

In the Shadow of the Modern Synthesis? Alternative Perspectives on the Last Fifty Years of Paleoanthropology

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In a recent article in *Evolutionary Anthropology*, Tattersall¹ discussed the development of human evolution in the last 50 years, specifically in the context of the history of evolutionary theory over the same time. His paper was rich in ideas and information, all clearly and elegantly stated, even if his admiration for most palaeoanthropologists' grasp of issues in evolutionary theory was somewhat restrained. His summary of many issues in the complex world of fossil hominins cut a swathe through much that is often obscure. Furthermore, the paper was clearly meant to be provocative, and in this it is a masterly success.

At the risk of oversimplification, Tattersall can be said to have made two main points. The first is that the last fifty years of palaeontological discovery and analysis have swept away the last vestiges of the unilinear and anagenetic models of human evolution and replaced them with a series of radiations and a pattern of diversity similar to that known for many other organisms. His second point is that this evidence should be seen as grounds for also clearing away the modern synthesis, which he sees as underlying a unilinear model. Multiple species, adaptive radiations, and diversity are taken to be evidence for macroevolutionary mechanisms and the dominance of a punctuated equi-

librium process of evolutionary change. Indeed, it can really be claimed that these two points are, in his mind, merely the two sides of the same coin, inseparable and indivisible. Multiple species and complexity cannot be accommodated within the modern synthesis, a theory of evolutionary change that Tattersall clearly sees as the crusty port of the biological establishment, ritually and uncritically passed from one select person to another, gradually deadening their senses.

His article left me in a dilemma. As someone who has championed the idea of multiple species, cladogenesis, adaptive radiations, and for well over a decade,²⁻⁵ I nodded wisely and cheered happily as he listed the fossil discoveries that have sealed, nail by nail, the coffin of unilinealism. But I am also a paid-up member of the modern synthesis, one who thinks that microevolutionary and adaptive processes account for the pattern we can see in the fossil record. If Tattersall were right, then I obviously could not have my evolutionary cake and eat it too. I would have to choose whether to sink all those wonderful hominin species together and champion a grand Darwinian unilinealism or else keep the species but throw away the theoretical glue that I saw holding them together. Which was it to be?

Of course, the question is, does it have to be either/or? What I want to do in this paper is to challenge the dichotomous equations that Tattersall has set up: multiple species = macroevolution; the modern synthesis = unilinealism. On these sets of equivalence hang his whole thesis, and therefore

his reading of the past and vision for the future of palaeoanthropology. I shall do this in three sections. The first will be historical. I shall argue that paleoanthropology, rather than being shackled for the last 50 years by the modern synthesis, has in fact remained blithely innocent of most theoretical issues, and that this, rather than rigid dogma, was the central problem. Second, I shall suggest that there is much within the classic microevolutionary synthesis that predicts the pattern we see. Much of Tattersall's outline of what falls within the modern synthesis is a simplification of a far more diverse field, one to which macroevolutionary theory has added little of substance. Third, I suggest that the future of paleoanthropology lies in a very different direction from the one Tattersall marks out, a direction that is less tied to the earth sciences but more integrated into the life sciences, particularly evolutionary genetics and evolutionary ecology.

NICE FOSSILS, SHAME ABOUT THE THEORY

Tattersall makes the important point that there was a major shift in the way human evolution was reconstructed in the middle of the last century. This shift is usually pinpointed to Ernst Mayr's⁶ pruning of the human evolutionary tree. In the appendix to his book on primate evolution, published in 1972, Elwyn Simons⁷ listed synonyms for hominin taxa. There are nine generic synonyms for *Australopithecus* and 17 for *Homo* (18 if you include *Eoanthropus*). Mayr⁶ reduced this to *Homo*, with only three

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species, basically in ancestor-descendent relationships. There was a good case for this, although *Australopithecus* refused to go away. Also, it is widely accepted that underlying the plethora of names were two factors. One was the fact that anthropologists and archeologists were often singularly bad at following the rules of zoological nomenclature; the other was that this reflected a view of the evolutionary process in which the species concept was very differently defined. In practice these two factors probably merge, as in many ways the naming of species and genera was simply a way of labeling specimens for reference. To my mind, rather than reflecting any deeply entrenched view of the evolutionary process, the practice probably derived as much from a straightforward need to communicate and describe clearly. Mayr's⁶ house-keeping exercise was sorely needed as the fossil record expanded and, no doubt, to someone as theoretically attuned as he is, it also made a major statement about evolutionary process. Species were about reproductive isolation, and as such the names should reflect that. It is a matter of doubt whether to paleoanthropologists this shift in meaning had as much effect as it seems with hindsight to have done. It could equally have been accepted as a rational change in nomenclature that reflected the growth of the fossil record, in which it was simply impossible for every specimen to have its own name. In that sense I wonder whether the change in terminology reflected quite such a change in theoretical outlook as is often thought.

If Tattersall is right, however, then all paleoanthropologists from then on were subscribers to the modern synthesis and operating within its framework. There is little doubt that the modern synthesis percolated into the thinking of the physical anthropologists at that time, and that there was a marked difference between them and their predecessors. It was then that paleoanthropology became decidedly unilinear, but it is less clear to me that this was due primarily to the modern synthesis. For the most part, palaeoanthropology was not explicitly theoretical, but was descriptive. There are, of course, clear exceptions. Loring

Brace was one, and he certainly did much to shackle the modern synthesis to unilinealism,^{8,9} as did Milford Wolpoff, who has repeatedly made explicit the links between his theories of human evolution and evolutionary mechanisms such as competitive exclusion,¹⁰ gene flow, and shifting balance.¹¹ Another is Joseph Birdsell,¹² whose textbook is one of the few that includes any explicit discussion of the hominin fossil record in the context of evolutionary theory. However, in contrast, his reading of evolutionary theory is both closely linked to the mod-

With a few exceptions, the anagenetic models of the 1960s and 1970s probably owed more to very general and often presynthesis notions of progress than to what Tattersall refers to as adaptive fine tuning. In that sense, unilinealism, such as is seen in the work of Weidenreich, another dominant figure at that time, often reflected orthogenetic rather than neo-Darwinian models of evolution.

ern synthesis and rejects anagenesis. What is interesting is that he explicitly rejects the single-species hypothesis for the Plio-Pleistocene australopithecines, casts serious doubt on it in the Middle Pleistocene, and offers a long discourse on "what the evolution of the horse really shows: a complex adaptive radiation." In this discussion he emphasizes both that evolution is about divergence, and that this idea goes back to G.G. Simpson, another of the architects of the modern synthe-

sis. It is striking that Louis Leakey, the greatest anthropologist of the time in terms of fossil discoveries, kept his evolutionary ideas, as well as his proclivities for naming new species and genera, decidedly in the mold of pre-modern synthesis. A further factor is that in practice fossil discoveries came into the literature by collaboration between the archeologists who dug them up and the anatomists in medical schools who described them. Archeologists and professors of anatomy seldom made a rich cocktail of Darwinian theory.

I think Tattersall overstates his case that unilinealism was an inevitable and limiting outcome of the modern synthesis. Where, then, did it come from? I think there are two important factors. With a few exceptions, the anagenetic models of the 1960s and 1970s probably owed more to very general and often presynthesis notions of progress than to what Tattersall refers to as adaptive fine tuning. In that sense, unilinealism, such as is seen in the work of Weidenreich, another dominant figure at that time, often reflected orthogenetic rather than neo-Darwinian models of evolution. The same is probably the case with Wilfred Le Gros Clark,¹³ who, while giving a perfectly clear account of Darwinian mechanisms, nonetheless interpreted patterns of change largely in terms of progressive change. There is no doubt that Le Gros Clark's view of primate evolution was strongly influenced by the idea of progressive grades or stages of evolution. This was probably fueled by both the paucity of the fossil record (relative to that of today) and the development of better dating techniques, which brought into sharper focus the chronological gaps that lay between specimens and therefore allowed ancestor-descendent relationships to be proposed more freely.

The second and, to my mind, more important factor was the nature of anthropological rather than biological ideas at that time, especially in the United States. Although the breakdown of the anagenetic model can be traced to the early 1970s, that model probably was never as widely accepted in Europe as it was in the United States. This is reflected in the greater persistence of anagenetic ideas, specifically multiregional mod-

els of modern human origins and the sinking of *Homo erectus* as a taxon, in America as compared to Europe.^{14,15} However, this geographical specificity of the unilineal model allows us to compare the modern synthesis with other intellectual influences. I think the primary such influence was, at one level, ingrained assumptions about human uniqueness, and at another, anthropological theory and training. In the discussions of the “single species hypothesis”¹⁰ in the 1970s (relating to whether *A. africanus* and *A. robustus* were really just one species) and the debate about Neanderthals and modern humans,¹⁴ the basic argument was that there is something unique about humans that prevents the formation of genetic or ecological barriers. Wolpoff¹⁰ argued that “culture” is the adaptation or niche of all hominins and, reiterated the point made by Mayr⁶ in 1950, that this would prevent the formation of species. His argument in relation to multiregional evolution in the Middle and Upper Pleistocene is similar, although based on models of isolation by distance rather than competitive exclusion.

There are two distinctive things to note about these views, both of which undermine Tattersall’s interpretation of the role of the modern synthesis in paleoanthropology. First, the thrust of most unilineal models in human evolution is that it is the uniqueness of humans, not the evolutionary mechanisms themselves, that is leading to anagenesis. Left to themselves, species—ordinary species, that is—simply get on with the business of speciating. But add the magic ingredient of culture and this stops happening. We can see this clearly in the writing of Mayr himself. The Cold Spring Harbor Conference on the Origin and Evolution of Man was undoubtedly one of the most influential meetings ever held in anthropology, and Mayr’s⁶ paper there the most significant in shaping the future (but see Box 1). He wrote: “How often has man speciated? The answer is that he has speciated only once. . . . This single event was the branching off of *Homo* from the anthropoid stock” (p116). Mayr recognized the importance, at this early evolutionary stage, of speciation as a mechanism. He then

commented on the absence of any evidence of further speciation, culminating in the question, “What is the cause for this puzzling trait of the hominid stock to stop speciating in spite of its eminent evolutionary success?”

What is so striking about these statements is that the problem for Mayr, a key figure in the modern synthesis, was to explain why speciation is not happening, for that is what evolutionary theory and inference would lead one to expect. As Tattersall and others point out, it is the uniqueness of humans that is the problem. We can well ask where Mayr and others

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acquired their ideas of the uniqueness of humans. While it is obvious that the notion of human uniqueness lies deep in Western philosophy, it must also have been buttressed by anthropological theory, which emphasized the all-embracing nature of human culture as humans’ mode of adaptation. Rather than the modern synthesis shaping anthropology, it may have been the other way around, with anthropologists persuading biologists that the unique cultural capacities of humans meant that speciation would

be inhibited, so that the course of human evolution would differ from that of other species. In this context it is interesting to note that both Kroeber and Kluckholm, key figures in the development of the American school of cultural anthropology, are both listed as participants at the critical Cold Spring Harbor conference in 1950. It is interesting to speculate that their influence may have been as critical as that of neo-Darwinism in setting in motion a stream of events that was to shape paleoanthropology over the subsequent two decades.

In other words, anthropologists undoubtedly read the modern synthesis as suggesting that there can be no cladogenesis, but rather than seeing the true nature of Darwinian theory they merely saw their own theoretical reflection. Tattersall’s wish that the anthropologists of the last half century had known more about evolutionary theory can perhaps be matched by the wish that many biologists had known less anthropology. “To your own self be true” seems to be the aphorism that the evolutionary biologists, who turned their attention to humans, forgot.

To add a personal note here, it was frustration with the combination of an absence of evolutionary theory in human evolution and assumptions about human uniqueness that led me to write *Another Unique Species*.² The title is an explicit reference to the fact that uniqueness itself is not a bar to the operation of Darwinian mechanisms; all species are unique. Human uniqueness, I argued, should be tackled from the perspective of straightforward Darwinian processes. One of those processes was divergence, and so one of the major themes of the book is that human evolution occurred as a series of adaptive radiations. I argued that there was every reason to expect multiple species, convergent evolution, and diversity of form and behavior rather than progressive trends. As far as I know, this was the first book to make explicit use of evolutionary theory to interpret the details of the fossil record. As Tattersall pointed out in his review at the time,¹⁶ it was depressingly limited (that is, neo-Darwinian) in its approach to evolutionary theory, but it

Box 1. Also Present at the Cold Spring Harbor Conference Were . . .

At the Cold Spring Harbor conference on the origin and evolution of man in 1950, Ernst Mayr's pruning exercise on all the genera and most of the species of human evolution became one of the most influential papers in human evolution. Perhaps it is for this, more than anything else, that the meeting is remembered. It is interesting, however, to look back at the conference and see that there were many strands of thought beyond unilinealism. For example, George Gaylord Simpson³⁷ was present, and his paper gave a very different reading of the view from the modern synthesis. He discussed how the principles of historical biology could more generally be brought to bear on human origins. Anagenesis is certainly not one of them. Rather, he emphasized the idea of species as evolving lineages in which diversity and parallelism can be expected to occur (p58). He also discussed the problems of muddling time and morphology (a recurrent theme over the subsequent fifty years), body size trends (even more familiar), and correlations of morphological characters and phylogenetic inference (little is really new!), and reversibility. Although Simpson's influence has not been as great as that of Mayr, his stress on the importance of looking at human evolution in comparative perspective is still fresh.

Unsurprisingly, Simpson also attacked orthogenesis and points out that the comments it inspired by W.W. Howells³⁸ show that unilinealism was by no means the accepted model. Referring to orthogenetic inferences and the general problem of seeing a linear trend in evolution, Howells said, "Evolutionary principles, properly understood, would

have warned us that something very different was to be looked for, and various instructive examples of phyletic histories should tell us what to expect, regardless of fossils. Jepsen (1940) has recently cited an instance in the apatemyids of the Paleocene and Oligocene, which not long since gave the appearance of an orthogenetic line, but which, because of a few recent discoveries, now appear to have a family tree sprouting roots and branches in new directions—a perfectly good parallel and lesson for the situation among the higher primates."

Howells then went on to say that Simpson can hardly have emphasized the point too strongly, that it is the paucity of the fossil record that makes one see particular lines, "links in a chain already visualised," and that the actual evolutionary history will be more complicated. Incidentally, he then berates Weidenreich for doing precisely that! The interesting point here is that Howells looked to Simpson for the general principles that should guide us in the way we look at human evolution, rather than the fossil record (or what we know about humans), and that single lines are not what to expect.

It is interesting to note that later in the same essay Howells goes on to talk about the complexities involved in understanding later human evolution. He forcefully emphasizes the paucity of the fossil record as a key problem, in interesting contrast to Mayr, who seemed to see that record as having filled out most of the picture already. Howells said, "The Pliocene still has the principal secrets of human ancestry." That statement shows where he was looking for the answers. In contrast, Mayr actually

focused entirely on the later *Homo* record, giving scant attention to the australopithecines.

As an aside, Howells also commented on the "spectacular synthesis" that had come about by the integration of genetics and palaeontology—presumably a reference to the Modern Synthesis. He then went on to say, "In anthropology such a synthesis has not taken place. Hypotheses as to race have not been made to jibe with hypotheses as to the general human origins . . . What geneticists may have to say about race has not been made to fit with what palaeontology has to say about the human line . . . Nor have the principles discussed by Simpson and Colbert been used correctly as often as they have been misquoted." The modern human origins debate beckons.

Indeed, presages of the future are to be found in many places in this volume, making it well worth reading even today. The list of participants alone reads as list of honor of American postwar anthropology, Birdsell, Boyd, Coon, Garn, Hooton, Howell, Howells, Kluckhohn, Kroeber, Lasker, Laughlin, Montagu, Neel, Spuhler, Steedman, Stern, Stewart, and Washburn. (There were only four participants out of the 130 who were not from the United States, which says something about either isolationism or the cost of those ocean liners.) There are many jewels to be found, not least a comment by Mayr himself that would have saved 1970s human paleontology a lot of ink: "The available evidence seems to me to indicate that man may be more closely related to the gorilla-chimpanzee group than this group is either to the orangs or the gibbons."

could hardly be called anagenetic in either spirit or substance. Indeed, he expressed his surprise that my adherence to such an outdated model of evolution did not stop me from promoting an adaptive-radiation interpretation of hominin evolution.

This impressionistic interpretation of the way the modern synthesis became incorporated into anthropology also helps explain why the impact was less strongly felt in Europe. In contrast to most European and other practitioners, paleoanthropologists in

the United States have been trained as anthropologists. While such training included much biology, it also would have led to a greater influence concerning the special role of culture in shaping human evolution. As Tattersall has pointed out (personal commu-

nication), Europeans interested in human evolution, such as Le Gros Clark and Trevor, may have known little about the emerging modern theories of evolution, but they also knew little cultural anthropology.

In sum, Tattersall is absolutely right to throw theoretical cold water on the anagenetic model of human evolution. I fully endorse his views on this. The problem lies, though, not in the dogmatic application of the modern synthesis, but its apparent abandonment in the face of a genuine dogma, the assumption that humans are not only unique but evolved by unique processes. The explicit reasoning of Dobzhansky¹⁷ and Mayr⁶ was anthropological in that it dealt with the special case of humans, not the general principles of neo-Darwinism. What this means is that Tattersall's equation, the modern synthesis = unilinealism, should have another term added to it: modern synthesis + culture = unilinealism. The question we therefore need to address is whether, without the additional element of culture and assumptions about human uniqueness, there is anything inherent in the principles of neo-Darwinism that means it cannot account for larger patterns of hominin diversity. Before doing that, however, it is worth briefly examining whether it was the failure of the modern synthesis that led to the appearance of so many new branches on the human evolutionary tree.

FROM LADDERS TO TREES TO BUSHES

If the anagenetic model of human evolution owed little to the dedication of paleoanthropologists to the modern synthesis, what led to its breakdown? Was it the rise of macroevolutionary theory? To answer this question, Tattersall looked to the highest authority known—the Editor of *Evolutionary Anthropology*—and found his answer incomplete. Fleagle¹⁸ has argued that the rise of multiple species in the hominin fossil record was due to three factors: simple empirical accumulation, such that it was simply impossible to hold down the number of species, even if one wanted to; cladistics, which depends on multiple species as a method; and more

rigorous use of statistics. To this Tattersall added the “more general appreciation of the complexities of the evolutionary process.”

It is worth spending a little time looking in detail at where and how the new species have appeared in the context of Fleagle's factors. Most of them have been genuinely new empirical additions. Ironically, three of these have been named by Tim White, not someone associated with multiple species models of human evolution. They are *A. afarensis*,¹⁹ *Ardipithecus ramidus*,²⁰ and

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Australopithecus gahri.²¹ But also in this category are *H. habilis*,²² which had the hardest battle being admitted to the status, and *A. anamensis*.²³ Others that might more ambiguously be put in this category include *A. aethiopicus*²⁴ and *Homo antecessor*,²⁵ which, had they been found in the 1960s, would certainly have been absorbed within existing taxa. If there is an intellectual stream running through this, it is, perhaps, that the job of getting new species

accepted has become easier and easier: *H. habilis* was resisted, strongly and *A. afarensis* was resisted less strongly, though there still were some sceptics, whereas the later taxa were accepted largely uncritically, certainly reflecting the greater willingness of paleoanthropologists to accept diversity.

The best example of a taxon arising out of cladistics is *H. ergaster*. This species has a somewhat mixed ancestry, being ultimately the untimely offspring of Colin Groves's²⁶ early cladistic approaches mixed with Wood²⁷ and Andrews's²⁸ attempts to differentiate Asian and African “*H. erectus*.” An equally good example of a taxon emerging out of statistical analysis is *H. rudolfensis*,²⁹ and the most dubious is *A. crassidens*.³⁰

This still leaves a number of taxa that would fit into Tattersall's additional factor, the appreciation of the complexities of the evolutionary process. One example of these might be the differences between *A. boisei* and *A. robustus*, which gained acceptance out of a judicious mix of the statistical and cladistic differences between these specimens and the recognition that there was a significant geographical patterning. This example, to which might be added *A. bahrelghazali*,³¹ can certainly be seen in this light, but the theoretical context for its acceptance is simply allopatry, a long-standing part of the armory of neo-Darwinian ideas.

The final group of species relates to later human evolution: *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. The recognition of these taxa certainly reflects the problem of evolutionary complexity but, even more strongly, it reflects the inadequacy of the appalling mess created by a polytypic *H. sapiens*.³² *H. heidelbergensis* has a strong cladistic and statistical basis, but its derived descendents are more problematic, not so much in terms of their endpoints as in the continuity that can be found between them and *H. heidelbergensis*. These seem to be species in the sense that Simpson meant—lineages with independent trajectories—but both the details of the fossil record and the scale of the process seem to rule out any punctuated events. Indeed, continuity between them, rather than disconti-

nunity, is the reason for the persistent problem of delimiting the taxonomic units in the later stages of human evolution and gives rise to the question of whether the species concept, which lies at the heart of macroevolutionary theory, is sufficiently fine-tuned to cope with evolution at this scale. The lineages of later human evolution seem to show simultaneously continuously evolving lineages and very distinctive derived endpoints, which are exactly what would be expected within the modern synthesis. They certainly highlight the problems of reconciling terminology with process.

This brief history of paleoanthropology in the last fifty years casts a very different light on the way our understanding of human evolution has changed than does that presented by Tattersall. There has clearly been a major empirical element driving it; new fossils do make a difference, although sometimes it takes time for this to have an effect. Changing methods and ideas have also played their part, and these have probably been interlaced with the way in which students entering the discipline have been trained. The modern synthesis certainly played a major role, but I hope that we can converge on the idea that it was the way anthropologists read that in relation to humans that was more crucial than anything inherent in the theory. More importantly, though, the end product is one on which Tattersall and I would be in close agreement: a picture of hominin evolution as a process of diversification and extinction, cladogenesis rather than anagenesis. To return to the question asked earlier, though, is this a challenge to neo-Darwinism?

DIVERSITY, DISPERSALS, AND RADIATIONS

The issue at the core of the differences between Tattersall and myself is the expectation and explanation of evolutionary diversity. We both agree on their existence in human evolution, as well as on the need to understand the pattern in terms of general evolutionary models rather than the specifics of human evolution. Where we disagree is on the question of whether or

not we need more than classic neo-Darwinian mechanisms to produce this pattern. While his paper is full of how liberating it is for those living under the constraints of the modern synthesis to embrace punctuated equilibria, it is short on the details of what mechanisms produce diversity.

One key point in neo-Darwinian theory, and the one most disputed by Eldredge,³³ Gould,³⁴ and others, is that macroevolutionary patterns—the rise and fall of species and higher taxa and the shifting distributions of lineages through time and space—arise from microevolutionary processes. Macroevolutionary patterns are not intrinsically a challenge to neo-Darwinism; few would dispute that they exist and require explanation. The challenge comes either from the inability of microevolutionary mechanisms to account for macroevolutionary patterns or from

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the alternatives offered by macroevolutionary theories being more powerful.

To my mind, microevolution offers perfectly good explanations for the shape of life on a larger scale. The key general principles are those derived from ecology, operating over short time scales, but repetitively built up over geological time.^{35,36} Local events are the precursors of large-scale evolution. There is little doubt that these small-scale events occur, for they are the essence of ecological observations, but the question is how they become the basis for macroevolutionary patterns. The link, it can be argued, is the way in which demographic changes have geographical outcomes. Populations expand where reproduction ex-

ceeds mortality, are spatially stable where they are in balance, or contract where mortality exceeds reproductive rate. It is these geographical processes that will mediate between microevolution and macroevolutionary patterns. Increasing populations will disperse, leading to expanded species ranges; declining populations will contract, leading to fragmentation, local extinction, and isolation of populations. Both these processes will lead to allopatry, small populations, local selective pressures, and genetic drift, all the classic mechanisms of neo-Darwinism that produce evolutionary change. The difference in theoretical emphasis lies here on the importance of dispersal rather than speciation itself as a signal of evolutionary significance. Evolutionary change may or may not produce speciation, but at the micro-level it will be a process of cladogenesis, not anagenesis. This emphasis on cladogenesis brings together both classic evolutionary theory and the main concern and interests of the macroevolutionary theorists. The outcome may be diversity, as the hominin fossil record suggests that has occurred many times (Box 2 and Fig. 1) or, if subsequent extinction wipes out the ancestral populations, it will take on the appearance of an anagenetic event. The microevolutionary process will nonetheless be cladogenetic. These ideas of an evolutionary geography as the basis for bringing together macro- and microevolution have been pursued and outlined for both early³⁵ and later hominin evolution.³⁶ Perhaps the key point to stress is that empirically most of the diversity seen in the hominin fossil record has a geographical basis, which is a major expectation for macroevolutionary patterns of neo-Darwinism.

It could be pointed out, of course, that evolutionary geography places insufficient emphasis on selection and adaptation for it to be truly neo-Darwinian. But the point to emphasize is that patterns of dispersal and contraction act as mediating factors between selection operating on populations, leading them to be successful and expand or unsuccessful and contract, and thus leading to the appearance and disappearance of taxa. They pro-

Box 2. The Pattern of Hominin Evolution as a Series of Adaptive Radiations

Figure 1 shows the overall pattern of hominin evolution as revealed by the fossil record and provides a broad, tentative picture of the currently recognized diversity. Needless to say, there is much here that is controversial in terms of the number of taxa recognized, their time ranges, and their evolutionary relationships.

1. Time ranges: the black bars show the time ranges of the hominin taxa currently recognized or suggested. These are very subject to the vagaries of the fossil record and the availability of dating techniques. There are likely to be minima, given that all taxa would have geographically localized origins and that their extinction would have occurred progressively over a time range, with small populations probably surviving in refugia for a considerable time after the species as a whole had contracted in range.

2. Phylogeny: the dotted gray lines indicate a possible phylogeny for the known hominins, although much of this remains uncertain and hotly debated. In particular, the extent of monophyly among the "robust" australopithecines is questionable.³⁹ The position of the new find *A. garhi* has been questioned,⁴⁰ as has the existence of *H. antecessor*. Further, the position of *H. antecessor* shown here is not that of the authors who proposed the taxa.²⁵ Most problematic of all is that there is no clear link between *Homo* and *Australopithecus*. Furthermore, the early *Homo* material has recently been placed within the australopithecines,⁴¹ and its monophyly is also still uncertain. Within later *Homo*, *H. heidelbergensis* is usually considered to be directly ancestral to *H. neanderthalensis* and *H. sapiens*,⁴² but an intermediate species representing a larger-brained common ancestor, *H. helmei*, has recently been proposed.³⁶ However, despite these caveats, this diagram probably represents reasonably well the emerging picture and scale of hominin evolution. In addition, the late Middle Pleistocene material from East Asia poses problems that have yet to be resolved.

3. Species: probably most controversial of all is the sort of taxa these "species" represent. It is unlikely that they are all biological species in the sense defined by Mayr.⁴³ Moreover, the fossil record is always likely to be

intractable to testing this species concept. Most species can be defined cladistically in that they possess unique derived traits, but variability and polymorphisms in both ancestral and descendent taxa often makes these hard to demonstrate. They are almost certainly species in the sense defined by Simpson—independently evolving lineages—and thus map the pattern of hominin evolution well. Clark⁴⁴ has recently suggested that the word "palaeodeme" should be used for all or some of these because it may better reflect the dynamic and unfixed nature of the evolving populations. It is unlikely that the species concept itself will be the most useful tool for unravelling what is, in effect, in comparison with much of the debate about punctuated evolution, a small-scale event, especially in its later stages (the last half million years).

Superimposed on the taxa are a series of radiations (gray shading) intended to represent the underlying pattern of hominin evolution. It should be recognized that these are abstractions of a continuous process. Broadly speaking, a radiation (adaptive radiation) can be considered to be a dispersal or series of dispersals of descendants of a common ancestral stock (the dispersal being the mark of their evolutionary success), leading to morphologically and systematically diverse forms, largely through allopatry, local adaptation, and drift. The ones shown here (numbered) are:

1. The radiation of the African apes in the later Miocene. This may have been a response to the invasion of Africa from Asia of an ancestral lineage,⁴⁵ with the African apes and the hominins being the outcome of these dispersals. *Ardipithecus ramidus* is very tentatively placed in this radiation.

2. The radiation of the bipedal apes (early australopithecines). All members of this group, occurring in the Pliocene, have bipedal adaptations. This seems to be the basis for a widespread pan-African (Chad, Eastern Africa, Southern Africa) series of dispersals. All members retain many generalized hominin cranial characters, although they also display a trend toward increasing megadonty.

3. The radiation of megadontic specialists is the dominant trend of

the latest Pliocene and early Pleistocene. This seems to be a radiation of more savanna-dwelling hominins, with adaptations toward the processing of coarse fibrous plant material. It is unclear whether this was a monophyletic radiation or part of a more general series of trends among the australopithecines, all of which show elements of megadonty. Indeed, this may be the trend that characterizes all the early (australopithecine) hominins, and may involve considerable homoplasy.

4. The radiation of earliest *Homo*. This is perhaps the most problematic of all the radiations as its phylogenetic position is extremely uncertain, and there is considerable variation within the group. *H. rudolfensis* retains megadontic adaptations, while sharing with *H. habilis* an element of brain enlargement. Whether there is more that characterizes this radiation than just a variant on the australopithecine themes of the preceding few million years remains to be seen.

5. The radiation of *Homo*. This, seen in *H. ergaster* and its descendants, may be suggested as a major shift in "grade" or adaptive complex from the australopithecines, shown in cranial and dental morphology and the postcranium, as well as behavior and technology. It furthermore gives rise to the first Eurasian dispersals, and so is geographically more extensive.

6. The radiation of larger-brained *Homo*. During the last half million years or so larger brained-hominins, often having very robust morphologies, developed in association with the expansion of Acheulean (Mode 2) and prepared core (Mode 3) technologies, and gave evidence of more human-like behavior. These radiations occurred in the context of major glacial-interglacial climatic cycles, so that the underlying biogeographical patterns may have led to repeated dispersals overlying each other³⁶ and giving rise to the complexity of the later hominin fossil record: the evolution in Europe of Neanderthals, and in Africa of *H. sapiens*.

7. The radiation of *H. sapiens*. This was a recent event, having occurred in the last 100 Kyr. It differed from preceding dispersals in that it involved far less morphological diversification and resulted in the first complete global colonization.

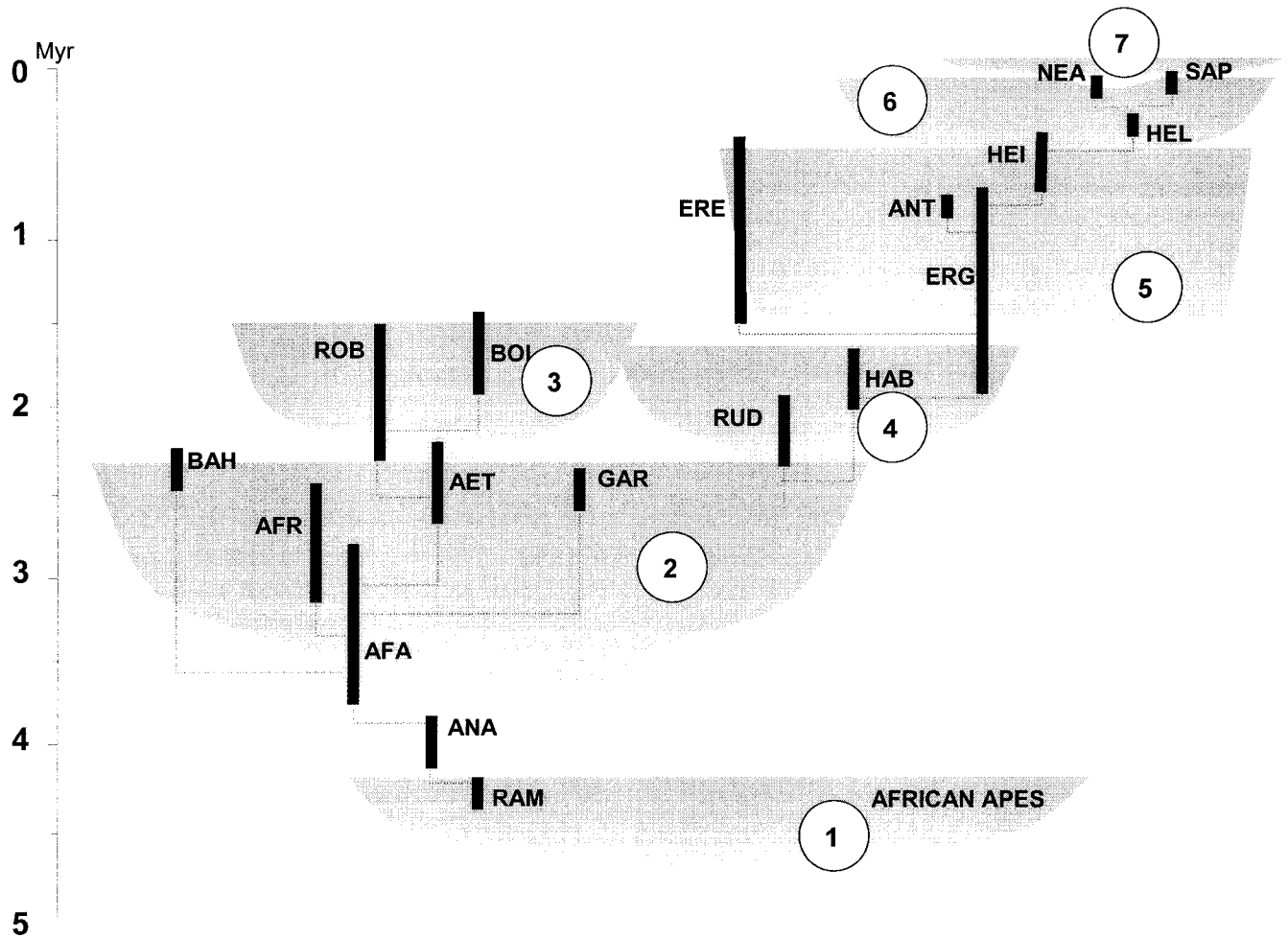


Figure 1. Pattern of hominin evolution as revealed by the fossil record. RAM, *Ardipithecus ramidus*; ANA, *Australopithecus anamensis*; AFA, *A. afarensis*; AFR, *A. africanus*; AET, *A. aethiopicus*; BAH, *A. bahrelghazali*; GAR, *A. garhi*; ROB, *A. robustus*; BOI, *A. boisei*; RUD, *A. or Homo rudolfensis*; HAB, *A. or H. habilis*; ERG, *H. ergaster*; ERE, *H. erectus*; ANT, *H. antecessor*; HEI, *H. heidelbergensis*; HEL, *H. helmei*; NEA, *H. neanderthalensis*; SAP, *H. sapiens*.

vide the link between microevolutionary mechanisms and macroevolutionary patterns. Speciation is an outcome of the operation of natural selection in this model, as is the pattern of extinction. This is not to say that the scale and nature of the observed macroevolutionary patterns are not influenced by many other factors—external change (for example, climatic forcing) and contingency, to name two favorite macroevolutionary concepts—but they are not decoupled from microevolutionary processes, a key claim in the various debates.

Can this sort of approach answer the question first asked by Gould and Eldredge³⁴ and posed again by Tattersall: “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?” To my mind, it can. For example, it appears that the species range areas of *Homo* were substantially larger than those of the African australopithecines, and thus the rate of speciation relative to range area was lower.³ The simplest explanation for this phenomenon is that an adaptive and behavioral shift among *Homo*—meat-eating being the most likely—led to a greater potential for range expansion. Thus the speciation patterns of *Homo* shifted from those of a typical catarrhine primate to those of a carnivore.

To sum up, it seems to me that microevolutionary mechanisms, those at

the heart of neo-Darwinism, can provide explanations for macroevolutionary patterns perfectly satisfactorily, and, indeed, that these mechanisms lead us to expect diversity in the hominin fossil record. There is no reason to accept the set of equivalences that lay at the heart of Tattersall’s paper: microevolution = unilinealism, and multiple species = macroevolution. My interpretation of the history of paleoanthropology over the last half-century is that it was either a lack of theory, or the misapplication of anthropological theories, that led to unilinealism. Furthermore, as I have tried to show, evolutionary geography provides the means of extracting multiple species out of microevolutionary processes.

PALEOANTHROPOLOGY: THE NEXT HALF CENTURY

The question is, where do we go from here? I think that for the most part Tattersall and I would agree. Indeed, I would say that he and I are closer in spirit than most paleoanthropologists are and, accordingly, should form our own segmentary lineage within the clan (there are some good anthropological theories!). We have both argued strongly that fossils cannot tell their own story, but that they need the comparative perspective offered by other areas of evolutionary biology. More specifically, interpretation requires explicit use of evolutionary theory. A lack of theory is a greater weakness than disputes over what that theory should be. I also agree with his prediction that an "expanding (fossil) record will show a strong signal of diversity, and will reveal an episodic history of evolutionary experimentation rather than a linear trudge toward perfection." Where I diverge from Tattersall's views is that I consider both the episodic experimentation and the overlaid trends we can observe (megadonty, encephalization, and technological complexity) to be the product of Darwinian processes operating on small populations of hominins.

Tattersall has suggested that paleoanthropology has been repressed by the heavy hand of dogma and is akin to a religious sect unable to see beyond its sacred texts. It seems to me that there is little evidence for this heavy hand in the last half-century of paleoanthropology. Rather, the empirical momentum of fossil discoveries has allowed the subject to remain atheoretical. Where theory has been used, it has been drawn more from inbuilt assumptions about the human species, and from anthropology. That should change and is changing. Theory is being brought in from cladistics and, more broadly, the comparative method, behavioral ecology, life-history theory and, most important of all, the emerging field of evolutionary genetics. Developmental genetics is likely to have an equally major impact. All these fields have two things in common. One is that they are all very much part of the life sciences, rather than the earth sciences, so that evolu-

tionary approaches will be less and less based on the fossil record alone. This will have the effect of integrating paleoanthropology more fully into the biological sciences, where mechanism and theory go hand in hand. The second is that they all are concerned with the larger-scale outcomes of the development and behavior of the individual. This is very close to the central spirit of the modern synthesis: working out how the large scale arises out of small-scale processes. It would be a shame if paleoanthropology were to abandon the modern synthesis at such a turning point.

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REFERENCES

- Tattersall I. 2000. Paleoanthropology: the last half-century. *Evol Anthropol* 9:2-16.
- Foley RA. 1987. Another unique species: patterns of human evolutionary ecology. Harlow: Longman.
- Foley RA. 1991. How many hominid species should there be? *J Hum Evol* 20:413-427.
- Foley RA. 1994. Speciation, extinction and climatic change in hominid evolution. *J Hum Evol* 26:275-289.
- Foley RA. 1995. Humans before humanity: an evolutionary perspective. Oxford: Blackwells Publishers.
- Mayr E. 1950. Taxonomic categories in fossil hominids. Cold Spring Harbor Symp Quantitative Biol 15:109-117.
- Simons El. 1972. Primate evolution: an introduction to man's place in nature. New York: Macmillan.
- Brace CL. 1964. The fate of the classic Neanderthals: a consideration of hominid catastrophism. *Curr Anthropol* 5:3-43.
- Brace CL. 1967. The stages of human evolution. Englewood Cliffs, NJ: Prentice Hall.
- Wolpoff M. 1971. Competitive exclusion among lower pleistocene hominids: the single species hypothesis. *Man* 6:601-614.
- Wolpoff M, Caspari R. 1997. Race and human evolution. New York: Simon & Schuster.
- Birdsell J. 1972. Human evolution. Chicago: Rand McNally.
- Le Gros Clark WE. 1949. History of the primates. London: British Museum (Natural History).
- Wolpoff MH. 1989. Multiregional evolution: the fossil alternative to Eden. In: Mellars P, Stringer CB, editors. The human revolution. Edinburgh: Edinburgh University Press. p 62-108.
- Wolpoff MH, Wu XZ, Thorne AG. 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In: Smith FH, Spencer F, editors. The origin of modern humans: a world survey of the fossil evidence. New York: Alan R. Liss. p 411-483.
- Tattersall I. 1987. Putting humanity in context. *Nature* 328:121.
- Dobzhansky T. 1937. Genetics and the origin of species. New York: Columbia University Press.
- Fleagle JG. 1995. Too many species? *Evol Anthropol* 4:37-38.
- Johanson DC, White TD. 1979. A systematic assessment of early African hominids. *Science* 203:321-330.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 366:261-265.
- Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science* 284:629-635.
- Leakey LSB, Tobias PV, Napier JR. 1961. A new species of the genus *Homo* from Olduvai Gorge, Tanganyika. *Nature* 202:308-312.
- Leakey MG, Feibel CS, McDougall I, Walker AC. 1995. New four million year old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565-571.
- Walker A, Leakey RE, Harris JM, Brown FH. 1986. 2.5-Myr *Australopithecus-Boisei* from West of Lake Turkana, Kenya. *Nature* 322:517-522.
- deCastro JMB, Arsuaga JL, Carbonell E, Rosas A, Martinez I, Mosquera M. 1997. A hominid from the lower Pleistocene of Atapuerca, Spain: possible ancestor to Neanderthals and modern humans. *Science* 276:1392-1395.
- Groves CP, Mazak V. 1975. An approach to the taxonomy of the Hominidae: Gracile Villafrancian hominids of Africa. *Casopis Mineralogeo* 20:225-247.
- Wood B. 1984. The origins of *Homo erectus*. Courier Forschungsinstitut Senckenberg 69:99-111.
- Andrews PJ. 1984. An alternative interpretation of the characters used to define *Homo erectus*. Courier Forschungsinstitut Senckenbergensis 69:167-175.
- Chamberlain AT, Wood BA. 1987. Early hominid phylogeny. *J Hum Evol* 16:119-33.
- Grine FE. 1989. The evolutionary history of the "robust" Australopithecines. Chicago: Aldine de Gruyter.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1995. The first Australopithecine 2,500 kilometers west of the Rift-Valley (Chad). *Nature* 378:273-275.
- Tattersall I. 1986. Species recognition in human palaeontology. *J Hum Evol* 15:165-175.
- Eldredge N, Gould SJ. 1972. Punctuated equilibrium: an alternative to phyletic gradualism. In: Schopf TJM, editor. Models in palaeobiology. San Francisco: Freeman. p 82-115.
- Gould SJ. 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6:119-130.
- Foley RA. 1999. The evolutionary geography of Pliocene hominids. In: Bromage T, Schrenk F, editors. African biogeography, climatic change, and hominid evolution. Oxford: Oxford University Press.
- Lahr MM, Foley RA. 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook Phys Anthropol* 41:137-176.
- Simpson GG. 1950. Some principles of histor-

ical biology bearing on human origins. *Cold Spring Harbor Symp Quantitative Biol* 15:55–66.

38 Howells WW. 1950. Concluding remarks of the chairman. *Cold Spring Harbor Symp Quantitative Biol* 15:79–85.

39 Skelton RR, McHenry HM, Drawhorn GM. 1986. Phylogenetic analysis of early hominids. *Curr Anthropol* 27:21–43.

40 Strait D, Grine F. 1999. Cladistics and early hominid phylogeny. *Science* 285:1210–1210.

41 Wood B, Collard M. 1999. The changing face of genus *Homo*. *Evol Anthropol* 8:195–207.

42 Rightmire GP. 1998. Human evolution in the middle Pleistocene: the role of *Homo heidelbergensis*. *Evol Anthropol* 6:218–227.

43 Mayr E. 1963. *Animal species and evolution*. Cambridge: Harvard University Press.

44 Howell FC. 1999. Paleo-demes, species clades, and extinctions in the pleistocene hominin record. *J Anthropol Res* 55:191–243.

45 Stewart CB, Disotell TR. 1998. Primate evolution: in and out of Africa. *Curr Biol* 8:R582–R588.
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Books Received

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