

# The Case for Saltational Events in Human Evolution

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**Summary.** Evolutionary saltation is a rather ill-defined Victorian concept that may contrast in various ways with gradual (linear) evolution. In comparing evolutionary modes it is thus more productive to bear in mind the difference between ‘transformational’ and ‘taxic’ mindsets, each of which sharply influences the way in which the evolutionary record is interpreted. It is also important to recognise the fact that, even under traditional notions of natural selection, we cannot think of the evolutionary process as one of fine-tuning the myriad systems that make up each individual and each taxon. Both individuals and species thrive or fail reproductively as the sums of their parts, not as the bearers of multiple features that can somehow be tracked independently of each other over vast spans of time. In this review I look at the human morphological and behavioural records in an attempt to discern pattern in human evolution, and particularly in the emergence of our own species, *Homo sapiens*, as narrowly defined. *Homo sapiens* is a variable species, although not notably more so than *Homo neanderthalensis*, which can itself be understood only in the context of its membership in a diverse clade of endemic European species. The record clearly indicates that both modern human morphology and modern human cognitive processes appeared rather suddenly, even saltationally, although not at the same time.

## INTRODUCTION

I HAVE BEEN ASKED TO SPEAK at this Symposium about saltation and the evidence for it in the human evolutionary record. This I am happy to do; but I should point out straight away that this title is subject to quite extensive interpretation. Saltation is an essentially Victorian concept that, even if only implicitly, contrasts notions of slow, steady, intralinear change with competing patterns of

abrupt change among species. In other words, it pits the views of those such as Thomas Henry Huxley ('Nature does make jumps now and then') against those of Charles Darwin ('*Natura non facit saltum*') (Huxley, 1900). However, while the Darwinian notion of gradual evolution (accurate or otherwise) is a pretty clear-cut one, saltational change may in principle embrace not only short-term, within-lineage, innovations, wherein the acquisition of new features is more than simply incremental, but also processes of taxic diversification within clades. Notions of saltation, in other words, may invoke both linear, unidirectional, transformational change, and taxically divergent patterns of innovation: it is the scale and suddenness of such innovation that is at issue.

Given the fact that a century of debate has failed to produce an agreed-upon functional definition of saltation ('evolution by jerks' is perhaps as close as we have got so far), perhaps it would be better to adjust our terminology a little, and to recast the two principal models of evolutionary change currently on offer as transformational vs. taxic, as Niles Eldredge did 20 years ago (Eldredge, 1979; Tattersall, 1994). It is, after all, this division, above everything, that separates today's two major mindsets of evolutionary thought. Under the transformational model, we are obliged to look upon evolutionary change as a process of gradual, generation-by-generation, fine-tuning within lineages. The signal being sought is thus one of continuity in character evolution. The taxic approach, in contrast, looks for evidence of systematic diversification: a process of evolutionary experimentation that involves the generation of new species, each of which is free, subsequent to its origin, to compete with its close relatives (and with species of more remote taxic affiliation) in the ecological arena. In this latter view, evolutionary outcomes, hence larger patterns, are at least as much a product of ecological interactions as they are of processes of genetic innovation and winnowing within lineages.

The notion of fine-tuning of adaptations within lineages, and over the aeons, via the action of natural selection, has proven to be a highly seductive one, no less in palaeoanthropology than in other areas of palaeontology and systematics. Indeed, by the time that the grand 'Evolutionary Synthesis' had established its grip over evolutionary biology in the 1930s, it had become almost universally self-evident to evolutionary biologists that the action of natural selection (in the traditional, Darwinian, sense) was sufficient to explain virtually every evolutionary phenomenon. Evolution had become reduced to small, incremental, gene/gene frequency changes within lineages over long periods of time. However, while almost nobody would deny, even today, that natural selection must be a central process in the fixation of inherited novelties in local populations, a moment's reflection is sufficient to reveal that this cannot, even in principle, be the full story. When we speak of 'adaptation(s)' we rarely refer to entire organisms interacting within their environments. To most palaeoanthropologists, 'adaptations' are intellectually dissected-out

characteristics of individual organisms and species. The formula seems to be: structure = adaptation. If a structure is there, it must be adaptive, for natural selection is ever vigilant, is it not? (Tattersall, 1994).

Well, as a matter of fact, no. Think about it for a moment. What is natural selection? It is any and all factors that result in a differential genetic contribution to the next generation by one individual relative to its contemporaries. And, crucially, every individual must succeed or fail in the inheritance stakes as the sum of its parts. Particular aspects of the individual genome cannot be differentially passed along to the next generation in isolation from others. Those specific attributes that we can, with sufficient ingenuity, characterise as ‘adaptations,’ are strongly, sometimes indissolubly, linked with numerous others in each individual; and each individual, in turn, consists of a huge number of such attributes. Individuals (and the populations to which they belong, for that matter) must necessarily thus compete in the genetic stakes as functional wholes, rather than as agglomerations of separate ‘adaptations’ that can be favoured or otherwise by natural selection. Certainly, new genetic innovations must arise as particularities *within* individuals; but their triage by natural selection has to take place inside the context of those individuals’ overall reproductive success. Conversely, structures may survive and be passed along between generations not because they are notably advantageous, but simply because they do not significantly impede survival and reproduction. In a profound sense, then, we are mistaken to speak of such things as ‘the evolution of bipedality’ or the ‘evolution of the brain,’ as if these attributes were susceptible to independent tracking over time, separable from the larger packages of which they are part, or entirely free of random influences.

The upshot is that the history of the hominid family, like that of all other taxa, sums out not simply as the abstract aggregate of changes in a number of body systems that we may conveniently follow and examine independently of others. Rather, this history is one of the differential successes of hominid taxa that succeeded or failed as the totality of their parts. Heritable evolutionary innovations certainly arose inside those taxa, indeed within individuals, but in the long term larger evolutionary patterns have been determined by the overall success of those individuals, and of the taxa to which they belonged. It is thus critical that we be able to identify those taxa: essentially, species. And whether, at the current state of the palaeoanthropological art, we are in a position to do this is highly debatable. Clearly, this severely limits our options. Recently, for example, I attempted to characterise the pattern of hominid brain size evolution since the beginning of the Pleistocene (Tattersall, 1998a). On one level, of course, there is no problem. Clearly, if we compare average hominid brain sizes 2 million years ago with those of today, the trend is clear: today’s brains are much larger. But if we wish to inquire beyond this, to address in more detail the matter of pattern in hominid brain evolution (even at the superficially simple

level of asking whether brain size increase was gradual or episodic), the difficulties immediately mount. There are relatively few hominid fossils that are sufficiently well preserved to indicate reliable brain sizes. Even fewer can provide brain–body size relationships. And, among those fossils that can do this to a reasonable approximation, fewer still are dated with the precision which this exercise demands. Most importantly of all, however, we need to know the species to which the specimens involved belong; for, individually, brain sizes are notoriously variable, and if we are to extract useful information we have to understand what the average brain sizes and morphologies are for each species in our family tree.

And this points up a huge gap in our knowledge of hominid phylogeny. We have no agreed-upon idea at all of the species diversity represented in the large and still growing hominid fossil record. The tradition has, indeed, been to obscure pattern in that record by sweeping a huge variety of morphologies into such meaningless groupings as ‘early *Homo*’ or ‘archaic *H. sapiens*’. The upshot is that, in the absence of anything even resembling a reasonable consensus on species diversity in the human clade, one is for the moment forced to give up on any useful attempt to discern pattern in human brain evolution. And, of course, until we have sorted out the basic systematics of the hominid record, we will be at a similar impasse in broaching most other questions, too.

### SALTATION IN HUMAN EVOLUTION

Yet, on another level, it must still be possible to look at the record to see whether the dominant overall pattern is one of continuity or saltation. And, indeed, it is. However, given the ambiguity of the concept of saltation, I would strongly prefer to couch this search in slightly but significantly different terms. The question I would prefer to ask is: Does the evidence point towards uniformity, or in the direction of diversity? Is the morphological signal one of steady within-lineage change, or does it suggest the multiplication of species (which were then triaged among themselves)? The practical problem here for palaeontologists is, of course, that while morphological differentiation among local populations of widespread species is a routine phenomenon, and may, indeed, be the principal mechanism leading to the establishment of heritable novelties (Tattersall, 1994), it is independent of the event of speciation itself. There is thus no specifiable degree of morphological shift that can be taken as a firm indication that a reproductive barrier has intervened. Species populations can undergo major differentiation without the intervention of speciation (the creation of effectively discrete reproductive units); and speciation can take place

in the absence of significant morphological innovation. In the first case, we risk overestimating species-level diversity on morphological criteria; and in the second we risk underestimation.

This is not a conundrum to which there is any clearly evident definitive solution. None the less, a survey of the living primate fauna makes it clear that it is the genus that is the *Gestalt* unit among Primates, and that species within genera do not typically contrast greatly in their hard-tissue characteristics. Thus, in any fossil assemblage in which two or more distinct ‘morphs’ can be discerned that display numerous hard-tissue distinctions, we may conservatively conclude that at least as many species are represented (Tattersall, 1986). This kind of non-quantifiable rule-of-thumb procedure may be less than perfectly satisfying intellectually; but in employing it we are much more likely to underestimate than to overestimate the number of species actually represented in our assemblage. This should mollify even those traditionalists who think it ‘unbiological’ not to regard virtually all variation as intraspecific. And, as I have argued elsewhere (Tattersall, 1986, 1992), to proceed in this manner will help ensure that we minimise any distortion of the actual pattern of evolution within the group.

However valid these musings might or might not be, however, some might find them a bit arid in the context of the subject of this Symposium, ‘The Speciation of Modern *Homo sapiens*’. For, practicalities aside, they only obliquely address the two questions that ideally first need to be asked: ‘How would we recognise a taxic event in the record of the origin of our own species?’ and ‘Who or what in the known record is our closest fossil relative?’ (Asking who or what our ancestor is would be expecting a little too much for theoretical as well as practical reasons.) What’s more, in our own case we face an additional difficulty beyond the routine one of morphological recognition: the behavioural innovations that characterise our species are at least as striking as the morphological ones (and have certainly been more fateful), and changes of the two kinds do not appear to have proceeded in tandem (Tattersall, 1998a, 1998b). With this in mind, what do the fossil and archaeological records themselves suggest about the origin of *Homo sapiens*?

## THE HUMAN RECORD

There is abundant evidence for diversity in the hominid fossil record during the long period in which our family was confined to Africa. At about 1.8 million years ago in Kenya, for example, we have clear indications that at least four hominid species shared not only the same continent, but the same landscape. Indeed, it seems that we modern humans have been profoundly misled by our current status as the lone hominid in the world (Tattersall, 2000). It is natural

enough for us to conclude that this is somehow the normal state of affairs, for this is what we are used to; but historically things have been otherwise and, in this regard at least, we should not permit the present to shape our expectations about the past. The dominant pattern we see throughout the human evolutionary record is, in fact, one of diversity rather than of linearity. It has also been one of highly episodic major innovation, so that overall our history fits the 'saltational' pattern, however defined. The 'archaic biped' body structure of the australopiths, for example, persisted for a very long time even as numerous species came and went, only to be superseded abruptly by the unanticipated appearance of *Homo ergaster*, the first hominid of more-or-less modern body form. Indeed, we have no inkling whatever as to the antecedents of this radically new kind of hominid; and even if we remove the species *rudolfensis* and *habilis* from the genus *Homo*, as Wood & Collard (1999) have recently and credibly suggested should be done, it is very difficult to find any evidence at all of the direct ancestry of *Homo* among the australopiths as currently represented.

What we do know, however, is that the subsequent fossil record of the genus *Homo* presents us with a picture of substantial morphological variety, although many traditionalists still apparently find it convenient to use the figleaf of 'archaic *H. sapiens*' to obscure this fact. And while it would be premature to claim that we understand the full nature of this diversity, there are powerful indications that during the later part of the Pleistocene a significant number of species was spun off within the hominid clade. The best regional example of this has come to light as the result of a reappraisal of the European and western Asian group to which the Neanderthals belong (Tattersall & Schwartz, 2000). It is as yet unclear what the exact affinities are of the 780 thousand-year-old species *Homo antecessor*, recently described on the basis of fairly sparse fossil evidence (Bermudez de Castro *et al.*, 1997). But it is becoming evident that there subsequently diversified in Europe a major hominid clade of which the Neanderthals are simply the best-documented component. Traditionally, effort in the analysis of this group of fossils was directed towards trying to force them into an essentially linear framework, under the guise of 'pre-*sapiens*,' 'protoneanderthals' and so forth; but predictably this has only served to foster confusion. Much of this confusion stems from the fact that (under the sway of linear thinking) time has often been considered paramount in the analysis of these fossils, as of others. Indeed, it is generally true that the ages of hominid fossils have often loomed far larger in exegeses of their phylogenetic relationships than have their morphologies. And while time is certainly a significant component of the fossil record, it has no necessary connection with phylogenetic affinity (Eldredge & Tattersall, 1975), although it is a factor available to be considered among others.

Morphological appraisal of this European record indicates the existence of a coherent clade that extends well beyond a single species. The best known

member of this clade is the species *Homo neanderthalensis*, represented from something more than 200 thousand years ago to less than 30 thousand years. *Homo neanderthalensis* is highly distinctive, possessing numerous characteristics that separate it from all other hominids. And while some still try to cram it into an enlarged concept of *H. sapiens*, if *H. neanderthalensis* fails the test of specific distinctness, it is hard to conceive of any taxon that would pass such a test. We might as well give up on the practice of systematics and extend *H. sapiens* to include virtually all hominids of the last 2 million years (which, paleoanthropology being what it is, has actually been suggested: Wolpoff *et al.*, 1994).

Neanderthal characteristics include medial projections and posterior swellings within the nasal aperture; substantial maxillary sinuses that not only restrict the width of the nasal cavities but swell out the face below (and inside) the orbits; an unusually forwardly-positioned face and upper dentition, with which is correlated an anteriorly-shifted mandibular dentition and retromolar space; double-arched brow ridges that roll smoothly back and up into the frontal plane; a suprainiac depression that provides upper definition to occipital torus centrally; horizontal orientation of the lateral part of the occipital suture; and numerous characters of the post-cranial skeleton. There are also many cranial features that are generally distinctive of Neanderthals, but whose expression is sufficiently variable to exclude them from any hard-and-fast diagnosis; these include the projection of the occipitomastoid/juxtamastoid crest complex relative to the mastoid process, enlargement of the molar pulp cavities, and so forth. Indeed, the substantial Neanderthal sample is particularly valuable not only in presenting us with a morphology that is consistent over a large tract of time and space, but that shows intrapopulation variation analogous to what we see in our own species. Neanderthals varied among themselves no less than modern humans do (Schwartz & Tattersall, forthcoming).

When we look a bit farther afield, however, and particularly farther back in time, we encounter in the European record some specimens that possess some Neanderthal characteristics, but not others. The cranium from the German site of Steinheim, for example, has certain Neanderthal features in the front of the skull, notably Neanderthal-like brow ridges and a large nasal opening within which is a hint of a medial projection. However, its face is not inflated by the maxillary sinuses; and at the rear the skull is not notably Neanderthal-like, despite possessing a horizontal lateral occipital suture and a weakly developed occipital torus and suprainiac depression. What does this mean? Traditionally, this combination of features has been taken to indicate that the specimen represents an early stage in the lineage leading to Neanderthals; but it seems more likely that the Steinheim cranium represented a distinct member of a clade whose common ancestor actually possessed certain features, large nasal aperture, smoothly rolled brow ridges, and so forth, that were also retained by the Neanderthals. In other words, the Neanderthals were not as autapomorphic as

even the staunchest advocates of placing them in *H. sapiens* normally admit they are. For, just like *H. sapiens*, they are a unique mixture of the primitive and the derived.

If Steinheim were a unique occurrence, of course, it might be possible to argue that Steinheim was simply a stage *en route* to Neanderthal status. But the picture is complicated by other specimens of not vastly different age. The best-preserved of these are from the Sima de los Huesos, in the Atapuerca Hills of Spain, and are about 300 thousand years old (Arsuaga *et al.*, 1997). While they also possess Neanderthal-like brow ridges, large nasal openings and horizontal occipital sutures, the Sima specimens are in other features clearly unlike both Neanderthals and Steinheim. The same can be said for other specimens from Europe, including the putatively ancestral specimens often referred nowadays to *Homo heidelbergensis*. Among the best cranial specimens thus classified are the 400 thousand-year-old Arago 21 and the beautifully preserved but uncertainly dated fossil from Petralona, in Greece. The species *H. heidelbergensis* has been considered ancestral to both *H. neanderthalensis* and *H. sapiens*; but the Petralona specimen, especially, displays intracranial (and most especially frontal) sinuses that are developed almost beyond belief. Since the primitive condition for the hominid clade is tiny cranial sinuses, and Neanderthal sinuses, while greatly developed compared with those of *H. sapiens*, are significantly smaller than those of *H. heidelbergensis*, it is hardly possible to regard the latter as a Neanderthal ancestor, as has been suggested from time to time. On the other hand, it could plausibly represent a distinct member of the larger Neanderthal-related clade that was particularly derived in this feature.

There is clearly much more to be done on the European Middle-to-Late Pleistocene hominid assemblage, but it already appears that we are unlikely ever to sort it out satisfactorily if we refuse to recognise taxic diversity within it. Whatever we have in Europe, it is not a steadily changing lineage, but an assortment of species whose interrelationships demand analysis. And this, in turn, points to a pattern of evolution that has involved repeated speciation. To put it another way, the dominant evolutionary mode in this case was clearly taxic rather than transformational. Whether it was saltational is, of course, another matter; in none of these cases (the listing of apomorphies aside) can we even hazard a reliable guess as to the historical nature of those speciations.

By about 200 thousand years ago, the Neanderthals seem to have achieved sole possession of Europe, a situation that persisted until their eviction by invading *H. sapiens* between about 40 and 30 thousand years ago. Exactly where these new hominids came from is unknown, although molecular studies and the sparse fossil evidence point to an ultimate origin in Africa (reviewed by Stringer & McKie, 1996). Analysis of the mtDNA extracted from the Feldhofer Neanderthal suggests that the *sapiens/neanderthalensis* lineages split well over 500 thousand years ago (Krings *et al.*, 1997), which seems reasonable;



and the very limited African fossil hominid record shows a substantial morphological variety over the past half-million years or so. About the most that can be said with certainty, however, is that this rather opaque record does not carry a clear signal of continuity. Again, the pattern was probably taxic rather than transformational.

### THE ARRIVAL OF *HOMO SAPIENS*

At some time around 40 thousand years ago, anatomically and behaviourally modern *H. sapiens* entered Europe, with dates of comparable antiquity coming from both the western and the eastern extremities of the continent. Here we have straightforward evidence for a short-term event, although it cannot strictly be defined as saltational and might have had several components to it. The arriving *H. sapiens* (the 'Cro-Magnons') brought with them a distinctive new 'Upper Paleolithic' industry whose origin is as yet unknown. What we do know, however, is that, along with this stone-working technology they brought, or very soon developed, a host of symbolic expressions that included painting, carving, engraving, notation, music, elaborate body ornamentation, burial with grave goods, social stratification, and much else with which living humans can identify particularly closely. In all of these attributes the Cro-Magnons contrasted strongly not only with the Neanderthals, but with their own direct predecessors, the earliest humans of modern body form. Thus, as far as is known, in Africa all hominids of 100–200 thousand years ago, the period in which *H. sapiens* putatively emerged, possessed Middle Stone Age stone-working technology. This technology was functionally equivalent to the Mousterian toolkit that was made up to about 40 thousand years ago in the Levant, both by Neanderthals and by those anatomically modern humans (Qafzeh 9, for instance) who had made their appearance at not much under 100 thousand years ago (Valladas *et al.*, 1988). In Africa there are some hints in the sparse archaeological record of early (250–100 thousand years ago) behaviours that may presage behavioural modernity: flint mining, long-distance transport of materials, blade production, possible bone-working (Brooks, 2000), and even use of living space (Deacon, 1993). But hints are all we really have, as in the case of eastern Asia, where the Ngandong hominids, the last of the *H. erectus* clade, may have been evicted as little as 40 thousand years ago or less, and where the first Australians, who must have been formidable navigators, left no convincing evidence of themselves prior to about 60 thousand years ago.

Little as we can say with certainty, however, there seems to be no doubt that 'morphological *H. sapiens*' emerged from a background of considerable taxic variety among hominids Old World-wide at least 100 thousand years ago. This emergence thus took place substantially before we have any evidence that

modern, symbol-mediated, behaviours formed part of the regular cultural repertoire of any hominid group. Of course, very occasional objects older than 40–50 thousand years ago have been interpreted as symbolic. But even if such interpretation is accurate, it only serves to underline that such expressions were not part of the larger cultural patterns of the societies that produced them. They were exceptions, not the rule. May we conclude, then, that the ‘early moderns’ (right back to the origin of *H. sapiens*) had possessed a potential for symbolic behaviours that remained fallow for at least 50 thousand years, until ‘released’ by some cultural stimulus? Certainly there is no evidence for any biological change (at least as expressed in the hard tissues) that could have had this effect; and in any event, perhaps we should not be surprised by this. For ‘exaptation’, or, if you prefer, ‘pre-adaptation’, has long been recognised as a key component of the evolutionary process. Birds, for example, possessed feathers for millions of years before adopting them as adjuncts to locomotion. The use of innovations is not necessarily confined to the contexts in which they arise.

It is possible to argue that all through the sporadic history of change and innovation in human prehistory, new species had mostly done what their predecessors had done, if perhaps a bit better, as the process of interspecific competition might determine. Only with the emergence of modern-behaving *H. sapiens* do we find this pattern disturbed. But it is disturbed with a vengeance. Modern-behaving *H. sapiens* is truly a new influence on the landscape, and is not simply an extrapolation of what went before. And if this is not an example of saltation, I can’t imagine what might be.

## DISCUSSION

**Questioner:** How is evolution of behaviour related to the anatomy?

**Tattersall:** Novelties, whether anatomical or behavioural, have to arise *within* species. Modern human cranial structure seems to have been established by at least 100 thousand years ago, and probably more, whereas evidence of significant hominid symbolic behaviours (hence cognition) is much younger than this. Therefore we must suppose that even if the potential for such behaviours was born with anatomically modern humanity, their expression had to await the invention of a cultural releasing factor (plausibly, language) some dozens of millennia later.

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