C. Richard Taylor

1939–1995

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
Ewald R. Weibel

NATIONAL ACADEMY OF SCIENCES

CHARLES RICHARD **TAYLOR**

September 8, 1939—September 10, 1995

Elected to the NAS, 1985

C. Richard Taylor

By Ewald R. Weibel

Charles Richard Taylor, who ultimately became the Alexander Agassiz Professor of Zoology and the first occupant of the Charles P. Lyman Chair in Environmental Physiology at Harvard University, was appointed director of the Concord Field Station of Harvard's Museum of Comparative Zoology in 1970, at the age of 31. One of the leading integrative physiologists, he strove to unravel the intricacies of how animals work by studying them as a whole—with particular emphasis on their energetics and efficiency of locomotion. In his 25 years as the field station's director, Taylor developed a unique research strategy, using the tools of comparative physiology and exploiting nature's diversity, to discover unifying principles of biological design. He was elected to the National Academy of Sciences in 1985.

Early life: fast track into science

Charles Richard Taylor, born in 1939 in Tempe, Arizona, was the third of four sons of Rosalind and Norman Taylor, a Methodist minister who had graduated from Yale Divinity School. The family moved to Culver City near Los Angeles in 1941. Richard (he favored his middle name) went to Los Angeles public schools before entering Occidental College, a small liberal arts institution. Even though he completed his undergraduate studies in record time, obtaining his B.A. in 1960, he actively participated in his biology professors' research project on the enigmatic diurnal variation of uric acid concentration in the blood of birds.

Experimenting with 123 birds of four species, making them fly at different times under controlled conditions and taking blood samples, Taylor found that the difference was related to flight activity. This study resulted in his first paper in *Nature*, with his mentor Jack W. Hudson, two weeks before his 21st birthday in 1960. In this period Taylor's characteristic strengths became evident: his enthusiasm for discovery, his tenacity in pursuing a goal, and his unbounded power in striving for success in his activities. On the basis of these characteristics, his mentors convinced him to apply to Harvard University for graduate studies in biology.

Nairobi offered Taylor very favorable conditions for developing a broad research program, one that combined well-controlled laboratory experiments with field studies in a great variety of environments, from savannas to arid deserts, and involved a wealth of species adapted to different conditions.

Entering Harvard's Department of Biology in 1960, Taylor pursued his studies with vigor, obtaining his M.A. in 1962 and his Ph.D. in 1963. One of his teachers in vertebrate biology was Charles P. Lyman, curator at the Museum of Comparative Zoology, who served as advisor for Taylor's Ph.D. thesis on "The thermoregulatory function of the horns of Bovidae." This topic arose from the observation, made by Harvard physiologist John R. Pappenheimer, that a goat's horns get hot when it is excited, suggesting they could have a thermoregulatory function.

Taylor approached the project systematically, first studying the blood supply of the horns by making corrosion casts; these experiments demonstrated an astonishingly profuse blood supply both at the surface beneath the keratinous sheath and around the horn sinus that is connected to the nasal cavities. Exercising goats on a treadmill, he measured surface temperatures, deep temperatures, and heat exchange (in relation to metabolic rate) under varying environmental conditions, concluding that the Bovid horn can indeed serve in thermoregulation, contributing 1 percent to 15 percent of total heat exchange. Finally, Taylor called on comparative studies to conclude that horns are most useful as heat exchangers in arid deserts, where the horny sheath prevents evaporation, or, conversely, in cold mountain areas, where heat exchange can occur without the need to change the insulation of the furry skin surface. In the course of these studies he extended his measurements to show that the horn can selectively control the temperature of the brain via an exchange of heat between the arterial blood of the carotid rete and the cooled venous blood returning from the horn.

In his thesis Taylor laid the groundwork for his future integrated-systems-biology research strategy, which combined morphological and experimental physiological studies with a comparative consideration of adaptation to variable life conditions. He was well prepared to embark on a career as comparative physiologist that would lead him from thermoregulation to the energetics of locomotion and finally to the study of the entire system for energy supply to the muscles (including the pathways for oxygen and substrate supply to working muscles).

First research program: how mammals control body temperature and water balance under variable environmental conditions

After completion of his graduate studies, Taylor became a research fellow in the Museum of Comparative Zoology of Harvard University (1964–1968), where he continued his collaboration with Lyman. In this position Taylor obtained his first grant from the National Science Foundation, allowing him to embark on large field studies in Africa on animals' thermoregulation. For this research he moved to Kenya, which had just become independent under President Jomo Kenyatta. Taylor found new animal physiology labs that had been built before independence for the University of Nairobi's Veterinary Faculty at Muguga. He was named attached research scientist of the East African Veterinary Research Organization and honorary lecturer in zoology at the University College.

In 1972 Taylor wrote on this undertaking: "About eight years ago I set out for Africa to try to find out if antelopes could survive in deserts without drinking; and if they could, to determine the physiological mechanisms by which they accomplish their remarkable feat."

Nairobi offered Taylor very favorable conditions for developing a broad research program, one that combined well-controlled laboratory experiments with field studies in a great variety of environments, from savannas to arid deserts, and involved a wealth of species adapted to different conditions. Primed by his thesis work, he asked how active animals regulate their body temperature where air temperature exceeds the physiological body-temperature range, particularly when water is scarce (thus limiting the main cooling strategy of evaporation). Field studies had identified species pairs—such as the eland and the oryx, two larger antelopes that survive for long periods without drinking water—that showed significant differences. The eland avoids arid deserts and uses the shade of trees to maintain its body temperature in the physiological range, whereas the oryx goes into open deserts and allows its core temperature to increase about 1–2°C above ambient temperature.

Taylor himself confirmed such differences in laboratory experiments on Grant's and Thomson's gazelles, two very similar small antelopes that herd together but differ in one important respect: Grant's gazelles are found in the arid desert zones of East Africa while Thompson's gazelles are not; and just like the oryx, a Grant's gazelle allows its body temperature to rise above ambient temperature when it rises to 45°C. But what happens when antelopes run—when they generate heat they cannot easily discharge because evaporation is limited (as the animals are dehydrated due to water shortage)? Taylor found that they store the heat and allow the core temperature to rise, up to 43°C in a Thomson's gazelle, without ill effects. This is possible because brain temperature can be kept close to normal because the carotid blood flows through the carotid rete—a set of smaller arteries that lies in the cavernous sinus, whose venous blood is cooled by the nasal mucosa (and also in the horns, as shown in Taylor's thesis). The arrangement of the vessels allows a countercurrent exchange of heat so that the blood reaching the brain is maintained at about 40°C, only about 1°C higher than at rest.

This first set of systematic studies that Taylor undertook in his four years in Kenya had all the basic characteristics of his later studies. He was asking an intriguing question about how life works under extreme conditions by testing the limits of functional performance. He took a systems approach by testing all related functions and sorting out their relative contributions—e.g., in cooling by evaporation through the skin and the lung; or through mechanisms for maintaining water balance under extreme dryness. And he sought answers to his questions by comparing two related species that were very similar but differed in one critical respect. This comparative approach proved to be particularly rewarding to Taylor in multiple research projects.

In a review in 1969, Taylor made a statement that was characteristic of his enthusiasm:

> *My competence in science, but not my interest, is limited to environmental physiology. Fortunately, this allows me to look at problems as different as the viscosity of blood, the temperature regulation of antelopes, and the metabolism of a snail. There are as many interesting problems as there are interesting animals…My problem is to find time for the things that interest me.*

But he did find the time and partners to look at problems that intrigued him—for example, the observation that in the very hot Sinai desert both the Bedouins and their goats wear black, whereas "common sense" would favor white. With Amiram Shkolnik and colleagues from Tel Aviv, Taylor approached both questions in later years. They found that the higher heat absorption of Bedouins' black robes does not affect skin temperature because the enhanced convection in the air space beneath the loose robe draws in cooler air from the bottom—a chimney effect—and in the cooler night the black robe is more comfortable. The researchers also found that black goats do absorb more heat than white goats, and thus need to drink more for cooling by evaporation, so there were other reasons why Bedouins choose black goats as their milk and meat producers. Black fur is a better protector against irradiation and absorbs more heat in the cooler winter; and black goats are easier to spot in the gleaming desert.

A similar question explored by the Taylor team concerned the survival of snails in the hot desert. It turns out that they are active only in winter and remain in a dormant state in summer, when they withdraw to the top of their shell, thus keeping temperature in the nonlethal range and reducing water loss.

Duke University (1968–1970): broadening the scope

In 1964 Knut Schmidt-Nielsen, the doyen of comparative physiology and professor of zoology at Duke University, published his seminal book *Desert Animals*, which broadly addressed the problems of heat and water in a hostile environment (Schmidt-Nielsen 1964). Before undertaking his studies in Kenya, Taylor went to see Schmidt-Nielsen to discuss the project. In his autobiography *The Camel's Nose* (1998), Schmidt-Nielsen confessed that at first he "doubted the wisdom of sending an inexperienced Ph.D. alone to Africa for a major research project." But when he visited Taylor in Muguga in 1964, a few months after Taylor had established himself there, Schmidt-Nielsen "realized that [here] was an exceptionally gifted and productive investigator. What he had learned about African mammals, [particularly] how they lived in the heat with very little or no water, exceeded all previously existing information combined."

After completing his African mission in 1968, Taylor joined Schmidt-Nielsen at Duke as a research fellow. There Taylor analyzed the vast amounts of data amassed from his various experiments in Nairobi, and he immediately joined in the exciting research program of his new mentor. The greatest influence on Taylor's further development was his involvement in studies on scaling—the effect of body size on bodily functions. His most important study at Duke dealt with the energy cost of running at different speeds. He and his colleagues studied mammals from the mouse to the dog and found that the minimum cost of moving a unit of body mass falls with size. The concept of scaling remained important in Taylor's further projects, and it was the key concept in our collaboration.

Figure 1. Concord Field Station laboratories in 1982.

Taylor's stay at Duke was short but most influential. The collaboration with Schmidt-Nielsen led to a lifelong partnership and deep personal friendship between the junior and senior biologist, who shared not only basic values of science but also a broad interest in all questions on what makes life tick. This partnership had a great impact on the development of comparative physiology, as we shall see. And, most important on a personal level, it was at Duke that Taylor met his wife Ann Boyd; they were married there in 1969. Their children Gregory and Caitlin came into their lives in 1978 and 1981, respectively.

Return to Harvard (1970–1995)

In the 1960s Harvard's Museum of Comparative Zoology was given 680 acres of natural forests and meadows in Concord, Massachusetts, to establish a field station; and the museum acquired an additional 80 acres in nearby Bedford, a half-hour's drive from Cambridge, that included an abandoned Nike missile range with several barracks that could serve as headquarters. By offering faculty and students facilities for the study of organismic and systematic as well as environmental biology, this field station would serve as a counterweight, in museum director Ernst Mayr's view, to the dominating discipline of molecular biology. In 1970 Mayr's successor Alfred W. Crompton invited Taylor back to Harvard to serve as the first director of the museum's newly established Concord Field Station and as an associate professor of biology; Taylor accepted within one week and was officially appointed in August 1970.

While still at Duke, Taylor planned and directed the transformation of the old military barracks into laboratories, offices, and animal holding facilities. Implementation had begun when he arrived in September, but it took several years and an enormous personal commitment to create a unique institution with a very modest budget (Figure 1). Taylor's vision was that the Concord Field Station should become a center for environmental and comparative physiology and be open to all members of the biological community at Harvard who needed fieldwork facilities. Meanwhile, Taylor engaged actively in the biology department's teaching duties, in time making the Concord Field Station a favorite site for students' work.

Energy economy in animal locomotion

Taylor's first projects at the Concord Field Station concerned how animals move, how much energy their different modes of locomotion demand, and how they can economize on the associated energy cost. Making use of his new facilities, ideal for holding animals of all sorts and nearly all sizes in large outdoor paddocks, he approached these issues through comparative experimental physiology, first making use of what he called "experiments of nature"—the great diversity of animals, large and small, fast and slow, mammal and bird. To test the mechanics and energetics of locomotion he would run the animals over force platforms; and to measure their oxygen consumption he ran them on a treadmill (Figure 2). Sometimes he combined these experiments with small interventions, such as loading a backpack on a dog, to "perturb the system." Continuing his studies at Duke on the scaling effects of body size on locomotor function, Taylor collaborated with Harvard engineer Thomas McMahon in seeking a mechanistic explanation as to why the speed at which animals change from trot to gallop depends on body size.

Figure 2. C. Richard Taylor running a goat on a treadmill for oxygen-consumption measurements at Concord Field Station in 1981.

An early question regarded the effect of locomotion pattern on oxygen cost. Among such patterns, that of the kangaroo is of particular interest because it is so complex. With Terry Dawson, Taylor showed that at low speeds (up to 6 km/h) kangaroos walk on "five legs," the heavy tail being the fifth, and that as the stride frequency increases their oxygen consumption increases linearly. At about 7 km/h they change to hopping on their hind legs; higher speeds are achieved by increasing stride length rather than frequency, and as the kangaroos hop faster the oxygen consumption remains nearly the same. The conclusion was that hopping is an efficient way to recover elastic energy stored from one jump to the next.

In a very systematic, complex, and profound study on bipeds, quadrupeds, and hoppers running on force platforms, Taylor explored, together with Giovanni Cavagna from Milano University and Taylor's graduate student Norman Heglund, the mechanisms for minimizing energy expenditure in vertebrates moving on the ground. The conclusion was that "the different modes of locomotion—bipedal or quadrupedal walking, trotting, galloping, and hopping—can all be reduced to two general mechanisms, a pendulum and a spring, to minimize the expenditure of chemical energy by the muscles for lifting and accelerating the center of mass within each stride." The pendulum is used in walking and the spring in trotting or galloping to recover, and thus save, energy.

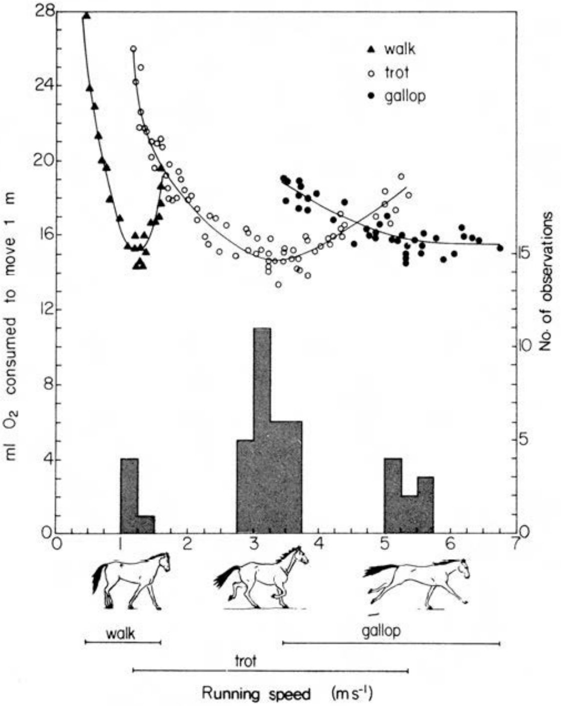

Figure 3. The oxygen cost of moving 1 m declines to a minimum when horses walk, trot, or gallop at increasing speeds. The histogram shows that horses choose their gait to correspond to the minimal cost of running.
(From Hoyt and Taylor, 1981) .

Another question was why horses change gait. Horses shift from walk to trot at about 2 km/h and from trot to gallop at about 4 km/h. By so doing they minimize energy expenditure because, in each mode, the energy needed to move one meter is curvilinear, with a minimum slightly below the transition speeds (Figure 3). As a result, Taylor and colleagues observed, "the natural gait at any speed indeed entails the smallest possible energy expenditure."

Taylor's African experience led to another question: How can African women carry large loads on their head with no increase, or only a small increase, in energy expenditure, whereas loads added to running animals increases the cost of running proportionately. This is where the inverted pendulum comes into play: as we step forward the center of mass is lifted, and as we fall forward the potential energy just gained is about 65 percent recovered. Heglund showed that African women are able to increase this pendular energy transfer so that they can carry a load of 20 percent of their body weight without increasing their energy expenditure. This mechanism also reduces the additional energy needed to carry larger loads, which can be up to 70 percent of the women's body weight.

In all these studies on the energy efficiency of locomotion, Taylor played with extraordinary virtuosity on the "experiments of nature," running even cheetahs and lions on his treadmill to compare their efficiency with that of their prey, such as antelopes. In his last experiment he went for the biggest by running with his colleagues alongside an elephant to measure its oxygen consumption, finding that the biggest terrestrial mammals move very cheaply, at about half the cost of human walking.

Symmorphosis: expanding energetics from consumer to supplier

In 1975 Taylor broadened his perspective and began to explore the organismic support system for the energy needed by working muscles. This is where my collaboration with Taylor began. That year I was on sabbatical (from the University of Bern) at Yale University, working on a cell biology project. I also spent a good deal of time at the Yale Medical School's superb library, looking for a solution to a paradoxical problem that had come up in my studies on the quantitative structural basis of gas exchange in the lung (Weibel 1973): In animals of different body size, from the 2-gram shrew to the 20-kilogram dog, the gas-exchange surface increases much more steeply than does oxygen consumption, whereas the surface is proportional to oxygen consumption in animals of different activity levels but of similar size. At the Yale library I came upon a new acquisition, *Comparative Physiology* (Bolis, Schmidt-Nielsen, and Maddrell 1973), in which the first article, by C. R. Taylor, was on "Energy cost of animal locomotion." Taylor reported that the ratio of maximal to resting oxygen consumption showed a bell-shaped curve with body size. When I plotted his data into my graphs, they seemed to fit the estimates of pulmonary gas-exchange surface. This suggested that by measuring average or standard oxygen consumption I had used the wrong reference parameter; I needed maximal oxygen consumption.

I called Taylor at Harvard and we met, for the first time, at the Harvard Faculty Club for lunch on May 5, 1975. Before we reached dessert, Taylor had proposed and sketched out a collaborative study based on an expedition to Kenya in which we could study an array of free-living mammals of all sizes. He would study their locomotion and energetics in the field, as well as in his former laboratory at Muguga; and I would collect samples of lungs and muscles for morphometric study in Bern. By joining forces we would thus examine the design and function of the entire pathway for oxygen, from the lung to the muscles, studying how the different parts of this system vary with body size in a natural population of mammals. This memorable lunch had shown Taylor at his best: a scientist with a broad vision and deep insight, with quick understanding of an issue and impressive imagination; and a man of incredible determination. For me it was clear I had met my partner in my own plans to quantitatively study the structural basis of respiratory function at all levels of an organism.

The deal was made, on the spot, by handshake. We both then convinced our respective funding agencies, in the United States and Switzerland, of the potential of this collaboration. We were even granted additional funds to expand our goals. By August 1976, full support was achieved.


Figure 4. C. Richard Taylor with Peter Gehr and Knut Schmidt-Nielsen during a field study in Masai Mara, Kenya, 1977.

The expedition to Africa took place in the spring of 1977. Its aim was to combine field studies on the locomotion of large mammals in Kenya's large wildlife parks (Figure 4) with laboratory experiments on energetics. Through his previous contacts in Kenya, Taylor had arranged for work facilities at the University of Nairobi's Muguga campus. Geoffrey M. O. Maloiy, professor of physiology and dean of veterinary medicine, offered laboratories for the physiological studies and also became an active collaborator. My group received support and laboratory space in the Department of Veterinary Anatomy chaired by Wangari Maathai, the 2004 Peace Nobelist. Taylor and his team of young physiologists stayed in Kenya for seven months; I could stay only for a few weeks but my experienced collaborator Peter Gehr did all of the anatomical work together with a small team. In both parts of the study, young African colleagues and technicians participated actively.

In this kind of study the work conditions are not always easy and many obstacles appear, often inadvertently. It was impressive to see how Taylor kept things on track; he would convince the authorities of the importance of this project by determination, diplomacy, and charm. That made it possible to obtain an array of animals caught in the wild—27 of them from 12 species, ranging in body mass from 500 g (the mongoose) to 250 kg (the eland antelope)— to bring them into the laboratory, and finally to sacrifice them for tissue sampling. But it was at least as impressive to see how Taylor could coerce wild animals the size of a wildebeest to wear a face mask and run for him on a treadmill up to their maximal running speeds!

The expedition resulted in a large mass of physiological data collected in the field and in the laboratory, and in a large volume of fixed tissue samples of lung and muscles on all animals studied physiologically. The material to be subjected to morphometric analysis was therefore tightly linked with the physiological data. These data were analyzed at Taylor's Concord Field Station of Harvard University, and the electron-microscopic and morphometric study was done at the University of Bern, with Peter Gehr directing the lung study and Hans Hoppeler the work on muscle.

When the Harvard and Bern groups came together for one week in 1980 to review the results of the different segments of the project, it was clear that in order to overcome the limitations of the reductionistic approaches of the individual studies, an attempt at systemic integration had to be made. In the structure-function model to serve this integration, a set of equations defined the physiological and morphometric parameters that determine the maximal flow of oxygen at each level: the lung, the circulation of blood, the muscle microvasculature, and the muscle cells with their mitochondria. In this way the variation of each functional or structural parameter could be related to the estimated functional limit—maximal oxygen consumption. Out of this transatlantic collaboration a set of nine papers with 19 authors resulted; they were published as a series in the journal *Respiration Physiology* under the title "Design of the Mammalian Respiratory System" (1981).

Taylor then suggested that we use a similar approach in comparing pairs of animals of similar body size whose maximal oxygen consumptions differ by at least 2.5-fold, implying that one is athletic and the other more sedentary—e.g., the species-pairs dog and goat, pony and calf, and horse and cow. The basic question was: Do they build the structures supporting the pathway of oxygen in proportion to the maximal aerobic energy demand? Two-dozen authors were involved in this study, which resulted in a total of 14 original papers, again published (in part) as a compact series in *Respiration Physiology* under the title "Adaptive variation in the mammalian respiratory system in relation to energetic demand" (1987).

The two studies asked how the structure-function relations in the pathway for oxygen are affected by two very different types of variation in maximal rates of oxygen consumption: allometric versus adaptive, or body size versus locomotor capacity. Could we draw some general conclusions? In our first joint paper on the design of the respiratory system, Taylor as first author had entered this sentence: "In undertaking this task we were motivated by the firm belief that animals are built reasonably." From this we then derived the principle of "symmorphosis," which postulates that the quantity of structure an animal builds into a functional system is matched to what is needed: "enough but not too much." The arguments for this hypothesis derived chiefly from Taylor's studies on the energetics of locomotion, in which he had shown that a load added to a working animal caused a proportional increase in energetic cost. Thus a useless amount of lung, heart, or mitochondria would add energy cost. Such an economic design must be the result of evolution, and comparative studies such as ours could therefore serve as test of the hypothesis.

The synthesis of these studies (1991) showed that both in allometric and adaptive variation, internal components of the system vary in proportion to maximal oxygen consumption, though not in a simple fashion: the amount of muscle mitochondria is directly proportional, but for capillaries and the heart it is the product of volume and the erythrocyte content of the blood (the determinant of oxygen capacity) that matches maximal oxygen consumption. At these three levels of the system the hypothesis of symmorphosis is supported. The situation is different for the lung, the interface between the body and the environmental air. The morphometric parameters that determine the lung's diffusing capacity for oxygen relate in a more complex manner to the variation in maximal oxygen uptake: they are larger in athletic species, but not proportional to the larger maximal oxygen uptake. We suspected that sedentary species have some excess diffusing capacity, and this was proven experimentally by Taylor and his collaborator Richard Karas: goats running at their maximal oxygen consumption level continue to run happily if the oxygen content of the inspired air is lowered, but dogs immediately stop running under this condition.

In allometric variation, the alveolar surface increases more steeply than does maximal oxygen consumption, so that large species need more surface area for absorbing the same amount of oxygen from air; this is related to the size of the peripheral airways, which reduces the oxygen pressure at the alveolar surface in large mammals (Sapoval, Filoche, and Weibel 2002). Thus the quantitative adaptation of structural components is not only gauged to the bodily demands but also to environmental boundary conditions. Ironically, this outcome of the study meant that the apparent paradox that had led to my collaboration with Taylor in 1975 was corroborated rather than eliminated; but it was solved by finding an explanation for the different requirements on the lung as interface organ.

Taylor suggested that the model be extended, as the pathway for oxygen was in fact too simple a test case for symmorphosis. Mitochondria also need to be supplied with fuel, carbohydrates, and fatty acids, at quite high rates; so it seemed possible that the design of structures such as the muscle capillaries was not related to oxygen delivery but rather to the supply of substrates for oxidation. Whereas the pathway for oxygen is, in principle, composed of a linear chain of transfer steps, the combined pathways for oxygen and substrates must be described by a network model with parallel limbs converging at the mitochondria. Oxygen and fuels differ, inasmuch as the latter can be stored whereas the former cannot. Oxygen must be supplied directly from lung to mitochondria when needed, while fuels can be supplied in two steps: from the capillaries to the cytoplasm, and from the cytoplasmic stores to the mitochondria.

To complement the Harvard and Bern teams, Taylor called on biochemists with expertise in carbohydrate and lipid metabolism, primarily Jean-Michel Weber of Ottawa University. In accordance with the study of adaptive variation to energy demand, the strategy was to compare dogs with goats running on a treadmill. The key result was this: structures related to both pathways for oxygen and fuels, mainly the muscle capillaries, are designed to satisfy oxygen supply up to the limit, but they are insufficient to supply fuels from the blood at the high rates required in exercise. Because fuels are stored in the muscle-cell cytoplasm, the capillary supplies of carbohydrates and lipids can occur at a slower rate but over a prolonged period of time; these supplies replenish the intracellular stores mostly in periods of rest. Substrates are drawn by mitochondria directly from the intracellular stores of glycogen and lipids; the dog’s needs for higher rates of substrate supply during running are satisfied by maintaining larger cytoplasmic stores of glycogen and lipid than are found in goats.

These latter studies were begun in 1992, and a set of nine manuscripts were completed in July 1995, while Taylor was spending a few days in Switzerland; they were submitted for publication in the *Journal of Experimental Biology* exactly one month before Taylor's death from a heart attack on September 10, shortly after his return to Concord from vacation with his family. Thus he did not see the publication, in 1996, of his last major oeuvre, which was further testimony to his extraordinary achievements as a leader in science (Weibel 2000).


Figure 5. C. Richard Taylor looking at the mountains above Ascona, Switzerland, with friends, during his last encounter with the author, in July 1995, at a symposium on symmorphosis.

The promoter of comparative physiology

I last saw my partner and friend C. Richard Taylor in July 1995—just 20 years after our first and all-important encounter (Figure 5). Together we had organized on Monte Verità in Ascona, Switzerland, a conference on comparative physiology—called "Optimization and Symmorphosis"—aimed at broadening our perspective beyond mammals and beyond the locomotor and energy-supply systems. The conference's proceedings were titled *Principles of Animal Design* (Weibel, Taylor, and Bolis 1998). This was one of the last of the biannual conferences—organized by the Interunion Commission for Comparative Physiology (ICCP) of the International Union of Physiological Sciences (IUPS) and the International Union of Pure and Applied Biophysics (IUPAB)—that had been initiated by Knut Schmidt-Nielsen, Richard Keynes, and Liana Bolis in 1971. The first conference was held in 1972 in Aquasparta, Italy, and the first paper in the proceedings (Bolis, Schmidt-Nielsen, and Maddrell 1973) was the very paper by Taylor that had caused me to contact him in 1975.

The commission's first chair was Schmidt-Nielsen. Taylor was a member and in 1982 became the chair until 1992, when the IUPS decided that the same people had been on this commission for too long and created a new roster with Malcolm Gordon as chair. Taylor's performance during his 10 years as chair was impressive, however. The conferences dealt with topics such as primitive mammals, sensory systems, design and performance of muscular systems, life in water and on land, differences of the sexes, and optimization and symmorphosis. The focus was generally very broad, aimed at fostering the integration of knowledge gained in various research approaches and thus helping to bridge the gap between reductionism and systems biology. Under Schmidt-Nielsen's and Taylor's leadership the International Comparative Physiology Conferences served this goal with repeated success. By organizing symposia at these physiology congresses, Taylor further promoted comparative physiology as an important approach for exploring integrated physiological systems.

C. Richard Taylor's legacy

Through his research and teaching, Taylor convincingly demonstrated the productivity of comparative physiology as an approach for clarifying the fundamental principles that govern organismic functions. He excelled in exploiting what he liked to call, following Aygust Krogh, "experiments of nature," making best use of the enormous diversity of animals in finding out what makes them different and successful. His work shows that this approach is particularly fruitful in connecting related results obtained by reductionistic research, be it morphological, biochemical, or physiological, into an integrated view of systems physiology or organismic biology.

The many researchers from all parts of the world that Taylor brought together in his large interdisciplinary projects experienced the rewards of generous and trustful collaboration across all boundaries. To his many undergraduate and graduate students, Taylor became a role model. He inspired their enthusiasm for looking into life processes deeply and broadly, with imagination, engaging energy, and persistence, and he showed them that science could be exciting—and fun.

REFERENCES

Bolis, L., K. Schmidt-Nielsen, and S. H. P. Maddrell (eds.). 1973. *Comparative physiology*. Amsterdam and London: North-Holland Publishing Company.

Hoyt, D. F., and C. R. Taylor. 1981. Gait and the energetics of locomotion in horses. *Nature* 292:239–240.

Sapoval, B., M. Filoche, and E. R. Weibel, 2002. Smaller is better—but not too small: A physical scale for the design of the mammalian pulmonary acinus. *Proc. Natl. Acad. Sci. U. S. A.* 99:10411–10416.

Schmidt-Nielsen, K. 1964. *Desert animals: Physiological problems of heat and water.* Oxford, UK: Oxford University Press.

Schmidt-Nielsen, K. 1998. *The camel's nose: Memoirs of a curious scientist.* Washington, DC: Island Press.

Weibel E. R., 1973. Morphological basis of alveolar-capillary gas exchange. *Physiol. Rev.* 53:419–495.

Weibel E. R., C. R. Taylor, and L. Bolis. 1998. *Principles of animal design: The optimization and symmorphosis debate.* New York: Cambridge University Press.

Weibel E. R., 2000. *Symmorphosis: On form and function in shaping life.* Cambridge, MA: Harvard University Press.

SELECTED BIBLIOGRAPHY

1960 With J. W. Hudson. Variability levels of blood uric acid in five species of birds. *Nature* 187:788–789.

1963 The thermoregulatory function of the horns of the family *bovidae*. Ph.D. thesis, Harvard University, Cambridge, MA.

1966 The vascularity and possible thermoregulatory function of the horns in goats. *Physiol. Zool.* 39:127–139.

1969 The eland and the oryx. *Sci. Am.* 220:88–95.

1970 With K. Schmidt-Nielsen and J. L. Raab. Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219:1104–1107.

1971 With K. Schmidt-Nielsen and A. Shkolnik. Desert snails: Problems of heat, water, and food. *J. Exp. Biol.* 55:385–398.

1972 With S. L. Caldwell and V. J. Rowntree. Running up and down hills: Some consequences of size. *Science* 178:1096–1097.

1973 With T. J. Dawson. Energetic cost of locomotion in kangaroos. *Nature* 246:313–314.

1974 With N. C. Heglund and T. A. McMahon. Scaling stride frequency and gait to animal size: Mice to horses. *Science* 186:1112–1113.

1976 With P. S. Chassin, N. C. Heglund, and H. J. Seeherman. Locomotion in lions: Energetic cost and maximum aerobic capacity. *Physiol. Zool.* 49(1):1–10.

1977 With G. A. Cavagna and N. C. Heglund. Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233(5):R243–R261.

1980 With V. A. Finch, R. Dmi'el, R. Boxman, and A. Shkolnik. Why black goats in hot deserts? Effects of coat color on heat exchanges of wild and domestic goats. *Physiol. Zool.* 53:19–25.

With A. Shkolnik, V. Finch, and A. Borut. Why do Bedouins wear black robes in hot deserts? *Nature* 283:373–375.

1981 With D. F. Hoyt. Gait and the energetics of locomotion in horses. *Nature* 292:239–240.

With E. R. Weibel, P. Gehr, H. J. Seeherman, G. M. O. Maloiy, H. Hoppeler, N. C. Heglund, O. Mathieu, D. K. Mwangi, V. A. Langman, J. M. Z. Kamau, A. Ammann, R. Krauer, S. L. Lindstedt, R. McN. Alexander, R. B. Armstrong, L. M. Cruz-Orive, A. E. Müller, H. Claassen, and V. Haussener. Design of the mammalian respiratory system: I. Problem and strategy; II. Measuring maximum aerobic capacity; III. Scaling maximum aerobic capacity to body mass: Wild and domestic mammals; IV. Morphometric estimation of pulmonary diffusing capacity: Critical evaluation of a new sampling method; V. Scaling morphometric pulmonary diffusing capacity to body mass: Wild and domestic mammals; VI. Distribution of mitochondria and capillaries in various muscles; VII. Scaling mitochondrial volume in skeletal muscle to body mass; VIII. Capillaries in skeletal muscles; and IX. Functional and structural limits for oxygen flow. *Respir. Physiol.* 44:1–164.

1982 With N. C. Heglund, M. A. Fedak, G. A. Cavagna, and G. M. O. Maloiy. Energetics and mechanics of terrestrial locomotion: I. Metabolic energy consumption as a function of speed and body size in birds and mammals; II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals; III. Energy changes of the center of mass as a function of speed and body size in birds and mammals; and IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97:1–66.

1984 With H. Hoppeler, S. L. Lindstedt, H. Claassen, O. Mathieu, and E. R. Weibel. Scaling mitochondrial volume in heart to body mass. *Respir. Physiol.* 55:131–137.

1985 Force development during sustained locomotion: A determinant of gait, speed, and metabolic power. *J. Exp. Biol.* 115:253–262.

1986 With G. M. O. Maloiy, N. C. Heglund, L. M. Prager, and G. A. Cavagna. Energetic cost of carrying loads: Have African women discovered an economic way? *Nature* 319:668–669.

1987 With R. H. Karas, E. R. Weibel, H. Hoppeler, J. H. Jones, P. Gehr, R. B. Reeves, K. E. Conley, S. R. Kayar, K. Rösler, H. Claassen, E. Uhlmann, L. B. Marques, M. Constantinopol, and F. Doffey. Adaptive variation in the mammalian respiratory system in relation to energetic demand: I. Introduction to problem and strategy; II. Reaching the limits to oxygen flow; III. Skeletal muscle: Setting the demand for oxygen; IV. Capillaries and their relationship to oxidative capacity; V. Limits to oxygen transport by the circulation; VI. The pulmonary gas exchanger; VII. Flow of oxygen across the pulmonary gas exchanger; and VIII. Structural and functional design principles determining the limits to oxidative metabolism. *Respir. Physiol.* 69:1–127.

1989 With J. H. Jones, K. E. Longworth, A. Lindholm, K. E. Conley, R. H. Karas, and S. R. Kayar. Oxygen transport during exercise in large mammals: I. Adaptive variation in oxygen demand. *J. Appl. Physiol.* 67(2):862–870.

1990 With R. Kram. Energetics of running: A new perspective. *Nature* 346:265–267.

1991 With E. R. Weibel and H. Hoppeler. The concept of symmorphosis: A testable hypothesis of structure-function relationship. *Proc. Natl. Acad. Sci. U.S.A.* 88:10357–10361.

1995 With V. A. Langman, T. J. Roberts, J. Black, G. M. O. Maloiy, N. C. Heglund, J.-M. Weber, and R. Kram. Moving cheaply: Energetics of walking in the African elephant. *J. Exp. Biol.* 198(3):629–632.

1996 With J.-M. Weber, E. R. Weibel, T. J. Roberts, H. Hoppeler, G. Brichon, G. Zwingelstein, G. McClelland, C. Saucedo, G. Ordway, R. Vock, H. Claassen, D. X. Y. Wu, and R. Billeter. Design of the oxygen and substrate pathways: I. Model and strategy to test symmorphosis in a network structure; II. Defining the upper limits of carbohydrate and fat oxidation; III. Partitioning energy provision from carbohydrates; IV. Partitioning energy provision from fatty acids; V. Structural basis of vascular substrate supply to muscle cells; VI. Structural basis of intracellular substrate supply to mitochondria in muscle cells; and VII. Different structural limits for oxygen and substrate supply to muscle mitochondria. *J. Exp. Biol.* 199:1643–1709.
