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Editorial

“Because I never was a damn geneticist” – the unique scientific approach and career of Eric H. Davidson

I once asked Eric how he could sustain his unique scientific approach even in the face of adversity and during periods where the gap between the depth of his theoretical insights and the available evidence was still huge. In his characteristic direct way, we all so much appreciated, he quipped: “because I never was a damn geneticist,” smiled, as he would on such occasions, and after a short pause, evaluating whether this was indeed a question worth pursuing further, began to think about it.

He wondered what I meant by unique. Was this even true? Clearly there was something different about his approach, but what exactly? “You tell me,” was the next, predictable, challenge, and so the spots where reversed and I had to defend my question, a situation that all of us who worked with him were all too familiar. These discussions were prone to last hours and required both logic and facts. Any hint of mere speculation would be met with a challenge to think more deeply and provide better evidence.

The question had come up because of our main joint project—to understand his investigative pathway, the discovery and theoretical formulation of the regulatory network paradigm as one of the core explanatory mechanism for development and evolution. We embarked on this journey about ten years ago. Eric, who had a keen interest in history, not only the history of science, but general history as well, had agreed to this project after a thorough “audition” brokered by our mutual friend Jed Buchwald. I had to convince Eric (1) that I was serious, (2) that I understood all the details of the science and its context, which meant to convince him that as a trained mathematical evolutionary biologist and historian (long story) working on the theory of developmental evolution I was not one of those who cared about variation in petunia colors, but about the deep questions of body plan evolution and especially about mechanistic explanations of phenotypic evolution; and (3) that the project would add insights. “We are not doing this just for the hell of it,” again, in retrospect, a totally predictable sentiment.

I succeeded. The audition, at a Saturday morning on his lovely porch, quickly turned into a deep conversation about the implications of GRNs for understanding evolution, the huge gaps within evolutionary theory to actually explain the hard and interesting challenges of phenotypic evolution and what we need to do to possibly overcome those and why we need to understand the “real” history of science in order to do better science. By real history of science Eric meant the logic of problems, experimental approaches, empirical evidence, and theoretical frameworks that define the “life history” of fundamental biological questions. He liked what he heard and we agreed that this would be a long project, if we do it right. And, of course, doing it right was the only option.

Our first conversation was almost immediately devoted to deep questions. He only had one concern with some aspects of my scientific pedigree. “So, you did your biology Ph.D. with Günter Wagner at Yale…pause…I know he is smart, but I don't understand the guy.” Clearly this was a challenge. It turned into an argument after I said that the two of them actually think very much alike, agree on both problems and eventual solutions, but come from different starting points. “What do you mean?” I had to explain how I could dare to say something like this. This meant going into papers from memory—both his and Günter's, extracting the logic, contextualizing the arguments. Time was flying and we had great fun (some of it in retrospect, as it was also exhausting at the time). Then came a classical Eric statement. I had argued how we (Günter and me) had taken a different approach to Evo Devo, how we argued for developmental evolution as a mechanistic science, already at the founding symposium a new section of what is now SICB, and how important it is to transform evolutionary biology. “Why are you wasting your time trying to convince people who think that they can understand body plans by looking at petunias.”

Because…Eric smiled. Not a question that could/should be answered at this moment. We proceeded to outline how we would approach the project we just agreed to. It had to be its own unique blend of history and science. As our meeting was during football season, Eric was going to drive into town to watch a game. This gave me time to recover—much needed as we would meet again for dinner and, of course Bourbon, at our friends Diana and Jed Buchwald's house

Our project turned into one extended conversation, where, over the years, we reviewed his investigative pathway, uncovered new and forgotten perspectives and continued our argument about the future of evolutionary biology. We collaborated on historical side projects, such as the paper on Boveri's long experiment (Laubichler and Davidson, 2008) and others that now need to be completed without him in person, but with his by now internalized voice guiding the process. As the main project continued it became clear that this could not be broken into smaller pieces or publishable units. We had a ritual. Periodically Eric would ask when I was going to write something about the project. I told him I am writing, but as this story is not modular or has any meaningful periods—as it is indeed one long and unique pathway that is not finished—I can't just publish these bits and pieces. We need to see where it goes. He bought the logic.

That Eric's investigative pathway is indeed one long argument became even more obvious after Isabelle and he finished their book (Peter and Davidson, 2015). Eric had talked for a while about writing something with Isabelle, who had been his congenial scientific partner for some time. He said that now that the regulatory logic is becoming much better supported by empirical evidence a broader

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synthesis is possible. I kept insisting that the evolutionary implications are also becoming clearer. It took him a while to make the decision to write the book and only after Isabelle agreed to do it with him. I remember when he started one of his outlines for the book. We were at a meeting in Berlin and one of the talks was going so off track that Eric lost any interest. We were sitting next to each other—pre-scooter days—and he began to type, in all capital letters, we were also familiar from his slides, a logical sequence of chapters. It was not quite the same as the eventual book, but close.

The book itself is its own masterpiece, a mixture of a clear logical framework and a wealth of empirical information that is the unique Davidson blend already present in the 1968 volume and a blend as unique as his favorite Bourbon (Davidson, 1968). The organization of the volume is a clear step by step exposition of a scientific paradigm: complex developmental and evolutionary processes are governed by a specific regulatory logic that can be uncovered, analyzed, modeled and applied. Expressed this way it sounds simple. And it actually is simple, once it had been formulated in such a precise way. Simple and elegant, as all important scientific insights. But knowing the history of what it took to get there, from logical insights to empirically supported specific cases and finally to computational modeling one can't help but wonder how this was possible within one investigative pathway. I discuss the book in much more detail in another context, trying to give it the attention that cannot be done here.

However, I do want to mention the two chapters that to me, as an evolutionary biologist, represent the major departure from all his previous books—the explicit discussion of computational modeling as a central approach in studying gene regulatory networks in development and evolution and an expanded discussion of the evolutionary implications of his work. The basis of this can already be found in the 1969 paper with Roy Britten, which ends with a long discussion of the evolutionary implications of the proposed regulatory network approach (Britten and Davidson, 1969) and in his long collaboration with Doug Erwin on explanations of macro-evolutionary patterns and processes. It is this last chapter on evolution that contains yet another important element of Eric's scientific legacy.

The last time I saw Eric in person was at the book launch party. He was characteristically curious, but uncharacteristically nervous. Would anybody care to read the book? After I told him I had read the whole book and found it brilliant, but wondered why they stopped so abruptly and did not delve deeper into what I consider one of its most transformative implications—an implicit reformulation of the core of evolutionary theory, we were right back to the discussion we started during our first meeting many years ago, petunias and all.

But this time I was determined to push harder and we ended up having a two-hour argument. Of course he realized what I said, namely that now we have the mechanistic core of developing an evolutionary theory that can account for both change and stability. Traditional evolutionary theory can explain the dynamics of evolutionary change reasonably well, but in order to account for the patterns of evolutionary history we also need to explain stability and with regard to this problem current evolutionary biologist behave like Ptolemaean astronomers, introducing one epicycle after another, while refusing to change their paradigm. Needless to say, Eric loved this analogy. The regulatory framework represents a different paradigm, one that can simultaneously account for the origin of variation and evolutionary change at different scales as well as the suppression of variation and therefore the specific patterns of stability we see in evolutionary history.

Why did you not go further, I asked. Why stop and leave those transformative implications unexplored. Of course he had a reason. The book is consistent as is, it is a layered argument and each section is backed by a wealth of empirical data. As such it provides the foundation for the new science of regulatory bioscience as he calls it and there is no room in the book for anything that is less grounded and more speculative at this point. So then we need to write a paper for an evolutionary biology journal to highlight these implications, I said. Why?, he grumbled. It is a waste of time to deal with the Petunia fanciers. I stood my ground, arguing that we need to get these ideas to the graduate students in evolutionary biology, so we need to reach them. This he accepted, having shaped countless young scientists at the MBL and beyond, most recent with the GRN course for which the book was written. He agreed to entertain such a paper, if Isabelle and Doug would also participate. Now, sadly, we have to do it without him.

But this last episode also sheds light on the question I asked him years ago. How did he do it? The answer is that Eric's science was Eric. A unique combination of crystal clear logic, a vast knowledge of even the most mundane facts of biological diversity, especially with regard to development, a deep sense of the real questions grounded in the history of the problems, a never ending curiosity, an intuition that was as much artistic as it was scientific, and a brutal honesty that did not allow him to even consider any shortcut. This explains the resilience to short lived fashions and distractions. The continuity comes from two sources: (1) stubborn as a mule (Eric about Eric and everybody else wholeheartedly agreeing with this statement) and (2) a sense of scientific tradition and humbleness towards his predecessors and intellectual heroes, such as Boveri, Wilson, Mirsky. Like all brilliant scientists, Eric was a bridge between many domains. Hidden in the quote about geneticists is a simple truth. Not that Eric had no regard for genetics—he clearly had—but that he did not follow a specific intellectual fashion, in this case to focus on a single gene in order to slowly understand a complex problem. His science was guided by theory in the most fundamental sense. And it connected the history and theoretical conception of problems with the best available evidence. For him this meant connecting molecular mechanisms with the logic and facts of differentiation studied by the leading experimental embryologists of previous generations. His unique knowledge of this earlier literature allowed him to be not only a bridge to the past, but also into the future that we now hve to help unfolding. He has given us so much. We owe him that.

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