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OBITUARY

Donald C. Jackson (1937–2020)

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Sic transit Gloria mundi

Brown University Emeritus Professor Donald Cargill Jackson died quietly on 7 January 2020 at a hospice in Providence, Rhode Island, USA, surrounded by his immediate family. He was 82 years old, and had been hospitalized for a few weeks due to heparin-induced thrombocytopenia following a minor heart surgery.

His numerous successful academic offspring, his seminal papers, and his service to the field, to the community and to his family have proven him to be a man of wisdom, grace and integrity. Now, the world is somewhat less than it was just a short while ago.

A genuine scholar and a gentleman

With Don's passing, we have lost an icon and leading figure in comparative cardiorespiratory physiology. For almost 60 years, his sharp, inquisitive mind provided novel insight into the regulation of ventilation and blood gases and he pioneered our understanding of anoxia tolerance in animals. The vast majority of his studies were performed on turtles, but his findings were always placed in a broader context and provided general insight into 'how animals function'.

In addition to Don's considerable scientific productivity, he was an attentive and supportive supervisor, a devoted teacher, and he contributed to academia at large by serving as editor for the *American Journal of Physiology* (1990–1995), on countless committees and on the editorial boards of many important journals in our field. He was funded by the National Science Foundation throughout his entire career and repaid that support by serving as an NSF Program Officer from 1991 to 1992.

A Socratic supervisor and a devoted teacher

Don was a passionate teacher, but calm, clear and challenging in his approaches, both in the classroom and in the laboratory. He favored the Socratic method, reinforcing the fact that every new idea or discovery only leads to more questions and the chance to be creative. When asked why he taught more than was required, he replied that in his position and career, he had great privilege and that gift should be recognized and paid forward. He always had undergraduate and graduate students, as well as postdocs in his lab, and was endlessly patient with them all. Lunch in the boss's office was a tradition that fostered conversation and debate, to the benefit of all. Many of the graduate students from other labs dreaded when Don's hand went up during their seminar or defense, not because Don was aggressive or demeaning, but because his calm and placid manner hid a razor-sharp mind that frequently caught errors in logic. His advising was not limited to the classroom and laboratory, and he offered his wisdom to his students long after they left Brown.

Doctoral studies on temperature regulation at the University of Pennsylvania

Don completed a BS in Biology from Geneva College in Pennsylvania in 1959 and enrolled thereafter in the physiology graduate program of the University of Pennsylvania on a National Institutes of Health pre-doctoral fellowship. At Penn, he came under the erudite supervision of Professor Ted Hammel and embarked on understanding temperature regulation in awake dogs in 1961. During this period, feedback regulation was enthusiastically being studied in physiological processes, with much of this conceptual transition originating from James D. Hardy, Hammel's supervisor a decade earlier. Hammel relocated to the John B. Pierce Laboratory in New Haven to join Hardy in the summer of 1961, bringing Don with him, where they implanted multiple thermodes to selectively warm and cool the hypothalamus in resting, sleeping and exercising dogs. The studies decisively demonstrated the pivotal role of hypothalamic temperatures in thermoregulation and documented a lowering of the hypothalamic set-point during sleep. During this period, Don also had the unique opportunity to study temperature regulation in Kalahari Bushmen in South Africa with Ted Hammel and Harold T. Andersen, and there still exist copies of a very entertaining movie with a mixture of safari footage and

'Gray hair is a crown of glory, which is won by a virtuous life' (Proverbs 16:31). Donald C. Jackson (1937–2020) analyzing lactate concentration in the shell of anoxic (and edible) Burgundy snail (*Helix pomatia*) during a research visit to Aarhus University in the summer of 2004. Photo credit: Tobias Wang.

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physiological measurements of body and surface temperatures, as well as metabolism.

Postdoctoral research at Duke University and getting hooked on turtles

As a newly minted PhD, Don was given the opportunity for a postdoctoral fellowship with Professor Knut Schmidt Nielsen at Duke University, commencing in the early fall of 1963. His first task was to study counter-current heat exchange in the nasal passages of kangaroo rats, and he was then encouraged to investigate whether toadfish behaved as oxyconformers, i.e. progressively reducing the rate of oxygen consumption in hypoxia. To account for anaerobic metabolism, Don attempted an experimental design combining direct calorimetry to measure heat formation with respirometry to measure oxygen consumption. Much to his vexation, it was impossible to perform the simultaneous measurements and he was left having to search for a problem that could be solved with the calorimeter. Fortunately, he suddenly recalled having read a recent paper by Eugene Robin reporting on extraordinary anoxia tolerance in turtles, and Don soon demonstrated that turtles dramatically reduce heat production within hours of being exposed to anoxia, which must mean that energy-consuming processes are reduced and that the turtles enter a hypometabolic state. Don was now hooked on understanding the physiology of turtles and the field of metabolic depression was born.

At a social event in Schmidt Nielsen's house, Don lost his heart to his future wife, Diana. It was love at first sight for Don; they married within 3 months and shortly after had a little family with their two sons, Tobey and Thomas. Diana became Don's life-long companion, and her artistic and spontaneous nature undoubtedly provided a stimulating balance to Don's more analytical approach to life. Together, the whole was more than the sum of the individual parts, and their companionship was a true inspiration to everyone who has ever spent time with them.

Back to Penn to study lung function and respiratory physiology of turtles

In the late summer 1965, Don (with Diana) returned to the University of Pennsylvania, where he devoted his research efforts to study lung function, blood gases and control of ventilation in turtles. As seminal findings, he demonstrated that turtles regulate neutral buoyancy by balancing lung gas volume and the amount of water in the bladder and the cloacal bursae. He also provided the first detailed description that the ventilatory responses to hypoxia and hypercapnia become more vigorous as body temperature increases, and contributed new data to awaken our understanding of the characteristic reduction in blood pH that occurs when body temperature rises. The latter pertains to the then-emerging alphastat hypothesis, a question that remained dear to Don's heart, and for which he coined the term 'Buffalo curve' in a review celebrating Schmidt-Nielsen's 65th birthday.

Climbing Ivy League academic ranks at Brown University

Don was appointed as Associate Professor of Medical Science at Brown University (Providence, Rhode Island) in 1973 and promoted to full professor in 1980. There, he continued to study turtle physiology, now including gas exchange across the skin, but the initial studies at Brown also provided very convincing demonstrations of a diffusive limitation for cutaneous gas exchange in amphibians. The relative roles of diffusion versus perfusion for cutaneous gas exchange was a much-debated issue in that period, but based on his quantitative analyses and precise measurements, it was difficult to argue with Don's conclusions.

His research broadened as more students were recruited and Don's laboratory provided the first demonstration of central chemoreception in reptiles, the fascinating finding that lungless salamanders also follow the Buffalo curve, reducing arterial pH with temperature. Microspheres were used to study blood flow distribution, and through the 1980s there was a progressive move into cardiovascular questions, including an early use of nuclear magnetic resonance to determine intracellular pH regulation and energy status of the heart during anoxia. With Peter Stewart as a colleague a few offices down the corridor, Don was also amongst the first to apply the concept of strong ion difference (SID) comparative acid–base physiology.

Extremely high lactate levels in hibernating turtles and the pivotal role of buffering by the shell

With Gordon Ultsch, Don also revisited the question of oxygen conformity in the toadfish, which began their long-lasting collaboration. Don and Gordon would go on to perform many detailed studies on the influence of anoxia on blood gases, plasma ions and metabolites in turtles. Don performed additional studies as part of a sabbatical at the Max-Planck Institute in Gottingen with Professor Norbert Heisler, and it became clear that anoxic turtles achieve astoundingly high lactate levels of more than 100 mol l^{-1}. Cardiovascular studies and acid–base regulation continued to be a major focus in the 1990s, with extensive comparisons amongst various species, where the inclusion of soft-shell turtles was particularly informative. These turtles did not fare well in anoxia, and pH plummeted much sooner than in hard-shelled turtles, further stimulating the idea that the shell actually partakes as an important buffer to alleviate the acidosis that ensues from the massive lactate levels.

To analyze the role of mineralized tissues of the carapace as buffers, Don utilized his quantitative skills and firm grounding in basic natural sciences to definitively demonstrate that the turtle's shell is absolutely essential for buffering lactic acid. In keeping with his comparative approaches, he examined these processes in other species of reptiles and amphibians, demonstrating this to be a generalized property of vertebrate bone, and even applicable to the carapace of crustaceans and snails.

Emeritus, (sort of) retirement and retrospect

Don retired from Brown University in 2007 and was celebrated with a 1-day symposium with talks from previous students and close colleagues. There was a large dinner, including friends and family, with many speakers expressing sincere gratitude and deep respect. Don did not, however, really retire. As an emeritus, he maintained a small office, and he continued – including in the fall of 2019 – to teach a course in comparative physiology based on his book entitled *Life in Shell* from 2011. He also taught at the University of New Orleans, near where he and Diana had bought a terribly charming apartment in the French quarter, providing a suitable hibernaculum far from the sinister New England winters. *Life in a Shell* is a highly recommendable, semi-autobiographical book based on the unique physiological problems imposed by being enclosed in a rigid shell, and the environmental stressors that turtles encounter. The book conveys the integrative nature of Don's research philosophy and the logical progression of his research; an inspirational guideline for any person interested in academia. The book also provides a fascinating example of being driven by genuine curiosity as well as the importance of serendipity: 'I did not grow up dreaming of becoming a turtle biologist… like a snowball rolling down a hill, my fascination with turtles grew, and soon I was hooked'. 'Looking back, I realize I could easily have chosen a different animal, but I chose the turtle'.