Chapter 1
Why Was Human Evolution So Rapid?

Ian Tattersall

Abstract Nowhere in the entire fossil record of life do we find more dramatically accelerated accumulation of evolutionary novelty than we do in the genus *Homo*. Quite simply, and by whatever criteria you measure it, our species *Homo sapiens* is more different from its own precursors of two million years ago than is any other species living in the world today. What might account for this unusually rapid rate of evolution? A major influence was almost certainly material culture, though not in the gene-culture co-evolutionary context envisaged by the evolutionary psychologists. Rather, material culture enhances the ability of hominid populations to disperse at times when conditions are favorable for expansion, while incompletely insulating the resulting enlarged populations from environmental stress when circumstances deteriorate. In other words, by facilitating expansion beyond normal physiological limits in good times, culture makes populations more vulnerable to fragmentation in bad ones. Over the course of the Pleistocene, short-term but large-scale local environmental changes became increasingly frequent over large tracts of the Old World, further amplifying the stress-and-response cycle. Since the fixation probabilities of evolutionary novelties of all kinds (as well as of local extinctions) are promoted by population fragmentation and consequent small effective population sizes, we see in the synergy between environmental effects and material culture a sort of ratchet effect which would have acted to leverage rates of accumulating change. This interaction explains the extraordinarily fast tempo of evolution within the genus *Homo* by invoking perfectly routine evolutionary processes; and it eliminates any need for special pleading in the hominid case, at least in terms of mechanism. Apparent recent diminution in human brain size may result from greater algorithmic efficiency.

Keywords Evolutionary rates • Tachytely • Hominids • Hominins • Material culture • Morphological change • Rapid evolution

There are many extraordinary things about our species *Homo sapiens*. The most obvious of these reside in our unique symbolic cognitive style, and in the physical correlates of our unusual form of striding bipedal locomotion. Much has been written about conspicuous features such as these, and about how they may have evolved. But there is something else about our species and its precursors that is equally striking, but that has somehow contrived to escape as much attention as it merits: namely, the rapidity with which the human lineage has evolved. By virtually any measure, *Homo sapiens* is more different from its own ancestors of only two million years ago, both in its morphology and in the way it processes information, than is any other contemporary mammal species.

The genus *Homo* has been in existence as a morphologically coherent entity for less than two million years (Myr) (Wood and Collard 1999; Collard and Wood 2015; Schwartz and Tattersall 2005; Tattersall and Schwartz 2009). Material culture, as inferred from the deliberate manufacture of stone tools, has been a property of at least some hominid lineages for a little longer: the earliest clear evidence for it goes back as far as about 2.5 Ma (Semaw et al. 1997). This also happens to be the age of the earliest claimed "early *Homo*" fossils (e.g., Schrenk et al. 1993; Kimbel et al. 1997), as well as of an inferred *Kenyanthropus* lineage (Leakey et al. 2001); but whether or not the fossils concerned are appropriately allocated, the current best guess is that stone tool fabrication was introduced into the hominid behavioral repertoire by archaically-proportioned australopiths (de Heinzelin et al. 1999). The earliest stone tool makers were thus terrestrially upright bipeds; but they were relatively small-bodied, and had archaic limb proportions and a host of morphological features, especially of the forelimbs and

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upper body, that attest to a partially arboreal way of life (Susman et al. 1984). Additionally, their skulls were constructed much as in today's great apes. They had large, protruding faces, hafted in front of tiny neurocrania that had contained brains no larger than one would expect of an ape of similar body mass. In all these features they contrasted dramatically with the tall, slender, long-legged *Homo sapiens*, which exhibits a large, balloon-like braincase with a tiny face retracted beneath its front (see Fig. 1.1).

Despite various "advanced" features reported in the newly described 2.0 Myr-old *Australopithecus sediba* (Pickering et al. 2011), the exact evolutionary roots of the genus *Homo* remain obscure. But on present evidence there is little doubt that it is from a form possessing the general morphological features of an australopith, and that lived at some time between about 2.5 and 2.0 Ma, that *Homo sapiens* ultimately descended. This represents a remarkable transformation that was accomplished very fast. It was not, of course, linear. Rather, as Fig. 1.2 shows, it was achieved in the context of vigorous evolutionary experimentation. Since the very beginning, numerous hominid species have apparently been pitchforked out on to the ecological stage, to succeed – or, more likely, to fail – over a period of intensely unstable climatic and environmental conditions.

A pattern of diversity of the kind represented in the figure is typical of successful mammalian families; but in morphological as well as in behavioral terms this particular transformation was distinctive by virtue of being both vast in scale, and exceptionally fast in time. To put it in perspective, two million years is approximately the amount of time that has elapsed since the divergence of the two species of *Pan*, *P. troglodytes* and *P. paniscus* (Stone et al. 2010). And while there are certainly noticeable differences in both behavior and morphology between these two species, they vanish alongside those separating an australopith from a modern human. To take another example, Fig. 1.3 compares the crania of two other hominoid genera, each one, like *Pan* and *Homo*, the other's closest living relative. On the right is a gibbon, *Hylobates*. On the left is a siamang, *Symphalangus*. What makes the comparison of these two morphologically similar genera particularly instructive is that, almost exactly as in the case of *Pan* and *Homo* (Stone et al. 2010), the best molecular estimate is that these two hominoids last shared an ancestor some seven million years ago, plus or minus a million years or so (Matsudaira and Ishida 2010).

The hylobatid case is a rather routine illustration of what G. G. Simpson (e.g., 1944, 1953) called "horotely," namely evolution at "normal" rates. The morphological differences between gibbons and siamangs appear to be pretty much what one would expect for closely related creatures with a divergence time in this general range (see reviews of primate evolutionary patterns in Hartwig 2002). The human/chimpanzee case, on the other hand, is very different. Nobody would dispute that modern humans are much more unlike

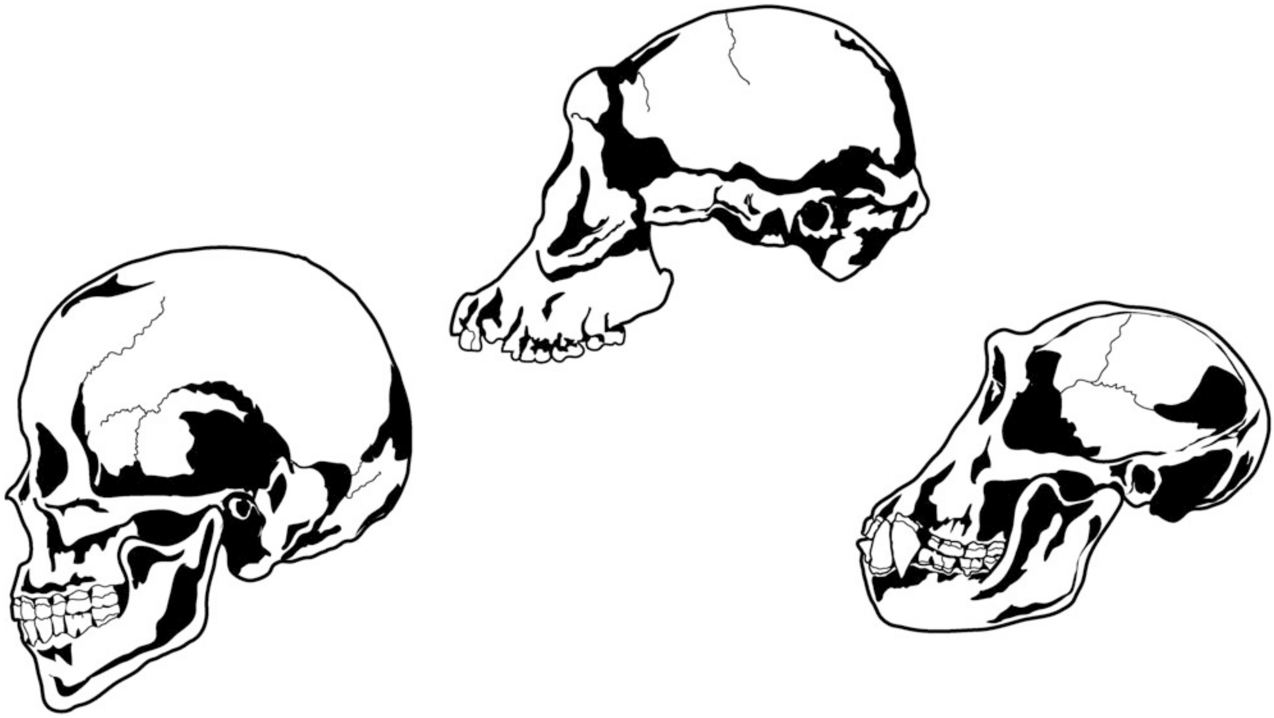

Fig. 1.1 Lateral views of the crania of: (*left*) a modern human, *Homo sapiens*; (*center*) *Australopithecus afarensis*; (*right*) a modern chimpanzee, *Pan troglodytes*. Drawing by Jennifer Steffey

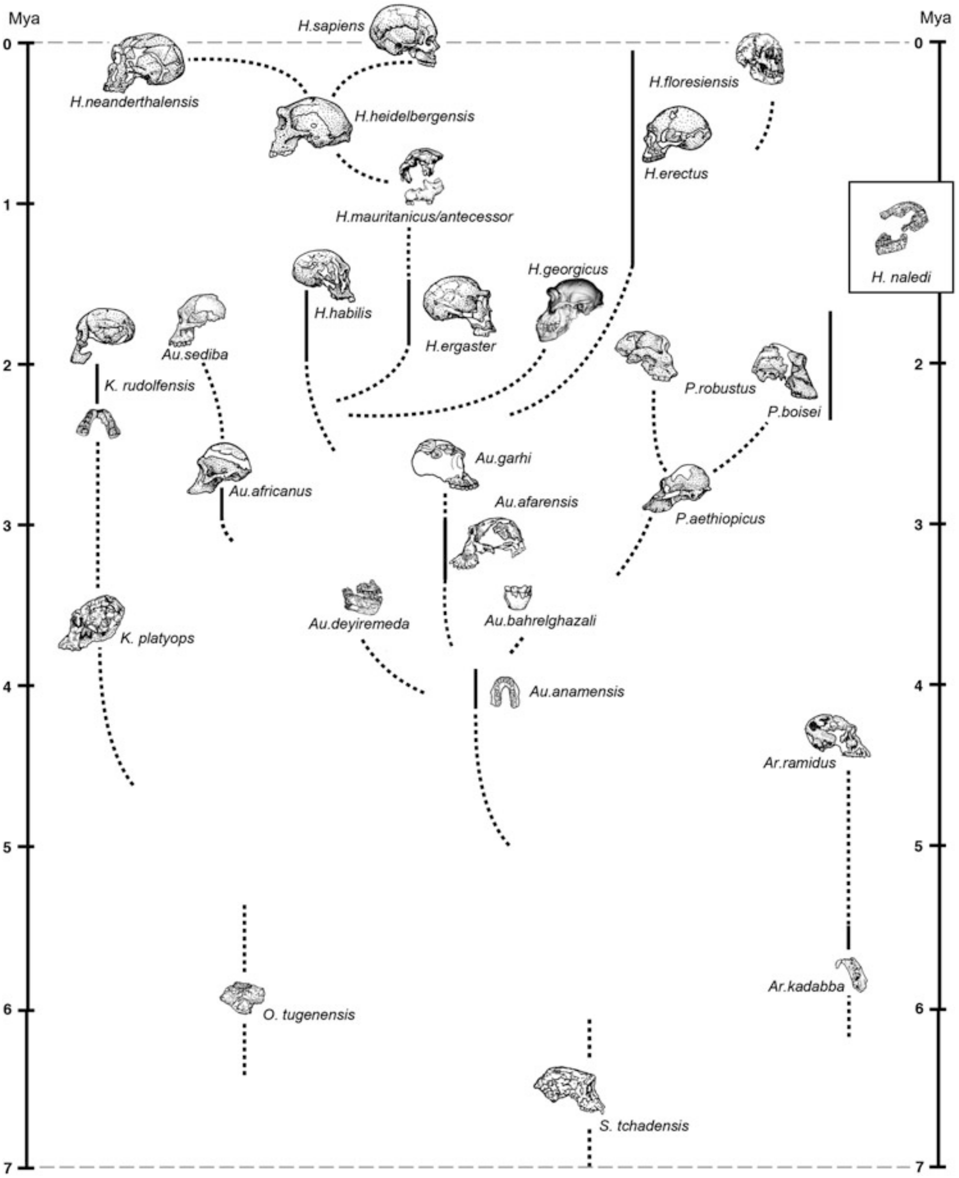

Fig. 1.2 Highly tentative phylogeny of the hominid family, showing the diversity of species currently known within the group, and indicating some possible lines of descent. Multiple hominid lineages have typically existed in parallel. Artwork by Jennifer Steffey

the common ancestor than modern chimpanzees are; and the human lineage thus seems to provide us with an example – and an extreme one – of what Simpson called "tachytely," the very fast accumulation of evolutionary change. Simpson believed that tachytelic episodes are often implicated in the origin of higher taxa, and by extension are responsible for many of the "systematic deficiencies" of the fossil record (Simpson 1953). He also observed that tachytely was to be expected when populations "are shifting from one major adaptive zone to another, and especially when a threshold is crossed" (1953: 334). This certainly appears significant when we contrast the hominoid cases just discussed. For it is certainly true that, while the brachiating siamang and gibbon lineages remain restricted to the ancestral closed tropical forests, human precursors crossed a major adaptive/habitat threshold on at least two occasions over the last seven million years or so.

The first time was when archaically-proportioned hominids committed themselves to an at least part-time terrestrial bipedal existence and a generalist diet (Sponheimer and Lee-Thorpe 2007), even as they retained a suite of climbing adaptations. The second was when early members of the genus *Homo* more or less entirely emancipated themselves from the trees, by acquiring basically modern body form and today's familiar striding locomotion. In one sense, then, the hominids conformed to Simpson's expectations by

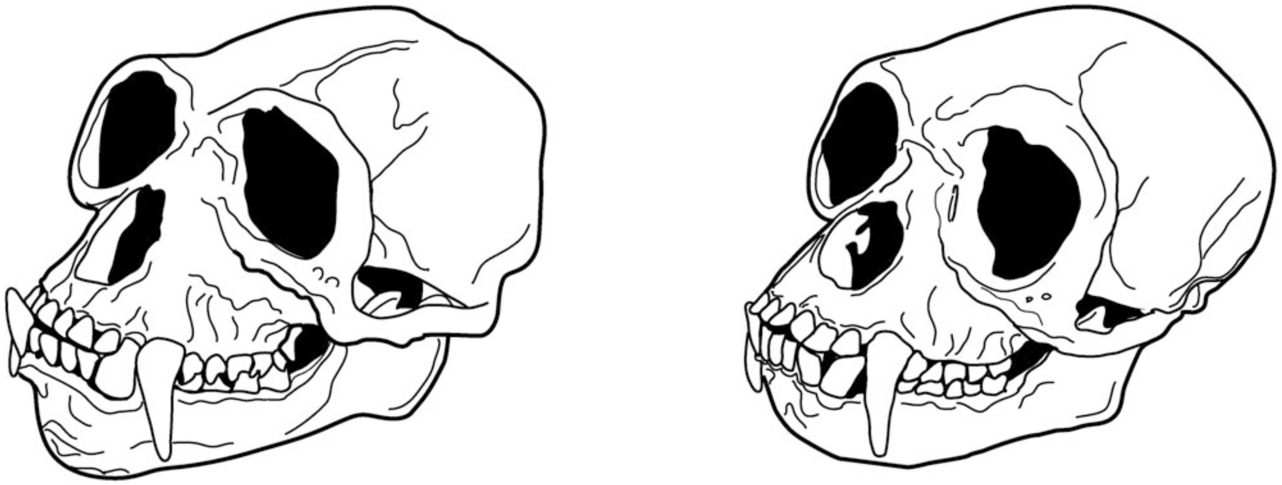

Fig. 1.3 Three-quarter views of two hylobatid crania. *Left*: siamang, (*Symphalangus syndactylus*). *Right*: gibbon (*Hylobates lar*). Drawn by Jennifer Steffey

undergoing rapid major morphological transformations in concert with major adaptive shifts. But in other respects – including having left an excellent fossil record of their transformation – hominids have departed dramatically from his predicted pattern. According to Simpson (1953: 333), "Evolution at exceptionally high rates cannot long endure. A tachytelic line must soon become horotelic, bradytelic [slow-evolving], or extinct." Yet, particularly since the birth of the genus *Homo*, when the last adaptive zone shift was achieved, high rates of both behavioral and morphological change have been remarkably consistent themes in hominid evolution. The most famous example of a consistent long-term hominid trend is, of course, the startling increase in brain size within multiple lineages of the genus *Homo* over the span of the Pleistocene (see data in Holloway et al. 2004).

Some two million years ago, hominids had brains that were, both absolutely and relatively, about the size of those of the already highly-encephalized apes. A million years later, the average hominid brain was twice as big. And today, after the lapse of another million years, it has doubled in size again. This observed increase in mean hominid brain sizes may well have been due to the success of larger-brained forms in inter-species competition for ecological space, rather than to the reproductive success of larger-brained individuals within in a gradually-modifying single lineage (Tattersall 2008). But whatever the case, this apparently steady trend represents a marked departure from the kind of tachytely that Simpson had in mind when he was seeking mechanisms for the origination of higher taxa. Clearly, the definitive abandonment of hominid dependence on trees has to count as one of the most radical shifts in adaptive zone ever made by any vertebrate, ever since the very first tetrapod heaved itself out of the water and on to terra firma. But once hominids had made their new ecological commitment – which eventually expressed itself in the occupation of an altogether remarkably wide range of open habitats – there must have been other factors at work to maintain both their persistently high rate of brain size increase and the associated morphological changes.

For reasons that are not entirely clear to me, morphologists have tended to avoid this issue, leaving the field clear for speculation by evolutionary psychologists. The reason for these scientists' intense interest is partly, of course, that the cognitive peculiarities of our species *Homo sapiens* are at least as striking as our physical ones. But perhaps more importantly, it is because if you are looking for a satisfyingly reductionist feedback scenario to explain the startling increases in hominid brain size – and, by extension, in cognitive complexity – over the span of the Pleistocene, nothing fits the bill better than a mutually reinforcing link between genes and culture. This link has been energetically promoted by evolutionary psychologists ever since Charles Lumsden and Ed Wilson published their book *Genes, Mind and Culture: The Coevolutionary Process* in 1981. There, with much mathematical folderol, these authors elaborated a notion of "gene-culture coevolution" in which, as they summarized it the following year:

> "culture is shaped by biological imperatives while biological traits are simultaneously altered by genetic evolution in response to cultural history" (Lumsden and Wilson 1982: 1).

Having made this sweeping general pronouncement, Lumsden and Wilson proceeded to apply its principles specifically to human cognition:

> "genetic and cultural evolution are inseverable, and … the human mind has tended to evolve so as to bias individuals toward certain patterns of cognition and choice rather than others" (Lumsden and Wilson 1982: 1).

A mini-industry had been founded.

Three decades on, the bandwagon continues to roll with undiminished vigor, led now by Peter Richerson and Rob Boyd. In their tellingly-titled book *Not by Genes Alone: How Culture Transformed Human Evolution*, Richerson and Boyd (2005) make a marvelous theoretical case for taking a hardened neodarwinian approach to understanding how humans acquired their extraordinary cognitive powers. From their viewpoint, evolutionary change sums out simply to the steady operation of natural selection on generation after generation of individuals, with a strong positive feedback between cultural and physical innovation. As a sweeping explanation for hominid uniqueness this is an appealing idea; after all, to smart members of a smart species, it seems intuitively obvious that being smarter is a Good Thing, and that even being a tiny bit smarter than your neighbor would be a significant advantage in the race for reproductive success. In fact, from a purely neodarwinian perspective it's hard to imagine how being smarter, or possessing any other excellent heritable quality, would not virtually *oblige* you to reproduce more successfully. In which case, as a result of the inherent feedback between genes and culture, human precursors were virtually condemned to become progressively more complex and intelligent, and by extension to have been predisposed to rapid and continuous evolutionary change.

But though it may provide reductively compelling examples in particular instances, maybe this isn't actually the whole story. For one thing, large brains are metabolically expensive as well as presumptively advantageous for reasons we cannot at present specify in any detail. For another, being smarter doesn't necessarily make you more reproductively attractive, or fleeter of foot, or keener of eye, or stronger, or more aggressive, or socially more adroit. Or any of the other things that, in a random and complicated world, might help to make you more fortunate – or simply less unfortunate – both reproductively and in simply staying alive. The bottom line here is that, in the end, it has to be the whole organism – an astonishingly complex and integrated genetic entity, with a limited number of genes doing a huge amount of work – that, for whatever reasons, succeeds or fails in the evolutionary stakes. Individually, none of the particular traits into which our orderly minds would like to dissect the whole organism can be singled out by natural selection for favor or disfavor – unless it has an unusually powerful effect on reproductive success not just at any particular point in time but consistently enough, and over a long enough period, to make a biologically meaningful difference. For most of the characteristics that paleoanthropologists are able to observe or to infer, this is rather improbable, especially in a world that was as unpredictable and constantly fluctuating as the one in which our Pleistocene precursors lived.

Still, these objections are as theoretical as the original argument; and to their great credit Richerson and Boyd readily concede how crucial empirical observation is in this context. In their words, "the world is *so* complex that without sound empirical data the theorists are blind" (2005: 257). The relevant empirical data must necessarily come from the archaeological record, which is our only source of reasonably direct proxies for ancient hominid behaviors. And, blurry and incomplete as the Paleolithic record may be as an archive of the undoubtedly rich and complex behavioral repertoires and social lives of earlier hominids, the picture it yields is not the pattern of gradual improvement that the neodarwinian feedback model of cognitive refinement predicts. Instead, we find just the opposite: major innovations tended to occur relatively suddenly, interspersed with immensely long periods during which nothing much occurred beyond the occasional refinement.

Thus, the first deliberately manufactured stone tools show up rather abruptly in the record at about 2.5 Ma (Semaw et al. 1997). There is then a wait of a million years, with one single outlier (Lepre et al. 2011), before a substantially new kind of tool is introduced, in the form of the Acheulean handaxe. And while handaxes became generally slimmer and more elegant over time, it was another million years before a new concept in stone tool making – core preparation – began to appear. To cut a long story short, what we are *not* finding here is a smooth increase in technological complexity and refinement over the past 2.5 million years. The spirit of questing and innovation we are so familiar with today simply was not expressed in the material expressions of our precursors until very recently indeed. What is more, in the period prior to the appearance of the new spirit, technological innovation (as opposed to refinement) was both sporadic and rare. What this simple observation clearly reveals, is that our modern cognitive style hardly serves as a reliable model for the ways in which our precursors dealt with information. Intellectually, they were not merely less gifted versions of us: they were doing business in entirely different ways.

This shows up in dramatic behavioral contrasts. While we modern *Homo sapiens* tend to invent new kinds of tools for new purposes, earlier hominids evidently responded to (sometimes rapidly) changing environmental circumstances by repurposing old tools. This is not to deny that those hominids were skilled, resourceful and intelligent. But it does suggest that their cognitive style was not ours. Indeed, perhaps the most telling of all of the innovations which begin to pile up toward the end of the Pleistocene was not the presumed bodily ornamentation, or the engraved symbols, or the cave art, or any of the other many striking individual expressions of the modern symbolic cognitive style that show up in that time range. Rather, it was a profound shift in the tempo of change itself. Technological innovation became the norm, rather than the exception. This implies a relatively abrupt, qualitative change in mental information processing, rather than simply an incremental improvement on what was there before (Tattersall 2008, 2012). What is more, the example of the non-symbolic and comparatively plesiomorphic but nonetheless large-brained Neanderthals demonstrates that neither our cranial configuration, nor our unusual cognitive status, can be interpreted as merely a passive consequence of our large brain size. We thus cannot view either of these modern human features as merely an extrapolation of long-running established trends.

All of this suggests that the apparent long-term feedback between culture and morphology in human evolution is an artifact of evolutionary model, rather than something we can hypothesize from empirical evidence. Indeed, even the culture/biology link seems tenuous, at least as proposed. But if the high average rate of morphological and cognitive change among hominids was not driven by the acquisition of modern body form; and if it was not driven in a linear way by a feedback between incremental cognitive/cultural improvements and reproductive success, then what *was* the factor that drove the extraordinary tachytely in Pleistocene *Homo*?

Perhaps oddly in light of what I have just said, in answering this key question I am nonetheless going to implicate culture, which has certainly been omnipresent as a central and basically unique fact of hominid life throughout the tenure of the genus *Homo*. Culture is, of course, a famously slippery concept, and the word means very different things to different people. By the narrowest definition, culture may not even be unique to humans (Mercader et al. 2007); and the issue is undoubtedly complicated by the fact that the incredibly complex behavioral expressions we see today in *Homo sapiens* are a reflection of our unique and recently acquired cognitive mode, rather than linear extrapolations of simpler behavioral forms that may have preceded them. Here I shall use “culture” in its narrow material sense, as reflected by the tangible products of technology, and the behaviors directly associated with manufacturing and using those products. I am not concerned with any wider social or cognitive implications.

This restricted definition has one singular advantage. For everyone can agree that, by substantially extending the phenotype, material culture constituted a major element in our precursors’ ability to respond to the external and adventitious climatic changes that regularly assailed them over the course of the Pleistocene (e.g., van Andel and Davies 2003). And it is in the context of those external changes, rather than as an expression of any intrinsic dynamic, that the effects of material culture would have made themselves felt among Pleistocene *Homo*. Here’s why. It has been clearly understood for many years that both small effective sizes and physical isolation are essential for the fixation of genetic novelty in populations of complex mammals like primates (Eldredge and Cracraft 1980). In large and continuous populations there is simply too much genetic inertia for either chance or selection to drive the incorporation of heritable novelties while, in contrast, within small ones the incorporation of such novelties – whether for chance or for selective reasons – seems to be routine. And, as it happens, the conditions in which Pleistocene members of the genus *Homo* evolved were hugely propitious for the fixation of genetic changes. These ancient hominids were almost certainly widely but thinly spread across the landscape, in small groups that probably belonged to relatively isolated population clusters. At the same time they were amazingly mobile, and it appears that demographic pressures toward expansion *within* those sparse populations were probably fairly intense, as we can fairly infer from the extremely rapid rate of spread of early *Homo* species. For example, hard on the heels of the first appearance of *Homo* in Africa, hominids widely considered to be of our genus had already ventured as far afield as Dmanisi in the Caucasus (e.g., Gabunia et al. 2000), even though the cool temperate environment there was very unlike any of the habitats the hominids’ predecessors had ever had to cope with in their home continent (Messager et al. 2011).

As an immediate consequence of their first known movement out of Africa, hominids were thus already occupying a range of environments far broader than any documented for even the most eurytopic of primates today. Almost certainly, this penetration of new ecological zones was made possible by some form of cultural accommodation to local conditions. Indeed, much as Phillip Tobias (1995) observed in another context entirely, it seems likely that even at this early point cultural *accommodation* had become more important than biological *adaptation* as a factor governing hominid history. Exactly what the factor was that facilitated the Dmanisi hominids’ penetration of the dry temperate zone must remain conjectural, since in terms of preserved technology there is no conceptual difference between the stone tools produced at Dmanisi and those that had already been produced in Africa for hundreds of thousands of years (e.g., Gabounia et al. 2002). But it seems reasonable to hazard that it was cultural accommodation that made it possible for the Dmanisi hominids to flourish in unfamiliar environmental conditions. And even were this not the case, it is evident that in later times it was material cultural innovations such as clothing, fire use, and shelter construction that eventually made possible later range expansions by *Homo* populations into yet more difficult environments to the north and west of the Caucasus.

Yet, while to some extent they almost certainly insulated hominids from the direct effects of biological selection, at least prior to the modern era technology and material culture had their functional limits. Of course, there can be little doubt that even simple material cultures would have had the potential to buffer hominid populations from some effects of the environment, and to allow its more efficient exploitation.

In favorable times cultural practices would certainly have facilitated geographic expansion of hominid populations into new environments. Equally likely, they would have made this occupation possible at higher population densities than would otherwise have been the case. But, in an age of dramatic climatic swings, material culture would not always have sufficed to maintain those larger populations in marginal zones when conditions became less propitious. At times of climatic deterioration, such as the onset of drought or extreme cold, hominid populations would have had to abandon difficult territories, becoming locally extinct where technological compensation failed. Even where culture may have allowed the survival of reduced and isolated population remnants, the new demographic and geographical circumstances would have enhanced the probabilities of biological divergence through drift alone, though it is not possible to preclude some biological adaptation to the new conditions.

From this perspective, one may consider material culture to be a factor that confers enhanced survival in isolation, and thus to be a potential initial trigger for both diversification and possible speciation. But by allowing generous range expansions in good times, material culture would also have made the "artificially" enlarged hominid populations more vulnerable to fragmentation in unfavorable conditions for which it could not completely compensate. Over the span of the climatically unsettled Pleistocene, multiply repeated sequences of such events would frequently have created the ideal conditions, in numerous and widely scattered hominid subpopulations, for the fixation of genetic novelties. Hence the tachytely we observe among Pleistocene hominids, expressed in parallel accelerated rates of accumulation of such novelties in multiple hominid lineages.

Of course, the basic dynamic involved here is a normal and fairly elementary feature of the evolving world. But, among hominids, cultural accommodation to unpredictably varying conditions would have created a sort of ratchet effect for evolutionary innovation. In good times, populations would have expanded into areas that lay climatically beyond their purely physiological limits. But when environmental conditions deteriorated beyond what prevailing material culture could cope with, those populations would have been fractured into small, genetically unstable units. If they contrived to avoid extinction these would, in turn, have been reunited when climatic amelioration occurred.

If speciation had intervened during the period of isolation, the result would have been competition among the newly reunited populations and the eventual elimination of some of them, potentially leading to the "trends" we discern in the fossil record. In the absence of speciation the entirely different phenomenon of reintegration would have occurred; but biologically it would have been equally significant, allowing the incorporation into the expanded population of genetic novelties that could never have become fixed if the earlier fragmentation had not happened. A further possibility is that cultural accommodation would have served to keep genetic novelties alive in populations that would otherwise have gone extinct, and have taken those novelties with them into oblivion.

Still, whatever the exact mechanism at work in any particular case, the possession by hominids of material culture in a fluctuating world would have had a profound effect on the evolutionary pattern we see in retrospect, reflected in the fossil record. In this perspective it is externally-mediated effects of this kind, rather than any internal dynamic, which place culture as such a powerful putative facilitator and accelerator of hominid evolutionary change, on both the physical and cognitive levels.

In a world of perpetual climatic and environmental oscillation, both the limits and the upside potential of technology provide us with plausible starting-points from which to examine the extraordinarily rapid rate of accumulation of morphological novelty in hominid populations over the last two million years. In its dual roles as facilitator of geographic expansion in good times, and as incomplete insulator in bad ones, material culture certainly seems more plausible as an explanatory agent for hominid tachytely than any amount of feedback between cognitive prowess – or any morphological factor – and individual reproductive success.

Finally, the most powerful metaphor for rapid hominid change over the Pleistocene is the remarkable rate of brain expansion in this group. Yet it is notable that, within the single surviving species *Homo sapiens*, the last 20 kyr or so have seen a trend toward brain size *reduction* (see Hawks 2011 and references therein). For example, Holloway et al. (2004) cite a mean brain size for a worldwide sample of recent humans of 1,330 ml. This contrasts with a mean of 1499 ml for a sample of 29 Late Pleistocene *Homo sapiens* calculated from Appendix 1 of the same source: a figure some 12.7% greater than the contemporary one. Various explanations have been put forward for this phenomenon, which cannot be explained by commensurately shrinking body size (Hawks 2011). Attempts have been made, for example, to associate endocranial volumes with climate, or more narrowly with prevailing temperatures (e.g., Beals et al. 1984). However, Bailey and Geary (2009) reject such climatic hypotheses in favor of a "dumbing-down" notion, whereby membership in increasingly complex societies placed decreasing intellectual demands on the individual. In essence, these authors argue that more elaborate social safety nets substituted for raw brain power. Wrangham (2011) blames "self-domestication" for the diminution of the human brain:body size ratio (brain sizes are typically reduced some 10–15% in domestic forms compared to their wild counterparts), while Hawks (2011) more vaguely associates smaller endocranial volumes with "higher fitness" resulting from unspecified causes.

Yet, one obvious explanatory possibility for brain diminution has been overlooked. The earliest anatomically modern *Homo sapiens*, known from eastern Africa in the period following 200 ka, had large brains that appear to have functioned much as the Neanderthals' equally large brains did (Tattersall 2012). The fateful shift to the symbolic information processing mode already referred to appears to have happened significantly later, in the period following about 100 ka. Once this shift had occurred, the metabolically expensive human brain found itself working on a new and different processing algorithm: one that was less dependent on the sheer volume of brain tissue than on the specific nature of the operations and connections within it. Quite simply, a more efficient algorithm may have permitted a reduction in the quantity of energy-hungry brain tissue, while simultaneously making possible a qualitative leap in processing power.

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References

Bailey, D. H., & Geary, D. C. (2009). Hominid brain evolution: Climatic, ecological, and social competition models. *Human Nature, 20*, 67–79.

Beals, K. L., Smith, C. L., & Dodd, S. M. (1984). Brain size, cranial morphology, climate and time machines. *Current Anthropology, 25*, 301–330.

Collard, M., & Wood, B. (2015). Defining the genus *Homo*. In W. Henke & I. Tattersall (Eds.), *Handbook of paleoanthropology* (2nd ed., pp. 1575–1610). Berlin: Springer.

de Heinzelin, J., Clark, J. D., White, T., Hart, W., Renne, P., WoldeGabriel, G., et al. (1999). Environment and behavior of 2.5 million-year-old Bouri hominids. *Science, 284*, 625–629.

Eldredge, N., & Cracraft, J. L. (1980). *Phylogenetic patterns and the evolutionary process*. New York: Columbia University Press.

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C. C., Ferring, R., Justus, A., et al. (2000). Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting and age. *Science, 288*, 1019–1025.

Gabounia, L., de Lumley, M.-A., Vekua, A., Lordkipanidze, D., & de Lumley, H. (2002). Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *Comptes Rendus Palevol, 1*, 243–253.

Hartwig, W. (Ed.). (2002). *The primate fossil record*. Cambridge, UK: Cambridge University Press.

Hawks, J. (2011). Selection for smaller brains in Holocene human evolution. arXiv:1102.5604v1.

Holloway, R. L., Broadfield, D. C., & Yuan, M. S. (2004). *The human fossil record, vol. 3: Hominid endocasts, the paleoneurological evidence*. New York: Wiley-Liss.

Kimbel, W. H., Johanson, D. C., & Rak, Y. (1997). Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *American Journal of Physical Anthropology, 103*, 236–262.

Leakey, M. G., Spoor, F., Brown, F. H., Gathogo, P. N., Leakey, L. N., & McDougall, I. (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature, 410*, 433–440.

Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J.-P., et al. (2011). An earlier origin for the Acheulian. *Nature, 477*, 82–85.

Lumsden, C., & Wilson, E. (1981). *Genes, mind and culture: The coevolutionary process*. Cambridge, MA: Harvard University Press.

Lumsden, C., & Wilson, E. (1982). Précis of *Genes, mind and culture*. *Behavioral and Brain Sciences, 5*, 1–7.

Matsudaira, K., & Ishida, T. (2010). Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. *Molecular Phylogenetics and Evolution, 55*, 454–459.

Mercader, J., Barton, H., Gillespie J., Harris, J., Kuhn, S., Tyler, R., et al. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Science, USA*, *104*, 3043–3048.

Messager, E., Lebreton, V., Marquez, L., Russo-Ermoli, E., Orain, R., Renault-Miskovsky, J., et al. (2011). Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: New palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. *Quaternary Science Reviews, 30*, 1439–1447.

Pickering, R., Dirks, P. G. M., Jinnah, Z., de Ruiter, D., Churchill, S. E., Herries, A. I. R., et al. (2011). *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*. *Science, 333*, 1421–1422.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

Schrenk, F., Bromage, T., Betzler, C., Ring, U., & Juwayeyi, Y. (1993). Oldest *Homo* and Pliocene biogeography of the Malawi Rift. *Nature, 365*, 833–836.

Schwartz, J. H., & Tattersall, I. (2005). *The human fossil record, vol. 3: Genera* Australopithecus, Paranthropus, Orrorin, *and overview*. New York: Wiley-Liss.

Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., et al. (1997). 2.5 million-year-old stone tools from Gona. *Ethiopia. Nature, 385*, 333–336.

Simpson, G. G. (1944). *Tempo and mode in evolution*. New York: Columbia University Press.

Simpson, G. G. (1953). *The major features of evolution*. New York: Columbia University Press.

Sponheimer, M., & Lee-Thorp, J. (2007). Hominin paleodiets: The contribution of stable isotopes. In W. Henke & I. Tattersall (Eds.), *Handbook of Paleoanthropology* (Vol. 1, pp. 554–585). New York: Springer.

Susman, R., Stern, J. T., & Jungers, W. L. (1984). Arboreality and bipedality in the Hadar hominids. *Folia Primatologica, 43*, 113–156.

Stone, A. C., Battistuzzi, F. U., Kubatko, L. S., Perry, G. H., Jr., Trudeau, E., Lin, H., et al. (2010). More reliable estimates of divergence times in *Pan* using complete mtDNA sequences and accounting for population structure. *Philosophical Transactions of the Royal Society B, 365*, 3277–3288.

Tattersall, I. (2008). An evolutionary framework for the acquisition of symbolic cognition by *Homo sapiens*. *Comparative Cognition and Behavior Reviews, 3*, 99–114.

Tattersall, I. (2012). *Masters of the planet: The search for our human origins*. New York: Palgrave Macmillan.

Tattersall, I., & Schwartz, J. H. (2009). Evolution of the genus *Homo*. *Annual Reviews of Earth and Planetary Sciences, 37*, 67–92.

Tobias, P. V. (1995). *The communication of the dead: Earliest vestiges of the origin of articulate language*. Amsterdam: Kroon Lectures, Stichting Nederlands Museum voor Anthropologie en Praehisoire.

Van Andel, T. H., & Davies, W. (Eds.). (2003). *Neanderthals and modern humans in the European landscape during the last glaciation*. Cambridge, UK: McDonald Institute for Archaeological Research.

Wood, B., & Collard, M. (1999). The human genus. *Science, 284*, 65–71.

Wrangham, R. (2011). Chimpanzees, bonobos and the self-domestication hypothesis. *American Journal of Primatology, 73*, 33–45.