An Interview with Philip C. J. Donoghue
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Q1: Could you tell us a bit about your journey into biology? What inspired you to specialize in paleontology and evolutionary biology?

R1: I guess that I should tell some tale about being a boy-naturalist or fossil collector, but I can't. I was raised in a steel town in South Wales that wasn't entirely compatible with an Enid Blyton style story of childhood. My love for palaeontology and evolutionary history developed much later, via geological history which captured my interest quite late in my schooling. I studied geology at the University of Leicester and I was seduced into palaeontology by two inspirational lecturers, David Siveter and Richard (Dick) Aldridge, who revealed to me the microscopic world of palaeontology – fossils of microorganisms like ostracodes, foraminifers, pollen and spores. I am sure that members of SESBE are very familiar with these groups, but I had no knowledge of them because of my ignorance of biology and, well, you need a microscope to see them! I was also excited by the (very simple) laboratory work that was required to recover these fossils, which made it feel more 'sciencey' to me than did the rest of palaeontology. I thoroughly enjoyed a Masters in palynology at the University of Sheffield, researching Silurian spores and acritarchs with Ken Dorning who was immensely generous with his time, before returning to a PhD at Leicester with Dick Aldridge and Mark Purnell on the palaeobiology of conodonts. Conodonts are an extinct group known almost exclusively from their tiny teeth which occur almost boundlessly in rocks of Cambrian to Triassic age. I quickly became embroiled in debate as to whether or not conodonts were vertebrates (spoiler: they are) and, as such, whether their teeth were the first manifestation of a mineralized skeleton in the vertebrate lineage (spoiler: they are). It was amazing. I was embedded in a community of researchers who fought like dogs over the interpretation of every shred of evidence that we could seek out of the conodont fossil record, applying any and every technique possible. Despite abandoning biology before high school, I had to wrap my head around vertebrate skeletal development, tissue and cell homology read from classical comparative histology, embryology and molecular expression. It was the opposite experience to many PhDs in that I was forced to embrace broader, not narrower research communities, and understand more diverse universes of data and methods. Somehow, this eventually segued through to two–year sabbatical working in Rob Kelsh's zebrafish lab, trying hopelessly to clone genes implicated in skeletal development from lampreys. This was an enormously enriching experience, diving back into a lab, with PhDs and undergraduate rotation students patiently trying to induct me in the dark arts of molecular developmental biology. I learned that my future did not lie at the bench, but I also learned a huge amount about comparative developmental biology and developmental genetics which, combined with phylogenetics and the fossil record, could be a powerful suite of data and methods for inferring evolutionary history.

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Q2: Can you share the main focus of your current research and some of the key questions you're trying to answer?

R2: I have never been accused of focus! I like to use my research as an excuse to learn more about natural history, exploring new branches of the tree of life. Most of my research has focused on early vertebrates and early animal evolution, but I have delved into early land plant evolution to provide myself with some perspective on the origin of animal body plans. At the moment, I'm trying to better understand the nature of ancestral land plants, from phenotypic and genomic perspectives. We've also tried to take a similar approach to understanding early microbial evolution, reconstructing the genome of the Last Universal Common Ancestor to infer its metabolism and, ultimately, its impact on the early Earth system. There is enormous scope for research in this area, made possible through the enormous numbers of microbial genomes that have been sequenced, but also as a consequence of the development of new methods for analysing these data. All of these strands of research involve entwining evidence from living and fossil organisms, but the challenge is often in calibrating the biological and geological evidence to the same timescale. I am therefore still very interested in the methods for establishing evolutionary timescales, using as much palaeontological and geological evidence as possible to constraining molecular timescales. I am fascinated by the heated debate that emerges from this work, with some molecular biologists complaining that our work does not allow the molecular evidence to speak for itself, and some palaeontologists arguing against any timescale other than a phylogeny stretched to the fossil record. Stuck in the middle, perhaps we've got it just about right.

Q3: How has the integration of molecular biology with paleontology changed the way we understand Earth history?

R3: It may be true that living diversity is a tiny fraction of historical diversity, but little of that historical diversity is recorded anywhere except in the genomes of living species. Palaeontology, uniquely, provides the means of calibrating molecular evolution to geological time, facilitating tests of hypotheses on the coevolution of, or competition between, evolutionary lineages in geological history. Palaeontology also allows us to understand how the evolution of the Earth system has affected biological evolution, such as through climate change induced mass extinction, and vice versa, such as the role of cyanobacteria in the oxidation of the atmosphere. The fossil record also provides direct insights into the anatomy of evolutionary intermediates of living lineages, constraining hypotheses of developmental evolution, such as in the assembly of the vertebrate head, the origin of tetrapod limbs and the mammalian middle ear. The data and methods of molecular biology and palaeontology are a winning combination that provide for an holistic understanding of evolutionary history.

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Q4: You've worked extensively on major evolutionary transitions. Which transition do you find the most compelling, and why?

R4: I am currently obsessed by eukaryogenesis – the evolutionary episode in which the two great scions of the tree of life, archaea and bacteria, were reunited in the assembly of a eukaryotic cell, the foundation of complex life on Earth. I am fascinated by the rich diversity of hypotheses that seek to explain the origin of eukaryotes through partnership between two or three or many more symbiotic microbial partnerships, as well as the complex mechanisms by which the many features of ancestral eukaryotic cell are envisaged to have evolved. I am also intrigued that different experts follow different definitions of what constitutes an eukaryote and so, effectively, their disagreements rest (at least in part) with the fact that they are trying to explain the evolutionary origin of different phenomena. So many of the competing hypotheses are rooted in arguments of plausibility, rather than phylogenetically-constrained evidence. This is such a rich and diverse problem that needs diverse perspectives if material progress is to be made and I am sure that in addition to molecular biology and phylogenomics, palaeontologists, philosophers and, I dare say, psychiatrists and therapists are sorely needed.

Q5: What lessons can we get from the fossil record to understand the evolutionary process?

R5: I'm not sure that I am especially well qualified to pontificate on this question, but you did ask! I think that it is important to remember that the fossil record only provides us with evolutionary patterns;

the evolutionary processes that underpin those patterns can only be studied in living organisms. However, the fossil record provides us with a temporal perspective on the patterns that have emerged from those processes and this has often led to proposals of higher level selection and non-uniformitarian evolutionary processes. I cannot say that I have ever been attracted by such proposals. To be sure, there is more to evolution than population genetics; its dynamics act within the context of accessible variation and that is constrained by the environment, which is a variable, and the burden of contingencies in evolutionary history of a lineage, among other factors. The effects of population-levels processes range in frequency and scale, and laboratory and field studies may underestimate the role of infrequent large–scale effects. However, I don't see a justification or scientific programme in explaining patterns in the fossil record through anything other than the lens of processes that we can observe in living organisms. The challenge is to bridge the temporal scale between modern processes and historical patterns and I think that progress is being made here. This is being achieved through palaeogenomics, where the sampling of ancient genomes for some lineages, like dogs, is approaching the level where population level processes can be inferred on millennial timescales. Initiatives like the Phenotypic Evolution Time Series (PETS) Database, is also trying to bridge this divide, collating data on phenotypic change at fine temporal resolution in both living and fossil lineages. I would love to see these two approaches combined to provide an understanding of the phenotypic effects of population level processes on geologic timescales, providing a framework for decoding the evolutionary patterns written in the fossil record.

Q6: How do you see evolutionary developmental biology (evo-devo) influencing future evolutionary studies? Are there any recent breakthroughs in evo-devo that have surprised you or challenged established ideas about the History of Life?

R6: Evo-devo has evolved so much over the last 30 years. I remember Chris Lowe complaining to me, perhaps 20 years ago, that he could not get funding for descriptive work anymore. I thought he was referring to the description of staging series but he was referring to gene expression assays in non-model systems. I was shocked by how much the field had moved on, but glorified expression-based studies still seem to make it into fancy journals from time to time. Regardless, there can be no doubt that evo-devo, however it is manifest, will continue to be an important field of evolutionary biology. How else are we

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to understand the relationship between genomic and phenotypic evolution (and everything else in between) which, surely, is a core aim of evolutionary biology?

I can't say that I have been especially surprised by the outcomes of any recent evo-devo studies, but I do not mean this as a criticism. The shock and awe discoveries of conserved regulatory genes and dorso-ventral axis inversion between chordates and protostomes, and of whole genome duplications between invertebrates and vertebrates, were made in the 1980s and 1990s. I'm not sure that there is scope for anything that could quite so effectively knock us off our feet. These discoveries prompted new questions that technology is only now beginning to allow the field to answer with any material level of resolution. As a palaeontologist, I've enjoyed following the studies of single cell transcriptomics from sponges through to bilaterians, perhaps because there is so much latitude in how the results can be interpreted in informing animal evolution. The advent of chromosome level genome assemblies has been equally exciting since many of the reference points are currently so phylogenetically disparate that there remains a lot of room for speculation about their evolutionary implications. I think there is a lot of scope for tears of both sadness and joy as new data emerge, challenging hypotheses of evolution, old and new.

Q7: You are a very collaborative researcher. Could you speak about the importance of interdisciplinary collaboration and how it has influenced your work?"

R7: I am attracted by interdisciplinary research, drawing together as many of the relevant strands of evidence that I can, to understand a problem in all its dimensions. Inevitably there is no practical way of doing this except through collaboration; if there was, it would be less fun. However, in my experience there are a number of challenges to interdisciplinary collaboration. Perhaps most fundamentally, it is important to understand the new discipline that you are engaging with, both in terms of its data and methods, so that you can discriminate and refine the questions that you want to ask of it. Differences in culture and semantics can also present challenges, especially when some of the terms are shared but they have different meanings. It is also important to recognize that other researchers have different priorities, interests and ambitions, and so they are not necessarily ready to stop what they are doing and focus on yours instead. So interdisciplinary collaborations can take time, discovering what is possible, how to communicate effectively and, above all, in finding the right collaborator whose research interests align with your own. But it can be enormously rewarding, both personally and professionally, and it can sometimes be impactful. I have especially enjoyed our recent work, with Earth system modellers, geochemists and philosophers, reconstructing ancestral metabolisms and exploring their impact on the early Earth system. The collaboration was confronted by all of the challenges that I have described, but we recognized these from the outset and found ways in which we could learn to speak a common language, align to the same research questions and establish an integrated interdisciplinary experimental protocol that allowed us to answer those questions. It was also a lot of fun!

Q8: Your research incorporates state-of-the-art techniques, such as synchrotron scanning. With technological advances accelerating, where do you see paleobiology heading in the next decade?

R8: That's an unfair question to ask a palaeontologist! We spend all our time thinking about the past. It's almost rude to ask us about the future. Palaeontology has certainly evolved as a discipline. Driven by the search for hydrocarbon reserves, a lot of effort was invested in documenting the stratigraphic distribution of fossil species and evolutionary studies have exploited those data. However, palaeontology has become increasingly analytical since the 1960s, with diminishing effort expended in field palaeontology, discovering new fossil data. Indeed, many palaeontologists decry the lack of funding and effort to expand our knowledge of the palaeontological record. In some senses, this is right and proper. Surely, we do not need to sample the entirety of the fossil record in order to establish and test hypotheses on the history of biodiversity. If we did, there would be no new data to collect so that we could test hypotheses. However, analyses of our existing sample of the fossil record have revealed that is extremely biased, especially in terms of spatial sampling, with the majority of collecting from Europe and North America. This is obvious to even a casual reader of *Nature* and *Science*, the pages of which have been filled with the discoveries in China of early animals, algae, flowering plants, fishes, amphibians, mammals and, of course, flocks of feathered dinosaurs, all of which have contributed to a reshaping of our understanding of organismal evolution in one way or another. China is special in very many ways, but surely these fossil discoveries have been so impactful because they have been made so late in our sampling of the fossil record. The retreat of Arctic and Antarctic icesheets will be equally impactful, exposing previously poorly sampled geographic regions, though it will doubtless be associated with the collapse of civilization, of which palaeontology is an essential pillar.

So I think that the future of palaeontology will be much as its past: a combination of new data and new methods for analysing old data. However, I think that palaeontology has to more than the study of the fossil record. It should be a discipline based on a set of core questions that transcend data and methods. Surely, palaeogenomics and, for that matter, comparative genomics and comparative developmental biology, naturally belong within the realm of palaeontology since they are all trying to infer the nature of ancient life. Similarly, sedimentary geochemistry, as a geological record of the metabolisms, speaks to the aims of palaeontology. So I think that palaeontology will become much more interdisciplinary in its outlook. But I would say that, wouldn't I?

Q9: How do you think new fossil discoveries might reshape our understanding of the early history of life? Are there any discoveries on your radar that could be transformative?

R9: There are surprisingly few people working on the Archaean (4000-2500 Ma) and Proterozoic (2500-538.8 Ma) fossil record and so there is a lot of potential for fundamental new discoveries. Even well-known and long-studied sites of exceptional fossil preservation, like the Gunflint Chert of Ontario and Minnesota (~1880 Ma) and Bitter Springs Formation of central Australia (~833 Ma) are overdue restudy using modern methods, like synchrotron radiation-based X-Ray tomography. My own exploratory examination of these deposits hint at a much greater diversity and disparity of organisms than has been described. However, the real challenge may be in establishing a framework for interpreting these microbial fossil remains. Living microbes, in all their biomolecular glory, can be difficult enough to classify without molecular phylogenetics, but their fossil remains are often limited to a resting cyst or, if you're lucky, a cell wall. It would be really helpful if we had an understanding of what happens to such cells as they pass through the processes of death, decay and the different modes of fossilization, so that we can constrain interpretations of whether features are absent because they were never present rather than because they have not been preserved. These sorts of questions can be answered through the sometimes grue-

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some field of experimental taphonomy, in which the patterns (and sometimes the processes) of death, decay and fossilization are studied under experimental conditions. We recently studied eukaryote organelles in this way, finding that chloroplasts and nuclei remain as substrates for fossilization months after cell death, providing support for claims of preserved organelles in Proterozoic fossils. This could be significant in discriminating between evolutionary grades of fossil eukaryotes, providing insight into the timescale of eukaryogenesis. Other research groups are applying new technologies to characterize the chemistry of Proterozoic fossil remains, finding signatures of chitin and chlorophyll, confirming the fungal and cyanobacterial affinity of otherwise problematic fossils. There is surely huge potential in extending these approaches to the microbial fossil record which would be transformative in calibrating molecular phylogenies to geological time.

Q10: What are the biggest challenges facing evolutionary biology today?

R10: I don't think I have anything useful to say in response to this.

Q11: What advice would you give to young researchers aspiring to enter the field of paleobiology or evolutionary biology?

R11: Personally, I think it is important that while you inevitably specialise, you maintain a broad knowledge of research discoveries in evolutionary biology. We're all time-poor and so there is a temptation to only read papers or attend seminars that are directly relevant to your main research topic. But where do you expect the new ideas to come from that will allow you to transform your field, as you seek fame and fortune? In my experience, these ideas are most readily 'borrowed' from studies of other groups, using different data or methods, or from entirely different fields. I think it's also important to be entrepreneurial in your scientific outlook. Science has fashions and your study group or methods may not always be à la mode. What other study systems can you exploit your skillset to have impact? What methods can you borrow from other fields to provide new insights on your study system? If you want a long and fulfilling research career, I think it helps to keep evolving, just like the organisms that you are studying.