CAREER NARRATIVE

EHAB ABOUHEIF

Streets and shorelines are named after my Uncle, Abdel-Latif Abouheif, otherwise known to the world as the 'Nile Crocodile.' He was World Professional Marathon Swimming Champion 1965, 1966, and 1968, and, in 1999, he was inducted to the International Swimming Hall of Fame (USA). His actions out of the water were equally inspiring – on 2 different occasions he donated his prize money to the families of swimmers (one English and one French) who had drowned or become paralyzed while competing with my Uncle. Inspired by his achievements, I trained intensively with a professional swim team hoping to be a champion and influence my generation, but my times were not fast enough and swimming was not to be my calling in life.

When I started studying Biology at Concordia University (Montreal), I thought a career in Medicine is where I could help change the world. Biology came easy to me--my grades were excellent--and it seemed the path was clear. That is, of course, until I met Geza Szamosi, Principal of the Science College, a unit of Concordia that broadly trains talented students in the sciences. He convinced me to join the College, and as a member, I had to take 3 courses in the history and philosophy of science and 3 independent research projects. This opened my eyes to a whole new way of thinking. During my Honors thesis project, my research led me to the disconnect between how evolution works at the level of the whole organism versus how evolution works at the molecular level. I sequenced a family of genes involved in salt stress tolerance in plants and found that the genes had significantly diverged in sequence at the molecular level but maintained their function in salt stress tolerance. This led me right to Kimura's *The Neutral Theory of Molecular Evolution* (Kimura 1985). Kimura argued that the major patterns of divergence of genes (the genotype) is driven by genetic drift of mutant alleles, which is in stark contrast to evolution at the level of the whole organism (the phenotype), where natural selection was thought to be the primary mechanism of adaptation. If I could unify these contrasting levels of evolution, I believed that I could greatly increase the predictive power of evolutionary theory and, as a consequence, improve biodiversity conservation, animal/plant breeding, and even medicine. I suddenly realized that I could achieve my dreams of making change in the world through my passion for evolutionary biology. I had no idea at the time that this 'black box' between genotypic and phenotypic evolution would consume me for the next the 23 years of my career.

I began my 23-year journey with fellowship from the Government of Quebec (FQRNT; 1993-1995) to start my MSc degree at Concordia University with Daphne Fairbairn (now Professor at the University of California, Irvine). Together, we discovered a general pattern of size dimorphism between males and females across the animal kingdom and coined it 'Rensch's Rule' (Abouheif and Fairbairn 1997, *American Naturalist*), and today it is my third most cited paper (263 citations). To establish this general pattern across species, I used statistical methodologies collectively known as 'The Comparative Method.' Because some species are more closely related to each other than others, this method assumes that species are not statistically independent data points. I believed that independence or non-independence of species data points should not be assumed but tested empirically. I therefore came up with a new test based on a statistic invented by mathematical genius John Von Neuman, and adapted it to evolutionary biology. This test is now known as the "abouheif test" and is now my second most highly cited article (Abouheif 1999, *Evolutionary Ecology Research*, 296 citations). These papers inspired a series of papers (Abouheif 1998; Abouheif 1999; Rheindt et al. 2004; Oakley et al. 2005) testing and developing new Comparative Methods.

In 1995, I received a PhD fellowship from the Government of Quebec (FQRNT; 1995-1998) to start my PhD in the Department of Ecology and Evolution at Stony Brook University (New York, USA) with Axel Meyer. In Axel's lab, I could finally study the black box between genotypic and phenotypic evolution in fish. I soon realized that the key to uniting evolution at these two levels into a common framework was organismal development, and this landed me square into the field of 'evolutionary developmental biology' or evo devo for short. Within two years, I published a paper in PNAS (Zardoya et al. 1996a) examining how genes regulating limb development evolve in zebrafish. This was followed by a series of conceptual papers on the concept of homology (Abouheif 1997; Abouheif et al. 1997; Wray and Abouheif 1998; and Abouheif 1999), which had significant impact on the field, both in terms of the number of citations (470 times total, *Google Scholar*) and their appearance in biology textbooks, e.g., Strickberger's *Evolution*. Two years after starting my PhD, Axel left Stony Brook to join the University of Konstanz (Germany) so I stayed in Stony Brook and joined Gregory Wray's lab, an early pioneer of evo devo.

This is when I began my work on ants. Like honeybees, nutrition, temperature, and social interactions can determine whether an egg develops either into a queen or worker. If the egg develops into a queen it lives for 30 years, develops fully functional wings, and lays millions of eggs, but if it develops into a worker it lives for only 3 months, is wingless, and has a significantly reduced reproductive capacity. Greg agreed that we would learn a great deal from ants about how genes, phenotypes, and the environment interact during development and evolution. I was seized by excitement and I could hardly wait to begin this new adventure with the ants, but I had to start from scratch. Although ants were a model for studying complex social behavior, almost nothing was known about their developmental and molecular biology. Before long, I had made significant progress in my research, and in 1999 I was awarded an NSF Dissertation Improvement Grant.

Greg Wray announced he was moving to Duke University so I moved labs once again and obtained my PhD from Duke. Within 2 years I made my first major discovery on ants, which we published in *Science* (Abouheif and Wray 2002). Our discovery focused on 'wing polyphenism,' which is the ability of ants to regulate their development of wings in response to environmental conditions. Wing polyphenism originated just once approximately 150 million years ago and is a universal trait of all ants–queens and males develop wings to take part in mating flights, while workers halt wing development to become completely wingless and live their whole lives underground. Before starting the work, we had predicted that because wing polyphenism evolved just once, that it would use the same conserved gene network as other holometabolous insects (flies, butterflies, beetles, and ants) to build wings in queens and males, and that this network would be interrupted in the same point in wingless workers in all ant species. To our surprise, we discovered that while queens and males did indeed use the same conserved gene network that controls wing development, the wingless worker interrupted this network in different places in different species. This revealed a fundamental disconnect between evolution of the phenotype (wing polyphenism) and evolution of its underlying gene network.

Before finishing my PhD at Duke, I obtained my first Assistant Professor Faculty position at McGill University (Montreal, Canada). Thankfully, McGill allowed me to first accept a 2-year HHMI postdoctoral fellowship with Nipam Patel (2002-2004) at the University of Chicago. 1 year after I joined his lab, Nipam moved to the UC Berkeley and so I followed him and helped him set up his lab. During this period, I learned a great deal about how to functionally manipulate the expression of developmental genes (both knockdown and overexpression) in non-model organisms. This experience laid the foundation and gave me the confidence to take my developmental and molecular work on ants to a higher level. With this added experience, I made it my goal to uncover how and why there is a disconnect between phenotypic and genotypic evolution in ants. I believed that if I could solve this mystery, that I would reveal fundamental rules about the way that genes, phenotypes, and environment interact during development and how this interaction influences the evolutionary process.

At McGill, I hit the ground running with an equipment grant from the Canadian Foundation of Innovation (2005; $600,000), an NSERC Discovery Grant (2005-2010; $32,000/year), and an FQRNT New Researcher grant (2006-2008; $20,000 CDN/yr). Soon after arriving, I was awarded a prestigious Tier II Canada Research Chair in Evolutionary Developmental Biology (2004-2009; $100,000 CDN/yr), and in 2006, I was awarded an Alfred P. Sloan Fellowship in Computational and Molecular Evolution (2006-2008; $50,000 US), which "seeks to recognize the achievements of outstanding young scholars in science, mathematics, economics and computer science. Past recipients of Sloan Research Fellowships have gone on to win 38 Nobel prizes, 14 Fields Medals (mathematics), and 8 John Bates Clark awards (economics)." I used all these newly acquired resources to take a multidisciplinary approach to understand the disconnect between evolution of the gene network that controls wing development and evolution of wing polyphenism in ants–I collaborated with mathematician Leon Glass and published a mathematical model (Nahmad et al. 2008) to make predictions about how the disconnect originates, and over the next several years, we tested the predictions of this model (Shbailat et al. 2010; Shbailat and Abouheif 2013). To understand whether the disconnect is a general feature of ants and other insects, I launched research to understand the genetic basis of reproduction, another defining trait of social cooperation in ants (Khila and Abouheif 2008, *PNAS*; Khila and Abouheif 2010 *Phil Trans B*). I discovered that this disconnect was clearly evident in other insects–I collaborated with Professor Locke Rowe at the University of Toronto on genetic basis of adaptation in the semi-aquatic bugs that resulted in three articles published in *Science* (Khila et al. 2012), *Evolution* (Khila et al. 2014) and *PLoS Genetics* (Khila et al. 2009).

Shortly after being promoted to Associate Professor, my lab made another major discovery (Rajakumar et al. 2012, *Science*), this time using supersoldier ants from the ant genus *Pheidole*. Dormant genetic potentials exist in all animals, as reflected by the sporadic appearance of ancestral traits in individuals that normally should not have them. These traits, such as bird's teeth and snake's fingers, are widespread in nature but are traditionally thought to be "freaks" that contribute little to the evolutionary process. We used supersoldier ants to show that these dormant genetic potentials, once triggered, act as raw materials for evolution, which changes the traditional view and provides a new way of thinking about evolution. This discovery attracted a great deal of media coverage: TV (e.g., *Global National New; Discovery Channel)*; radio (e.g., *CNN; CBC; NPR*); online news (*Over 2.5 million hits on Google Chinese & over half million hits on Google English, including BBC, CBC, PBS, MSNBC, Discover, Scientific American, Der Speigel, Le Monde*) and print (e.g., *Montreal Gazette, La Presse, The Vancouver Sun*). Not only does this work provide major insight into the disconnect between genotypic and phenotypic evolution, it opens future possibilities for harnessing dormant genetic potentials to advance medicine, biodiversity conservation, and animal/plant breeding. For example, after being invited to speak at National Breeders Roundtable, whose members are the largest shareholders in the poultry industry in the world, we published an article outlining a new protocol for animal and plant breeding based on artificially selecting desirable traits induced by the triggering of dormant genetic potentials (Rajakumar and Abouheif 2013). Shortly after, I was awarded the E.W.R. Steacie Memorial Fellowship, Canada's highest honour for a young Canadian scientist (2014-2016; $125,000 CDN/yr; 2-years relief of teaching and administration), and was recently inducted as a Fellow of the Royal Society of Canada's College of New Artists, Scholars and Scientists (2016), which gathers the best of the emerging generation of leaders in scholarship, science and art in Canada. I was also awarded an NSERC Research Tools and Instruments Grant ($132,000 CDN) and an NSERC Discovery Accelerator Grant (2016-2019; $40,000 CDN/yr).

Since this discovery, my career and research program are gaining even more momentum. I was promoted to Full Professor (2014) and continue to be sought after for invited seminars, public lectures, and keynote talks. To date, I have been invited to give more than 100 seminars and keynote lectures, many of which are at top-rank universities and institutes, including Harvard (2003, 2013), Rockefeller (2015), RIKEN (Japan, 2016), Keynote Address EuroEvoDevo Conference (July, 2016). My lab continues to publish articles of high impact: Alvarado et al. (2015, *Nature Communications*); Rajakumar et al. (2018 *Nature*); Rafiqi et al. (2020, *Nature*). I am frequently asked to write 'Perspective' articles in *PNAS*, *Current Biology*, and *eLife*, and some have actually been cited more than 30 times (Abouheif 2008, *Evolution & Development*). I serve as Editor-in-Chief for *Journal of Experimental Zoology: Molecular Developmental Evolution*, a top journal in the field of Evolutionary Developmental Biology.

I wanted, however, to advance the field in other ways. While Europeans had the *European Society for Evolutionary Developmental Biology*, no such thing existed in the Americas. In 2013, at an international workshop organized at the National Evolutionary Synthesis Centre (North Carolina, USA), I was elected to lead the establishment of a new evo devo society in the Americas. I used much of the time-off I had been awarded from the Steacie Fellowship to establish, as Founding President (2013-2015), from the ground up the *Pan American Society for Evolution Developmental Biology* (http://www.evodevopanam.org), and organize our first international meeting at UC Berkeley (August 2015). I am now serving as Past President.

Finally, the time came where I could finally build on the dreams inspired by my Uncle to use my success and influence to promote societal change on both local and global scales. Locally, I developed a McGill course that employs unconventional teaching methods, such as role-playing, to expose students to how theories of evolution affect our everyday lives. In recognition for these efforts, I won the 2013 Department of Biology Teaching Award. Globally, I began to engage the public through giving many open lectures promoting the integration and compatibility between science and religion. These lectures include a public debate in central London in front of 900 people where I argued for compatibility between Islam and Evolution. This debate received widespread media attention, with articles in *The Economist*, *The London Times*, *The Guardian*, *The Huffington Post*, and also *BBC Radio*. These lectures and debates inspired me to establish the *McGill Centre for Islam and Science* in collaboration with faculty members from Education and the Institute of Islamic Studies. The Centre aims to provide historical perspectives from the great scientific achievements of Islamic culture, to improve current science education in Islamic countries, and to identify pathways for future scientific innovation in those countries. For these efforts, I was recognized by the Canadian Arab Institute, and was named the "Canadian Arab to Watch" for September 2014.