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OBITUARY

In memoriam – Craig W. Hawryshyn (1954–2023)

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On August 29, 2023 a true pioneer in the fields of vision in fishes and ecology of vision passed away. Professor Craig Hawryshyn will forever be linked to ground-breaking work in the exceptionally challenging research areas of vision in the ultraviolet (UV) and polarized light detection. His experimental approaches to comparative vision science and visual ecology included behavioral, histological, biochemical, molecular biological and electrophysiological techniques. He also did field work to gather data about environmental factors relating to UV and polarized light fields underwater. His contributions, along with those of his students and collaborators, set the stage for much of what we now know about vision in the UV, including its cellular and molecular basis and its behavioural and ecological relevance.

Craig was born in Winnipeg, Manitoba, Canada on March 23, 1954. He received his BSc from the University of Manitoba (1972–1976) and completed his MSc in zoology at the University of Alberta (1976–1979). His PhD, at the University of Waterloo under the supervision of Ross Beauchamp (1979–1984), was the start of his passion for research on neuroscience and fish vision. After a postdoctoral fellowship at Cornell University with Bill McFarland (1984–1986), he held faculty positions at McMaster University (1986–1989), University of Victoria (1989–2006) and Queen's University (2006–2012). He was awarded a prestigious Canada Research Chair in recognition of his contributions to science and the esteem of his nominating colleagues. As can be seen from the citations below and his bibliography (see his profile on Google Scholar), Craig and his collaborators produced an extensive publication record, including 15 research and two review articles in Journal of Experimental Biology alone.

Three streams of data must converge if we are to understand the evolutionary trajectory leading to UV and/or polarized light vision in a particular animal. First, there are the characteristics of the receiver; the eyes and the rest of the visual system. Craig's early work used behavioral techniques, including heart rate conditioning and optomotor responses, to demonstrate UV and polarized light sensitivity in salmonids and cyprinids, and its ontogeny (e.g. Hawryshyn and Beauchamp, 1985; Hawryshyn et al., 1989; Beaudet and Hawryshyn, 1999; Hawryshyn, 2009). He collaborated on the identification of the visual pigments and cell types (including cone cell topography and mosaics) that underlie these sensitivities using microspectrophotometry, histology, gene expression (and the involvement of hormones such as thyroxine) and electrophysiological methods (e.g. Hawryshyn and McFarland, 1987; Hawryshyn and Harosi, 1991; Raine and Hawryshyn, 2009; Raine et al., 2010). He also developed and tested hypotheses about how polarized light sensitivity was achieved by the retina and how it

Craig Hawryshyn in Hawaii, 2015. Used with permission from his wife, Dianne Balfour.

was utilized by the animal (e.g. Hawryshyn, 1992, 2000; Kamermans and Hawryshyn, 2011). The second necessary input are the characteristics of the visual targets that make UV and/or polarized light detection adaptive. Craig contributed data on the nature of the interactions of potential prey with the photic environment and how these interactions could increase the likelihood of prey capture by increasing contrast via polarization and UV absorbance and scatter (e.g. Hawryshyn, 2010). Finally, the physical nature of the photic environment in which visual tasks are being performed must be known. Craig used spectroradiometry and polarimetry to measure these aspects of the photic environment in nature where the fish lived (e.g. Sabbah et al., 2011). Putting these three data streams together – a formidable and challenging task that few researchers manage to achieve – allowed Craig to develop ideas about the ecological relevance of such sensitivities to fishes at different times of day and along different developmental trajectories. These were particularly relevant for the changing visual system of salmonids as they matured from larvae to adults

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Word cloud image of the titles of the articles published by Craig Hawryshyn. Created on 29 November 2023 from Craig Hawryshyn's Google Scholar (©2023 scholargoogler.com) profile (https://scholar.google.ca/citations?user=FbBltk4AAAAJ&hl=en) with settings: minimum word frequency=2 and maximum word frequency=300.

moving from fresh water to marine environments and their relation to the sensory basis for their long-distance migration.

While publication and participation in large meetings are important for the dissemination of data and ideas, nothing can replace small, focused meetings that gather workers in well-defined fields. Realizing this, Craig motivated and participated in the planning and execution of two very important meetings devoted to UV and polarized light vision. The first was held in 1992 as a satellite meeting of what was at that time the American Society of Zoology. The proceedings of that meeting were published in a special issue of Vision Research that Craig guest edited (Hawryshyn, 1994). The second was held in 2000 at the University of Victoria where Craig was also the host. The proceedings of that meeting were published in a special issue of Journal of Experimental Biology (JEB) that Craig guest edited with Howard Browman (Browman and Hawryshyn, 2001). The presentations and discussions at these meetings led to many new collaborations and much new research.

The remembrances that follow make clear that Craig moved freely within the broad area of visual ecology, contributing to many of the various sub-disciplines that define the field. For those who aspire to achieve this, Craig's career represents an exemplary model. That is a fitting and commendable legacy.

Remembrances

Jake Sivak (colleague at the University of Waterloo, 1979–1984)

Craig loved science and his enthusiasm about science was infectious. Listening to him describe his research was like listening to a master chef describe how to create a Cordon Bleu culinary creation.

Howard Browman (postdoc at the University of Victoria, 1990–1993)

Craig was very generous in helping me to secure funding from what was then the Medical Research Council of Canada. That is, coaching me in writing a proposal on a research area in which I was a novice (the ontogeny of UV photoreception and of the UV cone in salmonids). This generosity continued during my time in his lab, and after. When I first arrived, Craig used an unusual amount of his time to train me – in theory and in practice – in many of the techniques mentioned above, and in how to interpret the data generated and write it up. It was all new to me at the time and I would not have succeeded without Craig's patient supervision. He was an exceptional mentor, with deep knowledge and skills. He imposed a very high standard for our lab's research, which was essential for work on discoveries that met significant resistance at the time; that is, UV vision based on a cone cell containing a UV-sensitive photopigment. I recall Craig preparing everyone in the lab for what was my first Society for Neuroscience conference; practicing our talks and going through the talking points for our posters. We were very excited with the prospect of all of the Nobel prize winners who would be in attendance. Thereafter, it was a running joke to express disappointment that no Nobel laureate had come to see our presentations. Craig and I stayed in touch through the years. In 1999 he came to Bergen and he and I co-taught an intensive course on 'Sensory Ecology of Aquatic Crustaceans and Fishes'. In 2000, he and I co-organized The Second Workshop on the Biology of Ultraviolet and Polarization Vision and co-edited the special issue of JEB referred to above. In the intervening 23 years, we stayed in touch and updated one another on our professional and personal lives. I last talked with him shortly before he died. We reminisced about how vibrant and exciting those days were when we were young and full of energy and ideas that led to many significant discoveries. What I learned from Craig – perseverance in the face of skepticism over a discovery, high standards for conducting and reporting research, generosity in sharing your knowledge,

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making and maintaining strong personal relationships with your collaborators – continues to serve me well. He was a great mentor and friend. I will miss him.

Luc Beaudet (PhD student at the University of Victoria, 1990–1997)

I first met Craig in the late 1980s while I was an undergrad working part time in the laboratory of M. A. Ali at the University of Montreal. Craig, who had moved to Victoria by then and was setting up his lab, had been invited to give a presentation on his work by Dr Ali, who also worked on vision in fishes. I was delegated the task of picking up Craig at his hotel and bringing him to the biology department; as I did not have a car then, we made the journey on the subway.

Despite the noisy subway environment, my poor English and Craig's embryonic French, he managed to explain his research to me and impart his enthusiasm for ultraviolet and polarized light vision in fishes. This exemplified his lifelong interest in disseminating research findings, and his deep respect for learners: Craig made me feel as if we were equals despite my complete ignorance of the subject matter. This never changed throughout our relationship.

Soon, Craig, postdoc Howard Browman, graduate student Daryl Parkyn, myself and support staff, formed the core of his newly established lab at the University of Victoria. These were exciting and formative times for all of us. Craig's trust in his team allowed us the freedom to explore new ideas and techniques. I cannot remember him ever saying anything to discourage a line of enquiry. Despite his hands-off approach, when the going got tough, Craig was there to provide support. Craig's role in shaping our futures cannot be overemphasized.

During our last visit together, not long before he passed, we reminisced about that ride on the Montreal subway that would, unbeknownst to either of us, lead to a lasting, yet too short friendship.

Shelby Temple (PhD student at the University of Victoria, 2000–2006)

Craig was a passionate graduate supervisor who held his students and himself to high standards. He had two sides: one that was highly compassionate and supportive for anything that involved our personal lives; and one that continually challenged you, often in unexpected ways. And while the latter was tough at the time, upon reflection, I am sure it made us stronger people and better researchers, which is likely why so many of Craig's students are still active in research today. One of the lessons I will always remember was his belief in the importance of making time and finding space to think. He encouraged his students to get out of the lab, to go fishing or spend time in nature to observe and ponder. And it was from this that I, and I am sure several others, learned the importance of serendipity in science.

Ted Allison (PhD student at the University of Victoria, 1997–2004)

It was always apparent that Craig was a relentless champion of his trainees and worked hard to see them succeed by ensuring they were in conversation with the world leaders (e.g. in visual ecology and visual system development). He was a highly integrative scientist and allowed us to be early adopters of emerging technologies (proteomics, chromatin immunoprecipitation, in situ hybridization, along with all the physiology, behaviour and ecology). Craig enjoyed being provocative in challenging dogma and revealing to others how animals see the world.

Shai Sabbah (postdoc at Queen's University, 2007–2012)

Craig's passion in the last several years of his scientific career was the color vision of the cichlid fish of Lake Malawi, Africa. These fish have evolved from a common ancestor in a brief period of evolutionary time, they are notable for their diversity in male coloration and sexual dimorphism in color patterns, and their mate choice heavily depends on visual communication. As he did throughout his career, also in the case in Lake Malawi cichlids, Craig systematically studied the properties of the receiving and transmitting fish, and the characteristics of their immediate environment. This work contributed to our understanding of the functional diversity in the visual systems of fish, and how evolution has shaped the properties of cone photoreceptors in the vertebrate retina. For example, through combined theory and experimentation, Craig and colleagues advanced the view that the large number of cone classes in fish evolved to enhance reconstruction of complex color signals under water.

Craig was also fascinated by the developmental changes taken place in the retina, and mostly in polarized light sensitivity. For example, salmonid fish use polarized light sensitivity for prey detection when they are young but for navigation when they are older. Craig and colleagues showed that the region of retina that is sensitive to polarized light switches during development such that the animal is well adapted to the different requirements at each life stage.

Craig's work significantly improved our understanding of the adaptive significance of developmental processes and species-specific variation in visual systems. His success in science, driven by his courage and persistence while battling health issues, is nothing but an extraordinary achievement. Even more admirable are the openness and honesty in which he talked about his struggles. Craig has been a role model for many of his trainees, who admit to not only finding an excellent supervisor, but to also finding a true friend.

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