

OBITUARY

Steven Franklin Perry (1944–2022)

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Steven Franklin Perry, or Steve to most of us, was born on 14 March 1944, in Brockton, MA, USA. He attended Middlebury College in Vermont, completing his BA (Biology) in 1966 with honours courses in agronomy and radiation biology at Cornell University, USA, and the University of Rochester, USA, respectively, before going on to undertake his PhD at Boston University, USA. Steve graduated in 1972 by dissertation titled ‘The lungs of the red-eared turtle, *Chrysemys (Pseudemys) scripta elegans*, as a gas exchange organ: a histological and quantitative morphological study’, which set him on the path to his life’s work in respiratory biology. Following completion of his PhD, Steve began a post-doctoral career that saw him work with some of the world’s leading respiratory physiologists, anatomists and morphologists. His post-doctoral research began at the Max-Planck Institute for Experimental Medicine in Göttingen, West Germany (1972–74), where he worked on the morphometry of lungs and gills with Prof. J. Piiper. He then moved to the University of Bristol, UK (1974–75) to work on trout gills with Prof. G. Hughes. From there, it was back to Germany to work with Prof. H.-R. Duncker (1975–77) at the Universität Giessen on the functional anatomy of lizard lungs. Steve then took up his first academic position as an Assistent at the Universität Oldenburg (1977). During his time in Oldenburg, Steve completed his Dr habil. (Zoology) through his Habilitationsschrift entitled: ‘The functional anatomy of unicameral and multicameral lungs and its implications for the evolution of the lung structure in amniotes’, published as Perry (1983), as he progressed to a fixed-term professorship (1984). Steve then moved to Calgary, Canada, in 1987 to work with Prof. J. Remmers on the morphometrics of developing sheep lungs and the neuronal control of breathing, and during this time he became a Canadian citizen. Steve accepted a permanent appointment as a professor at the Rheinische Friedrich-Wilhelms-Universität Bonn, Germany, in 1994, where he was the group leader for morphology and systematics in the zoological institute. Steve remained in Bonn for the rest of his life and career, formally retiring in 2009, after which he spent a year as a visiting professor at the Universidade de São Paulo in Ribeirão Preto, Brazil.

Steve was well known to everyone in the respiratory biology field and made an enormous contribution, publishing some 125 articles through his career (many in *Journal of Experimental Biology*) on an array of different animals and plants. Arguably one of his most important scientific contributions was the definition of the anatomical diffusion factor that described the ratio of potentially respiratory active surface area to the harmonic mean diffusion




Steve looking at the holotype of *Euromycter rutenus* at the Museum National d’Histoire Naturelle in Paris (2013), thinking and trying to understand the ventilatory mechanism of these basal synapsids.

barrier thickness (Perry, 1978). This paper provides a means of quantifying the ‘hardware’ (as Steve put it) of any respiratory organ, improving our understanding of all respiratory systems. Steve never liked publishing for the sake of it and would often comment ‘well let’s just do this in the Aardvark’ if we even contemplated it. A quirk of Steve’s career was that he only graduated three doctoral candidates, each of us beginning with the advice that our job was to think freely and exchange our ideas with our peers, an approach that was actively supported in lab meetings with cheesecake or, even better, facilitated in a local bar.

Steve established successful collaborations with several Brazilian laboratories throughout his career, resulting in a frequent exchange of students between Germany and Brazil. One of us (W.K.) examined one of Steve’s lingering questions on the division of the

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coelomic cavity in vertebrates and how it affects the respiratory pump. This research in the tegu lizard demonstrated how this structure prevents paradoxical breathing during locomotion (Klein et al., 2003) and provided insight into one of Steve's other passions: the evolution of the mammalian diaphragm (Perry et al., 2010). Thorough examination of long accepted paradigms was a fascination for Steve in how ideas become entrenched and accepted dogma, often with little supporting data. Research into the role of accessory breathing structures in birds (J.R.C.) was able to confirm one of his suspicions that the uncinat processes were in fact respiratory structures (Codd et al., 2005) and provided a mechanism for explaining how dinosaurs breathed like birds (Codd et al., 2008). Steve never lost his interest in reptiles or revisiting ideas he'd published, even in his retirement, to seek new and important insights. Research into the comparative anatomy of turtles (M.L.) followed on from Steve's own dissertation and demonstrated how these could be used to address systematic questions (Lambertz et al., 2010). A lesson we all learned was the incredible value of the 'old' anatomical literature even if it highlights Steve's early struggle with the German language, such as trying to literally translate Scheidewand. Steve searched for interesting questions, and never cared if these fitted the mainstream, encapsulated in his life's work on respiratory organs (Perry, 1989).

The integrative nature of a field like respiratory biology was something close to Steve's heart and this led him to organise the International Congress of Respiratory Science, held in 2006, 2009 and 2014, where he brought together scientists from diverse fields under one roof to break down barriers between different areas of science. The publication of his book '*Respiratory Biology of Animals*' (Perry et al., 2019) has set the foundations for this field moving forward. You can find much of Steve's philosophy of science throughout the book, perhaps best encapsulated by the quote from the preface: 'you may not find all the answers you are interested in, but instead will be confronted with persisting questions'. Steve was something of an exception in being someone who never tried to take possession of his field and would freely share his knowledge, passion and ideas, delighting when these would take root and produce new scientific outcomes, ways of thinking and research.

Steve loved teaching and got a real kick out of interacting with students throughout his career. He would begin many classes by reassuring the students that although he considered himself a Canadian, he had been speaking German longer than any of them! If you ever attended any of his classes in Bonn, these were notable for Steve's overwhelming enthusiasm for anatomy and functional morphology, which would variously include Steve breaking into song and insisting the students joined in (whether they liked it or not) with the chorus of 'it's a long way from Amphioxus' to making use of any unfortunate doctoral students standing around to demonstrate hypaxial musculature. A functional anatomy course

wasn't considered complete unless the obligatory 'so long and thanks for all the fish' was inscribed onto the blackboard in thanks. One important aspect of his teaching was the full immersion of the students into an animal's Bauplan. Steve memorably used to ask the students to close their eyes and visualize in their mind as he talked them through the pathway an oxygen molecule travels until ultimately reaching the mitochondria. Steve was an excellent anatomist and would expertly guide students through their dissections and facilitate their understanding of the changes in vertebrate structure and function through evolution.

Outside of his academic life, Steve had a lifelong love of music and song and was a musician at heart. Steve was a keen member of several choirs in Bonn and the Folk Club Bonn – never happier than when he could break into song, preferably wearing a flat cap and in Welsh or interchangeably with a Norfolk or West Country accent. We all have fond memories of Steve stopping by a busker on his way through the Weihnachtsmarkt in Bonn, just to get the beat.

Steven Franklin Perry died in Bonn, Germany on 13 November 2022 after a long illness, leaving behind his wife Regine. Steve lived a good life and made his mark as an academic but also as a friend and mentor to many. Those of us lucky enough to have studied and collaborated with him cherish the lessons he taught us through the memories of our time with him and we proudly carry his legacy with us.

Wilfried Klein, graduated 2001
Jonathan Codd, graduated 2004
Markus Lambertz, graduated 2015

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