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Life's flows – reflections on T. J. Pedley's career in biological fluid mechanics

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It is a real pleasure for us to look back over aspects of Tim Pedley's long and productive research career in the still evolving field of biological fluid mechanics. Tim's contributions have been influential in the development of the field from the early days, indeed from before the discipline was recognized as such a richly fascinating one for mechanicists to explore.

For a long time as modern science fashions grew, most developments in our understanding of physiological phenomena were driven by medical or biological science trained investigators. With a few notable exceptions, they were not fully versed in the physical and mathematical disciplines that underpin any full mechanistic understanding of the biological or medical processes. It was in the middle of the last Century that we began to see the emergence of the benefits of the shared approach to such problems with truly inter-disciplinary groups becoming established in various centres around the world. The pioneering Physiological Flow Studies Unit (the 'PFSU' as it became known universally) at Imperial College London was one such group. The Unit was established in 1966 under the leadership of the medically trained Professor Colin Caro and mentored by his long term friend and research collaborator Professor (later Sir) James Lighthill, then the Royal Society Research Professor at Imperial College.

It was shortly after this in 1968, through the encouragement of James Lighthill, that Tim joined the PFSU, with a concurrent appointment in the Mathematics Department at Imperial. Before that, he had studied plumes, bubbles and vortices for his PhD under George Batchelor in the Department of Applied Mathematics and Theoretical Physics (DAMTP) at Cambridge, followed by two years post doctoral work with Owen Phillips at Johns Hopkins; this classical work was the subject of his initial five papers in this journal. Without doubt, these early experiences were highly influential in establishing his way of scientific thinking and his approach to fluid mechanics – talents prized by James Lighthill.

Five influential years of research followed within the PFSU that helped further to shape his future academic direction. When he joined, the original research areas of

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cardiovascular and respiratory mechanics were already being investigated and many more questions than answers were being raised by the various experimental studies. Tim immediately took an interest in both fields and grappled with making mechanistic sense of the novel experimental information being obtained by his colleagues. He exhibited aptitude in applying his mathematical skills to messy real-world problems making good use of the limited, often somewhat inaccurate, data being gathered using difficult and novel experimental preparations and in helping to develop further ideas for realistic experimental work.

His early papers on respiratory mechanics, co-authored with Michael Sudlow and Bob Schroter, were seminal in describing, *inter alia*, the characteristic fluid mechanics and energy losses relating to steady laminar flow in the bronchial airways of the human and other mammalian lungs. Building on the group's recently obtained experimental measurements of velocity distribution in short bifurcating tube networks, the distribution of pressure drop along the normal or disease-narrowed bronchial airway path during inspiration and its dependence on lung volume were both predicted realistically. At the time, the description of flow in the lung – or any other branching tree such as the arterial tree – was rudimentary and not able to provide meaningful insight into the underlying mechanics and physiological processes. Much of today's received knowledge in this field stems, without recognition, from that work.

Another of Tim's talents that came to the fore at that time is his enduring ability to enthuse a public audience with his dedicated enjoyment in research and of its quality. There was one occasion, still in the memory of friends present at the time, when he managed to impress a largely senior medical audience with his belief that his theory to explain a particular process was vastly superior to the only available *in vivo* experimental evidence obtained with great perseverance by his colleague Tony Seed. He was trying to model the extremely difficult problem of the instantaneous varying heat transfer rate from a small heated thin film anemometer placed in the aorta where the adjacent blood flow oscillates strongly causing boundary layer reversal over the film. Graphically presented theory and laboriously and skilfully measured experimental data bore no relation to each other. Regardless, Tim had the temerity, with tongue in cheek, to suggest to the audience that all that was needed was more accurate experimental data – his theory would then be verified! He got away with it!

In 1973, Tim returned to DAMTP at Cambridge to join Sir James Lighthill and develop further his interests in biological mechanics. With the exception of a most productive interlude from 1990 to 1996, when he was Professor of Applied Mathematics and sometime head of his department, at the University of Leeds, he has remained at his *alma mater* ever since. Very soon at Cambridge, he was exposed to the fascination of scale effects in animal locomotion as he became deeply involved in the running, and subsequently publishing a book of the proceedings, of a seminal conference on the topic chaired by, and largely the brainchild of, James Lighthill. Up until then, Tim's experience had been focused on internal flows particularly relating to respiratory and cardiovascular mechanics; this new experience first introduced him to the fascinating research opportunities presented when studying the mechanics and external flows in terrestrial locomotion, flying and swimming – a topic that would prove a fertile research field for him later on.

Before leaving the PFSU, Tim and three colleagues (Colin Caro, Bob Schroter and Tony Seed) committed themselves to the monumental task of writing a basic textbook for teaching and research purposes on the mechanics of the circulation. This was to be a seamless treatise written jointly by all authors and to be intelligible to both those with a background in medicine and physiology and those of an engineering or physical science background. The resulting book took over six years to publish, with Tim commuting to London from Cambridge for weekly, vigorously conducted, debates on the latest draft version and the taxing demands of cross-discipline education of fellow authors; the intellectual effort involved has never been forgotten by any of them!

The value of this book (The Mechanics of the Circulation) to the field is that the first edition, published in 1978, has stood the test of time until today. The authors, all now retired professors in their respective disciplines, have recently published the second edition of the book with virtually no changes from the original text – the material covered has withstood huge scientific and technological developments and is still largely as relevant today as when first written.

Throughout the 1980s and into the 1990s, whilst at both Cambridge and Leeds, much of Tim's work was devoted to problems related to flow in collapsible tubes. In 1981, he organized a seminal meeting, (Euromech 137, Flow in Collapsible Tubes) on the topic, that brought together a group of mathematicians and engineers from Europe, the USA, Australia and Japan for an animated exchange of ideas in this newly emergent field. This meeting sparked the interest of many and initiated a period of rapid growth in interest in collapsible tube flows. Aside from being the first meeting of a new research community it attracted many established, as well as young, fluid dynamicists to the field. In the *Journal of Fluid Mechanics* alone the number of publications on collapsible tube flow rose rapidly following this event.

Tim's interests focused largely on unsteady flows, and in particular, on the mechanisms of self-induced oscillations, or flutter. In this context, he and his colleagues at Cambridge and Leeds (Matthias Heil, Xiaoyu Luo, Oliver Jensen and others) and his experimental colleague in Australia, Chris Bertram, investigated a variety of fascinating new phenomena. With Bertram's help, Tim was able to gather the experimental data needed to develop and validate the theoretical models being developed by his own group, and in a series of publications with Luo in the late 1990s, he presented a comprehensive two-dimensional model for flow-induced oscillation. During this period, Tim was able to attract, first to Cambridge and subsequently Leeds, some remarkable students and post doctoral colleagues, who launched their careers under his expert guidance, and who continued on to become leaders in collapsible tube flow and wall mechanics in their own right. Whilst some are mentioned here, there are very many more who benefitted from Tim's dedicated supervision and enjoyed his good humour.

Another field that captured Tim's attention in the 1980s was gas transport in the lung, in particular at breathing frequencies higher than normal, a therapy that was gaining popularity for the treatment of infants with respiratory distress syndrome. Tim's interest was stimulated by the tendency for chaotic mixing that could occur under conditions of oscillatory flow in curved tubes, a model used to capture the secondary flow behaviour found in bifurcating airways. This grew nicely from Tim's earlier work on pulmonary flows with Bob Schroter, and strengthened the collaboration with his colleague Roger Kamm who happened to be spending his sabbatical with Tim at Cambridge at the time. Again, the trademark of Tim's work on these problems was a series of elegant mathematical solutions to a collection of appropriately simplified models in order to provide new insights.

As should be obvious by now, one of Tim's greatest attributes has been his ability to both identify and popularize new fields of research at the intersection of the mathematics, engineering and biology communities. He also has an unusual knack for choosing problems that would grasp the attention of a much wider audience. In that connection, one of the most fascinating problems addressed by Tim's research has to do with why giraffes are able to avoid fainting when they stand with their head upright. If the arterial and venous circulations leading from the heart to brain were rigid conduits, then the flow rate would be independent of head elevation, but the intravascular pressures would vary from largely positive to negative, leading to massive changes in transvascular exchange. In the case of upright posture, Bindi Brook and Tim demonstrated that the veins returning blood to the heart are highly collapsed and that the flow is supercritical (analogous to supersonic, in that the flow speed exceeds the speed of wave propagation). In this situation, the viscous flow resistance is just sufficient to balance the change in gravitational head, so the internal pressures remain nearly constant. These studies were motivated by a published collection of experimental measurements by Alan Hargens and co-workers that Tim's insight and calculations helped to decipher.

Over more than twenty years, Tim, his students and post-docs and other colleagues, developed incisive insights into both formal and heuristic aspects of the fluid dynamics of swimming micro-organisms. What are the roots of this accomplishment? There is Tim's remarkable enthusiasm for developing formal mathematical models of 'just discovered' phenomena, and his superb ability to do so. Unlike many theoreticians he can distinguish between solid and wonky aspects of an experiment: from directly observing the thing itself, from still photos, and, in one instance, from second-hand tales of an experimental observation. His pleasure at solving puzzles and joy at developing rigourous quantitative insight into some newly uncovered mystery of nature are all mixed up with constructing fluid dynamic models that capture the essence of an observation.

How did Tim's involvement with the theory of swimming micro-organisms develop and capture major attention, after years of focus on the very different sort of problems described in previous paragraphs? John Kessler's demonstrations at DAMTP, featuring swimming unicellular algae as protagonists, their behaviour and that of the fluid in which they swim, modelled by rudimentary theoretical approaches, certainly played a part. But, just waiting to be triggered, there must have been some latent interest. This may have come as a consequence of Tim's mentor and friend, James Lighthill's extensive attention to modelling the locomotion of living, swimming organisms. His focus ranged from fast, large fish swimming in a regime of enormous Reynolds number, to micro-organisms swimming at $Re \ll 1$. Perhaps Lighthill's elegant expositions and publications set the stage.

Steve Childress' visit to DAMTP in 1983 may have given Tim another nudge toward looking at the collective dynamics of nominally independent but hydrodynamically coupled swimming microbes. Childress and colleagues had written wonderful and evocative papers on bio-convection and pattern formation by populations of the protozoan *Tetrahymena*. Their theory was in many aspects similar to the earlier one for the algal patterns, but the rational fluid mechanical model was much more detailed. John Kessler had focused particularly on changes in swimming direction, due to supplied or collectively generated rotational drag on the algae. Childress and co-workers had omitted gyrotaxis, the joint effect of gravity and rotational drag on the orientation of the organisms' swimming velocity. Surely it did not escape Tim that lots more was 'there' waiting to be looked at, measured and modelled. However, he was, at that time, more or less fully occupied with his current main research projects and administrative and other matters. In 1985 Nick Hill, who joined Tim in Cambridge, developed important contributions to the theory of micro-organism driven convection of their fluid habitat, resulting in several papers. This led to Tim focusing his interests more on the algal bio-convection problem.

Also whilst Tim was at Leeds, John Kessler demonstrated to him and Nick, who had also moved there from Cambridge, his new results concerning bio-convection of concentrated cultures of the bacterium *Bacillus subtilis*. This extension from algae to bacteria showed that there was universality in the underlying concepts. As the years progressed, Tim's interest and commitment to micro-organism dynamics became stronger, as demonstrated by the increasing fraction of his publications devoted to the subject, and the remarkable range of insights described therein.

After Takuji Ishikawa arrived on the scene, with new insights and new approaches to an extended range of phenomena, well beyond bio-convection, almost all of Tim's efforts, together with Takuji and graduate student Tobias Locsei, were concentrated on micro-swimmers, their fluid dynamics, interactions with each other and boundaries, mixing and enhanced transport.

Tim's contribution to the mathematical analysis of the fluid dynamics of low Reynolds number swimmers – collective, few-body, and single – is, and will remain, one of the essential foundations of the field. Although perhaps at first sight to some, not as immediately important as improved understanding of blood flow, air flow and such, it is likely in the long run that understanding microbial dynamics and ecology, will be at least as, if not more, useful in many key areas. Important examples are to be found in plankton dynamics, agriculture, water purification, and the operation of the digestive systems of creatures large and small, in which vast numbers of micro-organisms swim, mix, exude enzymes and process material to produce essential and beneficial, or sometimes poisonous, products.

Much of Tim's career has been taken up by public service, including heading DAMTP at Cambridge (2000–2005), heading the Department of Applied Mathematical studies at the University of Leeds (1991–1994), Director of Applied Mathematics at Gonville and Caius (1973–1989), and co-editing this Journal. All of these duties, and very many more, such as those relating to the standing of mathematics within the UK and mechanics worldwide, have been undertaken with considerable responsible care and dedication. His election to the Royal Society in 1995 is excellent testament to his influence and respect within his chosen field.

A lot could be put on record of his national and international professional service. However, we felt it fitting to focus the close of this brief article on a personal and defining note – Tim as a mentor. Throughout his career, Tim has always offered strong encouragement to others, especially students new to the field of bio-fluid mechanics, to enjoy their work, think broadly across conventional boundaries and discuss their ideas with others. His influence permeates the field, and his academic offspring populate universities and research labs around the world. Some were identified here, but there are others too numerous to mention.

We hope that Tim will continue to enrich the field of bio-fluid mechanics directly through his personal contributions for a number of years to come. However, Tim's legacy will also continue to grow in large part through his influence on the thoughts and activities of the many friends who have had the great pleasure of working with, or training under him over the years.