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PALAEOANTHROPOLOGY AND EVOLUTIONARY BIOLOGY

ABSTRACT: Palaeoanthropology has frequently been out of step with the rest of evolutionary biology. It was, for instance, late to subscribe to the tenets of the "Evolutionary Synthesis" which emerged during the 1930s; and in more recent years it has shown considerable reluctance to confront the fact that the evolutionary process is a more complex and multidimensional one than the Synthesis allows for. The principal legacy of the Synthesis in palaeoanthropology is a linearity of thought in which evolution consists of little if any more than the gradual modification of lineages under the guiding hand of natural selection. Under this construct the unravelling of our evolutionary past is little more than a matter of pure discovery, as of links in a chain. Yet the fossil record demonstrates with increasing clarity that the history of hominids consists of much more than a singleminded progress from primitiveness to perfection. Instead, it consists of a bewildering array of forms which require accurate recognition, and whose relationships demand analysis. Only when we incorporate systematic diversity into our evolutionary thinking will we be able to appreciate the true dynamics of the palaeoanthropological record.

KEY WORDS: Palaeoanthropology – Evolutionary theory – History – Evolutionary synthesis – Punctuated equilibria

INTRODUCTION

Palaeoanthropology has always enjoyed (if that is the right word) a somewhat equivocal relationship with the rest of evolutionary biology. Born out of the study of human anatomy, a specialization with a history, outlook and concerns entirely distinct from those of the comparative anatomical and geological studies that gave rise to other areas of palaeontology, palaeoanthropology has tended to stand apart from the evolutionary biological mainstream. Over the long term this insularity has, with a single exception, proved to be particularly true in respect to developments in evolutionary theory. However, the exception has turned out to be an extraordinarily powerful one, which, despite the passage of a half-century, still reverberates in palaeoanthropology today.

The first three decades of the twentieth century, following the rediscovery of the principles of genetics in 1900, were a fairly chaotic period in the history of evolutionary biology. There were almost as many theories of the evolutionary process on offer as there were biologists, and few among them (biologists or theories) accorded natural selection any primacy (see review by Mayr 1982). It was thus remarkable enough that, in the space of rather few years during the century's fourth decade, there occurred an extraordinary theoretical convergence on the evolutionary process among geneticists, systematists, palaeontologists and others. More remarkable still, though, was that this new unifying concept should identify natural selection not just as a necessary, but almost as a sufficient, condition for evolution.

Perhaps it was sheerly through exhaustion that the diversified and opinionated practitioners of what would become known as evolutionary biology finally agreed to pool their expertises into what became known as the "Evolutionary Synthesis." Based on mathematical

frameworks largely developed by J. B. S. Haldane (e.g. 1924–32), Ronald Fisher (e.g. 1930) and Sewall Wright (e.g. 1931), the geneticist Theodosius Dobzhansky (e.g. 1937), the ornithologist Ernst Mayr (e.g. 1942), and the palaeontologist George Gaylord Simpson (e.g. 1944) led the way to an all-but-universal acceptance of the notion that virtually every evolutionary phenomenon can ultimately be ascribed to gradual generation-by-generation shifts in population gene frequencies, under the benign hand of natural selection. It should be pointed out that each one of the founding triumvirate of the Synthesis was acutely aware from data in his own field that the evolutionary process must actually be more complex than this linear formulation implies. All were, for example, concerned in different ways with the evident discontinuities in nature, and with the need to account for their establishment. Nonetheless, as the Synthesis became more widely accepted, it also became "hardened" into a simpler and more unyielding formulation: evolution consists of gene-frequency change in lineages, period.

THE SYNTHESIS AND PALAEOANTHROPOLOGY

True to their tradition as consumers rather than producers of evolutionary theory, palaeoanthropologists had been little more than bystanders while all this was going on. Indeed, in general they continued right through the pre-war period to show remarkably little interest in the theory, implicit or otherwise, that lay behind their analyses of the human fossil record. Yet, unavoidably, as that record inexorably enlarged, a huge theoretical deficit was accumulating in palaeoanthropology: a deficit that would eventually have to be filled. And, in the postwar years, what better to fill it than the Synthesis, which was sweeping all before it in other areas of evolutionary biology? Thus it was that, at around midcentury, the bastion of palaeoanthropology fell to the Synthesis – and to the Synthesis, what's more, in its "hardened" version, shorn of the subtleties that had laced its earlier manifestations (see discussion in Tattersall 1995).

But it was not simply the theoretical vacuum that had existed at palaeoanthropology's center that opened the floodgates to the Synthesis. The architects of the Synthesis – notably Dobhzhansky and Mayr, ironically the pair with least first-hand knowledge of the hominid fossil record – actively took upon themselves the task of reinterpreting that record. And such was the majesty of their reputations that it became almost *prima facie* evidence of an antievolutionary stance to disagree with them. Dobzhansky was the first to share his insights on human evolution with his palaeoanthropological colleagues. As early as 1944 he applied the principles of "population thinking" (whereby it is recognized that individuals of the same species resemble each other because they belong to the same population, not the other way round) to the human fossil record, and concluded that the Java and Peking Man fossils were no more different from each other than representatives of different modern races. So far so good; but Dobzhansky went further, to claim not just that "as far as known, no more than a single hominid species existed at any one time level" (1944: 261–262), but that there *could* only ever have been one human species at any one time. "All the phylogenetic transformations in Hominidae," Dobzhansky declared, "were always taking place within a single genetic system, a species consisting of geographically, but not reproductively, isolated races." (1944: 262). This refrain was eagerly taken up by others, particularly as "culture" and "ecology" were added to the mix. Culture, it was alleged (whatever it was), had so broadened the human "ecological niche" that two kinds of humans could simply not coexist (e.g. Brace 1964).

It is thus evident that as early as the mid-1940s Dobzhansky had come to believe that all human evolutionary developments since Java Man had taken place within the confines of the single species *Homo sapiens.* Clearly he had been influenced in this by the recent arrival in New York of Franz Weidenreich, acclaimed today by its adherents as the father of multiregional continuity in palaeoanthropological thought. And even though Weidenreich is on record as saying that, by this point in his career, he was just too old to change his ways of thinking (Bobb Schaeffer and Ernst Mayr, pers. comm.), it is clear that his view of human evolution as a single braided stream was congenial to the Synthesis.

Ernst Mayr did not go quite as far as Dobzhansky in lumping fossil hominids, but in 1950 he published an influential paper in which he argued that all known fossil hominids belonged in the same lineage, leading from *Homo transvaalensis* (the australopiths), through *Homo erectus*, to *Homo sapiens* (including the Neanderthals). This simple schema had the decided advantage of sweeping away a huge detritus of unnecessary names that had accumulated in the human fossil record; but at the same time, with impeccable authority, it established a view of linearity in human evolution that was to grip the field of palaeoanthropology for the next half-century. Between them, Dobzhansky and Mayr had provided both an intellectual framework and a fossil interpretation that sustained the view of human evolution as a long, singleminded slog from primitiveness to perfection.

PUNCTUATED EQUILIBRIA

Yet, even in the 1950s, neither the hominid fossil record, nor the records of other groups of vertebrates and invertebrates, truly sustained the notion that the evolutionary process is a simple matter of perfecting adaptation within lineages. Instead, in retrospect the message has always seemed to be one of diversity, of consistent evolutionary experimentation. The appropriate metaphor appears to be a branching bush, rather than a

ladder to be climbed. And the "hard" version of the Synthesis – the form in which it had been absorbed by palaeoanthropology – makes little provision for such phenomena. Of course, if evolution indeed consists of no more than modification of lineages under natural selection, then fossils are essentially links – intermediates – in a long, continuous chain. Which in turn makes it remarkable that the fossil record is so signally lacking in such intermediates. Even so august a figure as Charles Darwin himself had found it necessary to invoke the fossil record's notorious incompleteness to explain the absence of the expected intermediates in the rock record as it was known in the mid-nineteenth century. Since then, many millions more fossils have been found, and many thousands more fossiliferous sequences have been investigated; but the essential observation remains unchanged. Thus, well over a century down the line from Darwin, the time was becoming ripe to ask whether in fact the famous gaps in the fossil record, far from being deficiencies to be apologized for, might not actually be telling us something biological, after all.

This impolitic question was raised in 1972 by the invertebrate palaeontologists Niles Eldredge and Stephen Jay Gould, who proposed that, far from being a stately, generation-by-generation process, evolutionary change actually tends to occur in short-term episodes, usually linked to speciation. For reasons of genetic homeostasis, they argued, most of the history of any species will be marked by non-change, or "stasis." The fossil record would thus be expected to show evidence of "punctuated equilibria" rather than of "phyletic gradualism;" and indeed, that is what we increasingly find. Species in the fossil record tend to have relatively sudden origins (in speciation), varying lifespans as recognizable entities (histories), and deaths (by extinction), much as individuals do; and, also like individuals, species may or may not give rise to offspring (successful or otherwise) during their histories. And even though some fine-tuning of the basic idea was needed – for example, it seems more plausible to me that significant novelties are incorporated into new species populations during the process of geographic diversification, rather than in conjunction with speciation itself (Tattersall 1994) – new analyses of both invertebrate and vertebrate fossil records have tended to bear the basic pattern out.

Predictably, there was much initial opposition to Eldredge and Gould's idea ("evolution by jerks" as one unkind critic called it) among evolutionary biologists of all stripes. Punctuated equilibria was attacked as being antievolutionary (which clearly it is not), or at least as being contrary to notions of natural selection (which it is not either; natural selection is clearly incorporated into its theoretical underpinnings). But knee-jerk reactions to the unfamiliar are standard fare in science, as in other areas of human experience, and to be expected. Equally predictable, though, was that, outside palaeoanthropology, evolutionary biologists would not take long to recognize that punctuated equilibria is complementary, rather than antagonistic, to the dictates of the Synthesis. Particularly, most evolutionary biologists have come quite readily to appreciate the special role that punctuated equilibria permits entire populations and species to play in the evolutionary process, and to accept the value and significance of Gould and Eldredge's (1993: 224) observation that: "Most macroevolution must be rendered by asking what kinds of species within a clade did better than others (speciated more frequently, survived longer) or what biases in direction of speciation prevailed within a clade."

In palaeoanthropology, however, the picture has been very different. Slow to absorb the principles of the Synthesis, the science of human origins has been equally slow to abandon them, or even to augment them with the insights into the complexities and patterns of the evolutionary process that have been brought by punctuated equilibria. Once again, palaeoanthropology has declared itself independent from the regularities of nature as expressed in the evolution of non-hominid organisms. At one level this could, of course, be seen as no more than a reversion to palaeoanthropological habit: simply the pursuit of business as usual. But at a more basic level it reveals, I think, an ingrained conviction that human beings – and thus also our ancestors, our lineage – are somehow, and intrinsically, *different* from other organisms. Our species *Homo sapiens* is the lone hominid on Earth today, and we naturally tend to believe that this is the "normal" state of affairs. Put another way, if there is at present only one hominid species in the world, then, somehow, this must always have been the case. Yet time and again it has proven inappropriate to extrapolate *Homo sapiens* into the past as a "living model" of its ancestors. And while Palaeolithic archaeologists have absorbed this lesson to their great advantage, palaeoanthropologists have yet to do so. Clearly, something extraordinary happened with the birth of behaviourally modern *Homo sapiens* (Tattersall 1998); but it is precisely because of the emergent and unpredictable nature of this event that we cannot use our remarkable selves as the key to our own past. *Homo sapiens* is not simply an extrapolation of what went before, whatever the giants of the Synthesis may have told us.

Yet, even though the sheer size and exuberance of the human fossil record by now makes it no longer possible to squeeze the known diversity of extinct hominids into a single linear sequence, the mindset lingers. There is still today a strong tendency in palaeoanthropology to minimize the number of species we acknowledge, as if by doing this one might genuflect to the Synthesis and approximate a linear sequence as closely as possible. As long as we can squeeze a mind-boggling array of fossils into "archaic *Homo sapiens,*" for example, we can cling to the notion that our living species emerged from the gloom by a process of perfecting adaptation, while still acknowledging at some level that the early forms in question were not exactly ourselves. And we spare ourselves, of course, the onerous task of sorting out the variety of morphs involved, and the

relationships among them. Yet, if we look objectively at the hominid fossil record, it is impossible to avoid the message of evolutionary experimentation that it carries. The morphological variety in that record is enormous, and it has only been possible to ignore it by the device of ignoring morphology itself. In turn, this sophistry has been made possible by fundamentalist adherence to the tenets of the Synthesis; for, if all hominid fossils are links in a single chain that courses through time, then their place in the sequence of evolutionary events is most directly revealed by their age. In this way, dates in palaeoanthropology have largely replaced morphology as the keys to the significance of individual hominid fossils.

This, then, is the legacy of the Synthesis in human evolutionary studies. In its day, this new perspective on the evolutionary process produced the same salutary effect on palaeoanthropology as it did in the study of evolutionary theory. For in both cases, it effected a much-needed clearing-out of outmoded ideas and outright mythology. From the new vantage point thus created, it should have been possible to build a new structure in palaeoanthropology based on a keener appreciation of the subtleties of the evolutionary process and on a rapidly expanding human fossil record. Alas, once the post-war euphoria of the new evolutionary perspective had worn off, the insularity of palaeoanthropology reasserted itself, and the hardening Synthesis took on the form of dogma. Only when we finally extricate ourselves from the dead hand of this dogma will we have a chance of coming to grips with, and experiencing the true excitement of, the marvellously expanding human fossil record.

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