Palaeontologia Electronica
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RECLAIMING EVOLUTION FOR THE FOSSILS

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The recognition of how unimportant fossils are in evolutionary studies would come as a great surprise to the average person. In the popular mind, fossils equate to evolution: the very word conjures up dinosaurs and their extinction; or perhaps the string of fossil hominid fossils, a particularly elderly example of which has just been unearthed.

That is the **public** perception; but what of the professional one? There, I think it is fair to say, fossils have virtually no influence at all. Unconvinced? Here is an example, and a distinguished one at that: Mark Pagel, in the new **Encyclopedia of Evolution** of Oxford University Press (2002), wrote the entry on Evolution, and it does not feature the word "fossil" once. Neanderthals get a tiny look in, but towards the end of the article (Vol 1, p. 331) he concludes that **"Biological evolution, stripped to its bare essentials, is nothing more than the temporal changes in the genetic makeup of populations"**. "Fossils" **per se** do not even get an entry at all in the encyclopedia.

How fossils came to be manœuvred out of evolutionary studies – or perhaps more properly, why evolutionary studies moved in a non-fossil direction – is a matter for the historians of science. Perhaps it was Huxley's disappointment with **Archaeopteryx** in his schemes for deriving birds from dinosaurs; perhaps it was Haeckel's desire to be able to extract ancestry from ontogeny that led to fossils becoming obsolescent. Or perhaps (more likely) the 20th century new discipline of genetics led to a focus on quantitative methods in which fossils had no place. Either way, G. G. Simpson's contribution to the neodarwinian synthesis, although notable overall, really restricted fossils to a side-line: more tempo and less mode. But modern evolutionary studies are less interested in the history of events, and more in the (apparent) processes.

In reaction to this downgrading, palaeontologists – above all, Stephen J. Gould – have emphasized the aspects of the subject that might still yield mechanism, but mechanism above the population level – the grand topic of "macroevolution". Many of the big palaeobiological themes over the last thirty years or so have focused on just this area: punctuated equilibrium, coordinated stasis, mass extinction (two words are most catchy, it seems), clade selection, to name but a few. The implication (rarely even whispered, but there) is that fossils can tell us something about the mechanism of evolution that we can't learn from looking at living populations

Frankly, I think these attempts are misguided, if they are meant to make fossils "contribute" to evolutionary theory as a whole. For a start, and rightly or wrongly, they lead neontologists to regard palaeon-

Budd, Graham, 2002. RECLAIMING EVOLUTION FOR THE FOSSILS. **Palaeontologia Electronica,** vol. 5, issue 1, editorial 2: 3pp., 80KB; http://palaeo-electronica.org.

tologists with suspicion, almost as crackpots, as if they haven't yet fully grasped what Darwin (and others after him) worked out about How Evolution Works. Second, I suspect that, when it comes down to it, population processes are what evolution is all about. Even if there are really high-level "mechanisms" – such as mass extinctions, say, they do not seem to connect up with population processes. And here, I would like to say, with Wittgenstein: "a wheel that can be turned though nothing else moves with it, is not part of the mechanism". Why, then, bother being a palaeontologist? Well, accepting population processes are "what evolution is all about", this does not mean that the outcome of evolution is entirely governed by them, even if it is composed of them. Let us look at Darwin's concerns in the **Origin:** he was interested in the shape of horses, the perfection of the eye, the flightlessness of certain ducks. What is notable is his (then, inevitable) discussion of these interesting topics without any reference at all to genetics. Indeed, Darwin's own theory of heritability was, let us say, somewhat wide of the mark. In an ideal world, the added insights that genetics gave us would have been added to Darwin's concerns: instead, they replaced them. The reasons why this happened, I think, are clear: no-one knows what the relationship between the two is. Let me give an example: the origin of the limbs of tetrapods. One can tell a palaeontological story here, even a rigorous one based on phylogeny, about the sequence of events; and one can investigate the genes involved in patterning limbs, and even wonder about how they took place in a population setting (an interesting problem in itself). So, now we might end up with the relatively boring statement: Limbs evolved like this, and a large number of population-process driven genetic changes took place as well (I'm leaving out the "saltational" possibilities here as beside the point). And, for now, it seems, that is all we can say, and it is not very interesting. We cannot see the population processes going on that might have led to the tetrapod limb, nor is the fossil record anywhere nearly detailed enough to show it to us. Thus, the relationship between the two is based entirely on trust. To put it another way, we do not have a general theory of how – or better, which - population processes give rise to morphological evolution. Modern evolutionary biologists are only now really waking up to the problem that this presents them, although the basic difficulties have been known for 50 years. The truth is that no-one understands how genes relate to morphology. Or, perhaps Günter Wagner at Yale understands – but I don't understand him. The old rigid way of thinking "these genes imply this phenotype" – the view that leads to the thought that what actually happens in the phenotype is not very interesting – is crumbling. In its place is coming a recognition of the incredible subtleties of the genome – its networks of interactions, bufferings and sensitivities, all of which lead to an inevitably complex relationship with the phenotype that ultimately rests on it.

How can we examine this relationship – a real Missing Link in evolutionary studies, if ever there was one? There are three requirements at least. First, we need a much greater understanding of how the genome works – and palaeontology is not likely to contribute much to this end. Secondly, we need to understand how the phenotype (and for us, especially morphology) actually evolves: the ground rules that control it. Amazingly, even though Darwin and a few others have pondered this question, morphologists have not really thought about this problem – it is generally considered to be too particular to be able to have a general theory (with the exception of a few comments here and there about "exaptation" and "redundancy"). We need to make sense of our palaeontological data in this way, so that they can be presented to the genetic world in an ordered way. Finally, and here is the really difficult part – the causal link between ordering of the phenotype and ordering of the genotype needs examining, and this difficult conceptual and modelling work will give rise (one hopes) to a general theory of biological change. The "bare essentials" of gene frequency change in populations will then be seen to be an interesting but relatively small aspect of this more rich theory. Palaeontologists need to get their own house in order, to present and think about their data, not as a mass of details about tooth length and tusk curvature, but in the light of the modalities of change that will be revealed by mass-inspection of all the data out there. Only then will we really be invited back to the evolutionary table to eat, and not just brought on as the after-dinner entertainment.