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Interview by Ute Deichmann with Douglas Erwin

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Douglas Erwin is the Curator of Paleozoic Invertebrates at the Smithsonian Institution of the National Museum of Natural History, Washington, DC, and external professor at the Santa Fe Institute, NM. He received his Ph.D.in Geology from the University of California, Santa Barbara, in 1985. Most of his current research focuses on major evolutionary transitions and evolutionary innovation, where he attempts to understand both the role of developmental invention in generating novel morphologies and how new niches are constructed to facilitate the persistence of these new inventions. Much of his work has focused on the events of the early radiation of animals about 540 million years ago (the Cambrian radiation). From 1990 to2005 he examined causes and consequences of the great end-Permian Mass Extinction that occurred 252 million years ago and then conducted research on the generation of evolutionary innovations that followed these and other mass extinctions.

Macroevolution and criticism of Neo-Darwinism

UD: How did you become a paleobiologist?

DE: In the U.S., people who are interested in invertebrates usually study in geology departments. People who are interested in vertebrates or in paleobotany study in biology departments. So my training was originally in the geology department but I had a background in biology as well. So I started in paleontology in the geology department.

UD: Your work has focused, at least in recent times, on major evolutionary transitions and novelties which result in innovations – or innovations resulting in novelties?

DE: Novelties may produce innovations. So to me, novelties are individuated morphological or phenotypic structures, whereas innovation is when they become evolutionarily and ecologically significant. So there are often lags in the fossil record between identification of a novelty and one that becomes ecologically significant.

UD: How did you become interested in these questions?

DE: I was interested in them at least since college. I've always been interested in big-picture questions, probably because I'm lousy at detail! So when I was a graduate student, I was initially very interested in the Cambrian radiation. It's the origin of animals. And I've always been interested in that, but for two decades I worked on the Permian mass extinction. Not actually because I was interested in the extinction, but because I was interested in the recovery afterwards. So I've always been drawn to the large-scale or macro questions.

I got to graduate school in 1980, which was a time when there was a lot of interest in paleontology in macroevolution and mass extinctions – that's what everyone was talking about at the time.

UD: Was there a particular scientist whom you followed or who became a model scientist for you?

DE: Well my advisor, Jim Valentine, at UC Santa Barbara – the reason I went to Santa Barbara was to work with Jim. And he had been interested in those questions for a long time.

UD: Was there any long-range influence of Stephen J. Gould?

DE: Certainly there is. We all read Steve Gould when I was an undergrad and I met him in my senior year, but I also knew that my grades weren't good enough to get into Harvard.

Steve was a lousy advisor, actually, so I wouldn't have been – most of the students who went to Harvard I don't think were well-served by Steve. He wasn't a very good mentor. But certainly a lot of Steve's writing had an impact on what people thought about.

UD: If I understood correctly, you are critical of certain claims of Neo-Darwinism, for example uniformitarianism and adaptive radiation through environmental pulls that allegedly cause biological inventions. Paleontologists have always been critical of Neo-Darwinism but some have rejected evolution altogether, right? In your case it is different and I am curious to find out what caused you to become critical.

DE: It's not that I think that there is necessarily anything wrong with Neo-Darwinism in particular types of questions, it's just that I view the evolutionary process as being broader, as a lot paleontologists do. That there are patterns that you see in the fossil record that don't seem to be explicable by processes of the traditional Neo-Darwinism of the 1960s and 1970s. I'm not quite sure how I got interested in the question of how the evolutionary process had itself evolved, but at some point, 10 or 15 years ago, I realized that there was this implicit assumption within Neo-Darwinism that mechanisms generating variation were essentially fixed over time. That was an assumption that they had to make in the 1940s, the 30s really, to combat orthogenesis and a lot of other anti-Darwinian views that had developed from the late 19th century before the Modern Synthesis. So I don't fault Simpson and Mayr and Wright because in a sense that was an assumption that they had to make. And I don't think that most of them realized that they were making this assumption about Neo-Darwinism – that evolution was a uniformitarian process. But to a geologist, there was this assumption that the evolutionary mechanisms had not themselves changed over time. And interestingly enough, in Steve Gould's book, *Structure of Evolutionary Theory* in 2002, there were three places where he sort of "dances up" to almost asking that question, but then doesn't go farther.

John Maynard Smith and Eörs Szathmáry in the 1995 *Major Transitions* book do explicitly raise the question because the idea of major transitions with different levels of selection is inherently non-uniformitarian. And Maynard Smith recognized that. He has got a paragraph on that but it doesn't do anything about it. So he never seems to have thought further about that. But I think that my interest in these questions comes out of the fact that I have always loved history; I read a lot of history and archeology just for fun. Coupled with my training as a paleontologist this has tended to give me a more historical perspective on evolution that I think is perhaps true of people in biology. And Eric [Davidson] also had a really deep love of history – an incredible knowledge of history.

UD: Yes, he did.

Developmental mechanisms in evolution and Eric Davidson

UD: That brings me to my next question. How did you become interested in developmental mechanisms, especially related to gene regulatory networks, in evolution?

DE: Ah - that was the topic of my senior thesis in college! So when I was a junior, I discovered a paper that Jim Valentine had written with his then-wife, Cathy Campbell, which took Eric's 1971 and 1973 papers and asked what their implications for macroevolution were. It was a paper that they published in 1977 in *American Scientist*. It came out about the time I was an undergraduate and I was fascinated by it. The thought that you could link understanding the processes that we see in the fossil record to the gene regulatory networks, sort of captured my imagination and that's why I wanted to work with Jim at Santa Barbara. And my senior thesis was actually on the evolutionary implications of reverse transcriptase. This was in the late 1970s before HIV was discovered or recognized to be a retrovirus. So by 1981 I had probably read about 80% of all the papers that had been written on reverse transcriptase – because there weren't that many.

UD: They were discovered in the 1970s, right?

DE: Well, they were predicted in 1968 and discovered in '72 and then Temin and Baltimore got the Nobel Prize for it in 1975. So there wasn't a huge literature. There was feline leukemia virus and there were a bunch of other retroviruses known, but it was really easy even for a stupid college kid to read this stuff! And so my senior thesis – which was awful – was on how retroviruses, or what we now call retrotransposons, could modify gene regulatory networks and how that might influence evolution.

So I read Eric's work. But the problem was, when I got to graduate school, to figure out how as a paleontologist to do a thesis that was actually science instead of just arm-waving. I kept my interest in that and I took an advanced seminar in gene regulatory networks that was given in biology at Santa Barbara. But I couldn't figure out how to get any traction scientifically with it.

UD: And later on did you contact Eric or did Eric contact you? Much later, of course.

DE: Yes, much later.

In 1997 or '98 I knew Kevin Peterson, who was originally trained as a paleontologist. He's now at Dartmouth, but he was a grad student at that point at UCLA with Charles Marshall and then was doing a post-doc with Eric. And Eric was coming back to Washington [D.C.] and wanted to see the Burgess Shale. And Kevin said, "Oh, I have a friend who is the curator of the Burgess Shale. I'll email you and you can go over and see it." And so Eric, Mike [Levine] and Ellen [Rothenberg]– we got in contact and they came over. They were going to see the head of NASA to convince him to put more money into developmental biology.

But they wanted to see the Burgess Shale so they came over and I showed them through it. And Eric was somewhat flummoxed to discover a paleontologist who actually had read his papers. And I had been reading his work ever since I was in graduate school, and he was sort of surprised by this. And when he discovered that I was from Los Angeles, he said, “the next time you’re visiting your parents, why don’t you come to Caltech?” And so I went over for an afternoon and then I stayed for three or four days. And then one thing led to another.

I should also say that before I met Eric a lot of paleontologists were very interested in the Evo-Devo revolution. So in the late 1990s, just before I met Eric, there was one of the early Evo-Devo meetings that Rudy Raff organized in Indiana and there were four paleontologists there – Steve Gould, who was giving the plenary address in the best Gould fashion, Jim Valentine, me and Dave Jablonski. And Jim and David and I wrote a couple of papers trying to interpret events of the Cambrian Radiation in light of this new information from developmental biology. So we published a paper in *American Scientist*, and one in *Developmental Biology*. Namely, three papers about that time. But none of us were developmental biologists and it was clear that there was a limit to what extent we actually understood the experimental data or understood what experimental data was useful for and what we should ignore. So when I met Eric, it was clear that by collaborating with him I could get farther than I could with Jim and Dave.

UD: On a philosophical level, Eric tried to put forward the idea of a mechanistic evolutionary biology. Do you know if there was any research going on along these lines before him? And, do you think it will be possible to find out the mechanisms of macroevolution based on the genome in a clear-cut way in the future?

DE: Well, the answer to the second question is yes. There are a number of people pursuing this. There are a number of vertebrate paleontologists – Neil Shubin who is interested in early vertebrates. And he knows Sean Carroll and Cliff Tabin very well. They have known each other for 20 years or something. And they had been very interested in looking at the origin of vertebrate limbs, and that’s a system that developmental biologists know very well, so it’s an easy way to combine paleontology and a mechanistic understanding of vertebrate development. And there are other people, there’s a young guy who just got his PhD between Eric and David Bottjer who is interested in these problems with echinoderms [Jeff Thompson]. And certainly there is a lot of information in arthropods. I don’t think it’s been utilized well to understand early arthropod evolution; I think that’s another possibility. I think there are other people that are beginning to do this, and hopefully they'll do it a lot better than I can now that Eric is gone.

UD: I was wondering why it is, if I understand correctly, that most evolutionary biologists are Neo-Darwinists. For instance, Carroll writes about developmental gene regulatory networks and their possible relationships with evolution but he also thinks that small mutations are enough to bring about major changes.

DE: The reason that most people of my generation still feel that way is that their initial training in evolutionary biology comes from population genetics. I took population genetics too, it's just that by the time I took it I was in graduate school and that's where my best grade in graduate school came from. But I was already suspicious of the extent to which it could be applied by the time I took it. But it's just like geologists who are trained before the revolution of plate tectonics that happened in the early 1970s. Most of them have never been able to quite wrap their head around the shifting plates and mountain building and things like that because their training came in an era where they didn't know how to make mountains and they didn't have plates moving around and things like that. And so I think their initial training, for most people, tends to have a big influence on their thought processes. And still, most evolutionary biologists have their initial training in population genetics; it is a theoretical core of evolutionary theory.

I don't think Eric ever actually took an evolutionary biology course. We always discussed his suspicion of population genetics. But the training that developmental biologists get has been, until recently, very distinct from the training that evolutionary biologists got. And Eric never was trained or never adopted a lot of the conceptual baggage that comes with training in evolutionary biology.

UD: I think one of the reasons Eric had a problem with population genetics was that it was predominantly applied to bacteria. Or to single-gene phenotypes. And from the beginning Eric dealt with the complex phenotypes and complex organisms.

DE: There are also a lot of people that work not just with yeast but also with flies and with Arabidopsis and things like that. So there are non-microbial systems. But Hopi Hoekstra's [at Harvard] work on coat color in rodents also is at the distal part of a gene regulatory network and the genetics of it is relatively simple.

I think one of the things that evolutionary biologists have not been able to understand is that Eric had a fundamentally hierarchical view of how the genome operated in development and if they are looking largely at the distal ends of those networks they're not going to see the complexity that he saw or that most developmentalists saw.

Methodology and epistemology

UD: Jumping forward to availability of big data, genomic sequencing data: They were also very important for Eric's systems research. On the other hand, big data has given rise to claims which he fundamentally opposed. People would question the value of man-made hypotheses and experimental testing, focusing instead on mathematical and statistical description. I would like to know which role do hypotheses, explanation and causality play in your work?

DE: I think it's essential. In paleontology big data tends to be trying to put all the described fossils in a computer so you know how many fossils of this type were found in those hills versus some other hills.

UD: Which data from these fossils do you put in?

DE: It is basically, found this fossil in these kinds of rocks at this locality.

UD: So you don't measure the fossils.

DE: Sometimes there are links to photographs but it's mostly a description of the fossils, locality, and kind of sediments. The big data in biology is much more about genomics and proteomics and metabolomics and every other sort of "omics", transcriptomics, and I guess ultimately I see it as a useful set of tools, but I don't yet see that it is necessarily going to eliminate the need to understand what the mechanisms are. I don't see how that kind of data is actually going to produce the kind of understanding of evolutionary mechanisms that we're looking for. For one thing, most of the people who are doing that work are doing it on taxa that are not the ideal ones for evolutionary studies. If you think about most model systems, they're very useful from the laboratory experimental point of view and they are absolutely the worst thing you could ever use if you are interested in evolution. No evolutionary biologist in the world would have picked C. elegans or birds or Drosophila -

UD: - or human beings.

DE: Humans are sort of highly encephalized apes. But from an evolutionary standpoint there are a whole lot of taxa that are going to do much more revealing about the evolutionary process than most of the model systems are. It's happening, I mean the development of CRISPR-Cas-9 is going to allow a lot of techniques to be extended much farther beyond model systems. My most recent graduate student Sarah Tweedt just finished in December [2016] and is now working with Gunter Wagner at Yale. Her undergraduate training was in developmental biology and her PhD was from the biology group at Maryland but through me, so it's in paleontology/macroevolution sort of stuff. But her postdoc is going to be going back and looking at single-cell transcriptomics of sponges with Gunter. So she has the advantage of training in both fields, paleontology and more mechanistic studies. And I think she's only one of a new generation of people that are coming from a different conceptual framework that can make use of a lot of these new tools. But I think it's still going to be hypothesis driven and they are still trying to understand the mechanisms of evolution. I don't see the argument that people have made that if you get enough data then somehow, magically, the answer will just come out.

UD: Yes, mathematically in a formula.

DE: There's a wonderful book, I don't know if you know it. I've just been reading it. It's called, *Probably Approximately Correct*, by Leslie Valiant.

I was at the Institute for Advanced Studies in Princeton, NJ in October with two colleagues from the Santa Fe Institute – Walter Fontana who is now at Harvard, and Eric Smith. They were both talking about this book. And one of the points the author makes is that there are theoryful and theoryless disciplines. So theoryful disciplines are ones that can be easily mathematized – physics being the primary example. Theoryless disciplines are ones for which a robust quantification of the discipline is much more difficult and possibly impossible. So different approaches have to be used. And evolutionary biology, which he discusses in this book – he's primarily a computer scientist actually - evolutionary biology is a wonderful example of a theoryless discipline and a systems biology approach is still likely to fail unless an underlying theory is developed. And I'm not sure whether a formal theory of evolution can be worked out, because it is a historical discipline.

UD: But once evolutionary biology has become a mechanistic science you might be able to do that.

DE: I think you'll be able to get a lot closer to it. The question is whether the mechanisms change or have enough variation in their outcome that

UD: Evolutionary biologists don't seem to look for mechanisms apart from small mutations and selection.

DE: Maybe it's a lot harder. It's a lot easier to find a correlation than to understand the causality. Part of the reason that I think that Eric and I were compatible is that one of the big problems in paleontology is that paleontology used to be built on correlations for 180 years. That happens at this time, so this caused that. Well, often it turns out that if you do a lot of hard work you can actually figure out, or you can constrain the probability or likelihood that not only are A and B correlated but that there's actually a causal connection between them. Sometimes you find out with high-resolution studies that they're not actually correlated. They're correlated because of coarse graining of the timescale. But with a finer timescale you realize that the two events were not actually lined up. So there are ways of getting those questions. But because of my frustrations with that problem in paleontology, I think Eric and I hit it off better than might have been true with other paleontologists.

UD: So paleontology is one of the fields in which science has been based on correlations long before the advent of big data, and your and Eric's works seem to be a new and promising approach to overcome the limitations of correlations.

Another question – you wrote that you are creating "mathematical models of biotic recovery after mass extinction and test them against fossil data." Is that correct?

DE: I was. We may start doing that again next year; I sort of went off in other directions. One of the things that we were trying to do with understanding what is happening during the Early Triassic, and, in a sense, to Cambrian as well, is to figure out whether it is possible to build robust models that will -

UD: Mathematical models?

DE: Mathematical models that will explain, or help us understand, the process of recovering after mass extinctions.

UD: What are you modeling exactly?

DE: This is completely different from the work with Eric. The main thing we're trying to understand is how you build new niches. That is the process of construction of a new niche. There is a lot of work on what is called niche construction or ecosystem engineering in modern ecology. But it looks at it in a different framework from an evolutionary one.

So I did some work with Ricard Solé, who is a physicist who is very interested in biological problems. He's in Barcelona. We published a couple of "toy models" out of the recovery process, but I need to collaborate with somebody who has the mathematical skills as well as at least biological insight to develop more sophisticated models. I did one paper with David Krakauer from SFI [Santa Fe Institute] in 2009. David is a pretty big theoretical biologist but he needed to recruit another friend of his who is actually a real mathematician to do some of it. But David and I are hoping to get a post-doc next summer who will be able to spend about two years trying to understand how the niche space opens up after these extinctions.

UD: On which data do you base these models?

DE: The models are primarily based on existing ecological models.

UD: So what are you measuring? I wonder how the mathematics comes in there.

DE: The way this works is that we're trying to develop a suite of models and then test those with data from the fossil record, so that the data from the fossil record doesn't go into building the model.

UD: Because that would be tautological.

DE: Yes, but we are hoping to test the models against the data we have in the fossil record. The interesting problem is that there are a couple of potential outcomes and one is that the data we have now from the fossil record may not have been collected in the right way to actually test the models yet. So the models may inform paleontologists of how we have to gather data in order to evaluate different models of the recovery process.

UD: How can you measure a niche? What are you measuring – the spaces, the temperatures?

DE: Essentially, a suite of environmental parameters, which can be both physical (such as temperature, substrate dependence, salinity tolerance) and biological (dimensions that are generated by organisms in the environment). What we're coming up against is a longstanding assumption that niches exist independently, so if you make the chess board with each of the different squares being a niche, there are people, and have been since the 1960s and 70s, who think that these niches exist independently of the organism that occupies them. And then they have a lot of empty niches. So a mass extinction is wiping the pieces off of the chess board. And then the recovery is just reoccupying.

To me, that's nonsense. Because what happens is that the chessboard collapses. And the question is how does it get rebuilt? And we think there are models that exist in ecology that we can use to develop – such ecological models through time in which these niches would open up and one niche might facilitate other niches for other organisms.

UD: Organisms create the future?

DE: Right. It turns out, oddly enough, which I didn't realize until a paper two years ago from Marcus Feldman's group that this is actually very similar to problems in cultural evolution. So there is a really interesting paper that Nicole Creanza from Mark Feldman's group at Stanford wrote in *PNAS* a couple of years ago which describes a model that's sort of like what we're looking for, but the question they were asking was about cultural innovation, not about niche construction. But because of the similarities in the model which she developed, we may perhaps use it. So they were basically asking how new technologies, novel technologies, were developed in cultural evolution, the Neolithic revolution. That sort of thing.

It's a mathematical model based on some assumptions about cultural evolution. They tested different assumptions. There were some similarities between that modeling process and what we want to do. We still have a lot to work out.

UD: Maybe it will turn out not to be so similar?

DE: It's possible, yes.

History and Philosophy of paleontology

DE: And as you know I've gotten a lot more interested in the philosophy of science, but it's only been in the last five years that I've had the luxury of being able to devote myself in that. So there have been a couple of small projects that I'm working on. Trying to figure out whether there is something that I contribute in history and philosophy of evolution.

Dave Sepkoski and I actually had a couple of conversations about the philosophy of paleontology because there's a study by Derek Turner, who had a book on philosophy of paleontology (Paleontology: A Philosophical Introduction, 2011). Another interesting topic is the information content of fossils.

UD: But there is no data there.

DE: But the fossils themselves have information. For much of the last 30 years of paleontology has had an enormous amount of emphasis on what is called "taphonomy", which is the study of how organisms decay and are preserved as fossils. What information is preserved, what kind of information is lost, and how you can get information out of the fossils. I think if you look through that taphonomic process you get back to the biological data. Paleontologists actually spend an enormous amount of time on how to deal with the information content of the fossil record in a practical way. But philosophers of science have completely missed that, probably because the philosophers of science that are interested in paleontology are almost entirely interested in macroevolution.

UD: Or in Stephen J Gould.

DE: Anybody who is interested – if Steve didn't write about it, it's not interesting. But there are actually a lot of paleontologists, some of them of incredible significance like Dave Raup [formerly of University of Chicago] whom philosophers of science have never thought about. There are many more interesting philosophical questions in paleontology than those that Steve worked on. Some people feel like they have to defend Gould against any criticism.

There's a recent paper by Doug Futuyma. He's a microevolutionist and it's his response to macroevolution. One of the points he makes, and I think it is really important, and that is that critics of Neo-Darwinism forget about the setting of the 1930s and 1940s. That is that in order to establish the Modern Synthesis biologists had to fight the orthogenesis of Osborne and all sorts of other nutty ideas.

UD: I thank you very much for all this valuable information and your views.