography, *The Camel's Nose* (1998). It recounts his unusual personal history, living in three countries and experiencing the war. Besides its rich anecdotes about expeditions, people, and animals, it provides a powerful statement of the utility of studying animal function in both field and laboratory. But its greatest interest, and as he told some of us he intended, lies in how he lays bare his personal problems in order to offset any purely triumphalist view of a well-rewarded life and to show how one can compartmentalize one's life to do good science while otherwise experiencing difficulties.

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His books retain their value-any one of them, from first to last, provides an excellent entry point for a person intent on entering the field of comparative physiology. And his influence will long be felt-in particular his stress on the importance of clear articulation of what science discovers specifically and of the reality-based world view of the scientist in general.

Successful scientists fit no simple social stereotype, ranging from brash extroverts to shy introverts. Schmidt-Nielsen cannot be readily placed on such a one-dimensional scale. While certainly shy and quiet, he was at the same time outspoken and opinionated-but in ways so informed, so subtle, and so effective that his views usually prevailed. He had an eloquent style and a soft manner but a firm and well-reasoned position on issues extending far beyond his area of science. Most often he prevailed, whether editing a thesis with a student or a paper with a coauthor or whether calming a university after faculty and president at Duke did public battle over the location of the Richard Nixon library. In the department his was a consistent voice for intellectual quality, whatever the field of an applicant or the nature of some initiative. Outside the department he was a force for broad culture, liberalism, and urbanity in a part of the world that received these only late and grudgingly.

Knut Schmidt-Nielsen was a giant in the field of physiology. His high standards, compelling intellect and language, his deep appreciation of the complexity of the natural world and the process of science inspired those who worked closely with him. His influence in the field of comparative physiology has been profound, and he will be deeply missed. Still, his legacy will remain through the students, post-doctoral fellows, and collaborators who carry the tradition of his field in a rapidly changing world.

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