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Chapter 2

GENETIC DRIFT IN RECENT HUMAN EVOLUTION?

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ABSTRACT

Among the several main reasons for the present gradual demise of the hitherto dominant hypotheses of 'modern' human origins, the replacement or 'out of Africa' models, are the issues of genetic drift and introgression. The operation and consequences of genetic drift are considered, especially in terms of their effects on the evolution of the human species during the Late Pleistocene period. The complexity of the subject is reviewed in the light of several relevant frames of reference, such as those provided by niche construction, gene-culture co-evolutionary theories, and by the domestication hypothesis. The current cultural, genetic and paleoanthropological evidence is reviewed, as well as other germane factors, such as the role of neurodegenerative pathologies, the neotenization of humans in their most recent evolutionary history, and the question of cultural selection-based self-domestication. This comprehensive review leads to a paradigmatic shift in the way recent human evolution needs to be viewed. This article explains fully how humans became what they are today.

INTRODUCTION

Although the notion of genetic drift dates back to the work of Seawall Wright (1929), it was properly developed only in the second half of the 20th century—as indeed applies to the discipline of genetics generally (Mendel 1866). Kimura formalized the idea in his 'neutral theory of molecular evolution' (Kimura 1968, 1983), which to this day remains central to the issue. It postulates that most evolutionary changes at the molecular level are caused by a stochastic process of drift of 'selectively neutral mutants'. Genetic drift thus refers to accidental random events that influence allele frequency, i.e. the forms of the DNA sequence of a particular gene at a given position on a chromosome. It thus contrasts sharply with the

process of natural selection (Darwin 1859), the second major evolutionary determinant, which favors gene variants on the basis of reproductive success alone. In both cases allele frequencies change over time, but they do so by quite different mechanisms. Genetic drift derives initially from the fact that the alleles in offspring are random samples of the parents', but the law of large numbers in probability theory ensures that the cumulative effects of drift are very small in large populations: the random nature of the process will average out, even though only a fraction of all zygotes become mature adults. Another aspect of genetic drift is the role of chance in determining whether an individual organism thrives, survives and reproduces. Numerous eliminating effects in nature are completely random, such as volcanic or tectonic events, wildfires or tsunamis; they are not very effective in any Darwinian sense. Thus genetic drift is an evolutionary process that does not produce adaptations.

Due to chance assortment of chromosomes at meiosis, not all of the alleles of a pair of diploid sexually reproducing parents are transmitted to their offspring, especially in species with low reproduction numbers (Suzuki et al. 1989: 704). In very small populations, genetic drift tends to lead to the rapid loss of some genetic traits and the establishment of traits unrelated to the reproductive or survival value of the alleles involved. Such small populations are very common in nature, especially in demes and specific environmental or geographic settings. Genetic bottlenecks and the founder effect are specific expressions of genetic drift, and in contrast to both natural selection and drift, they can often be empirically tested or demonstrated. Examples are the low genetic variability of the cheetah and the northern elephant seal. The latter's population was reduced to fewer than twenty animals by 1890, and the present recovered population, over 1500 times greater, offers an extreme example of the effects of genetic drift. The changes to the genome of the elephant seal over less than 200 years have very little to do with natural selection; they are attributable to population depletion by over-hunting.

The founder effect can be illustrated with such examples as the Icelandic cattle, differing genetically from the Norwegian deme they derive from; or with the fruit flies of Pacific islands. There are also relevant instances of human cases, e.g. the lack of blood group B in American indigenes, or the genomes of reproductively isolated groups, such as the Amish. More dramatic examples are provided by the endemic insular populations recently reported from Flores and Palau. The first island has provided skeletal remains of a Late Pleistocene primate some claim to be a new species, *Homo floresiensis* (Morwood et al. 2004; Morwood and van Oosterzee 2007), while others perceive in them evidence of congenital or genetic conditions probably attributable to a combination of founder effect, genetic isolation and a high inbreeding coefficient (Henneberg and Schofield 2008). On Rock Island, Palau, Lee R. Berger has excavated dozens more tiny human skeletons. These are about the same size as the first Flores specimen, with adult body weight estimated to be as low as 28 kg, and they, too, exhibit distinctive traits often interpreted as primitive. These include reduction of the absolute size of the face, pronounced supraorbital tori, non-projecting chins, relative megadontia, expansion of the occlusal surface of the premolars, rotation of teeth within the maxilla and mandible, and dental agenesis. But in contrast to the Flores team, Berger had no hesitation defining the Palauan specimens as 'fully modern' *Homo sapiens sapiens*, subjected to founder effect that has perhaps caused Laron Syndrome (Hershkovitz et al. 2007).

It is far more difficult to find direct, empirical evidence of natural selection in humans (the sickle cell allele and lactose tolerance being notable exceptions), although that process was recognized much earlier than genetic drift. Multiple adaptive peaks and the random

fixation of less fit alleles are among the factors ensuring that natural selection does not yield theoretical optimum results (Suzuki et a. 1989), as is commonly assumed. Since species often evolve in the form of demes, i.e. in relatively small populations, genetic drift is perhaps far more effective in speciation. In *allopatric* or geographic speciation, biological populations become completely isolated, usually through sea level fluctuations or tectonic plate events, although severe climatic changes may have the same effect, and in some species even minor separation can suffice. Given enough time (and speciation may take as much as a million years), the populations then evolve separately and differently, and may eventually become different species, i.e. they can no longer produce fertile offspring. *Peripatric* or *parapatric* speciation can occur when a small part of a larger population enters an isolated niche and because of it becomes genetically so isolated that the same applies. *Sympatric* speciation is the process by which, in theory, a new species originates from another without being geographically separated from it. Although common in bacteria, it is thought to be an uncommon process in multicellular life forms, by which genetic divergence (through reproductive isolation) of various populations from a single parent species and inhabiting the same geographic region leads to the creation of new species. Despite a number of empirical examples having been reported in recent decades (e.g. Lodé 2001; Barluenga et al. 2006), these could perhaps just be variations of the parapatric speciation theme. Examples of sympatric speciation tend to invoke selection rather than genetic drift.

In this chapter, however, attention will be focused on the articulation between genetic drift and other factors contributing to the development of just one species, our own, during a very short period of its evolutionary history, the Final Pleistocene (its last forty millennia). Expressions of genetic drift in the current human genome will be considered together with the several other factors that have shaped that genome. More specifically, the involvement of introgression, niche construction, and selective breeding or domestication will be examined at length, and gene-culture co-evolution will be identified as the prime mover of recent human development. All of these explanations of evolutionary processes contrasting with plain natural selection are at significant variance with the currently still dominant paleoanthropological and archaeological model of recent human evolution, the replacement hypothesis (‘African Eve’) and the various other Out-of-Africa (OoA) models, which have governed most relevant discourse over the past few decades. How was it possible that such a highly unlikely demographic scenario, completely lacking any archaeological, paleoanthropological or even credible genetic evidence, was ever capable of gaining such prominence? Although ‘absence of evidence seldom slows the spread of fashionable ideas’ (Bickerton 2010: 90), this is an issue that does cry out for detailed historical examination. The hypotheses were initially derived from the claims of an academic charlatan, Professor Reiner Protsch ‘von Zieten’ (the aristocratic title was as bogus as his second doctorate; Schulz 2004), who invented the notion of a recent rise of ‘anatomically modern humans’ exclusively in Africa, from where they conquered the world (Protsch 1973, 1975; Protsch and Glowalski 1974; Protsch and Semmel 1978; Henke and Protsch 1978). By the late 1980s, the academic memes created by this idea, of mitochondria mutations and OoA, were taking over world archaeology (Cann et al. 1987), despite the voices cautioning against this notion even then:

> This does not mean that there was a single female from whom we are all descended, but rather that out of a population numbering perhaps several thousand, by chance, only one set of mitochondrial genes was passed on. (This finding, perhaps the most surprising to us, is the

> least disputed by population geneticists and others familiar with genetic drift and other manifestations of the laws of probability.) (Curtis and Barnes 1989: 1050)

Before any aspect of recent human evolution can be considered meaningfully, it is essential that paleoanthropology be entirely purged of these refuted hypotheses, a process that may still take many more years. In this chapter, only a short explanation can be given before moving on to more important matters.

THE AFRICAN HOAX

The OoA or short-range model of recent human evolution perceives a sudden cultural change occurring in Europe about 35,000 years (35 ka) ago, which it attributes to an incursion of African immigrants of superior cognition and technology, often linking it to the introduction of language (Davidson and Noble 1989, 1990; Noble and Davidson 1996). It rejects all evidence of symbolism and many other markers of human modernity prior to the advent of these gifted Africans, at some point between 100 ka and 200 ka ago, and regards any cultural complexity in the rest of the world as having been introduced by these colonizers. Sometimes called the 'discontinuist' model (d'Errico and Nowell 2000), its first version, by Protsch, was emulated by the 'Afro-European *sapiens'* model (Bräuer 1984a: 158), followed by the 'African Eve' complete replacement scenario (Cann et al. 1987; Stringer and Andrews 1988), the 'wave theory' (Eswaran 2002) and the 'assimilation theory' (Smith et al. 2005). Of these, the mitochondrial Eve model is the most extreme, in the sense that it demands a complete lack of interbreeding between its African species and any other humans. It therefore has no choice but to postulate that these Africans, which it calls 'anatomically modern humans' or simply 'Moderns', are a species different from the robust recent humans they either displaced or exterminated. The more moderate varieties of the short-range model accept the occurrence of mixing between robust and gracile forms and therefore are merely variations of the multiregional theory (Weidenreich 1946; see Relethford 2002; Relethford and Jorde 1999), simply claiming a strong inflow of African genes.

These various hypotheses are of considerable relevance to this book because the only possible explanation for the perceived speciation required to yield these Graciles is genetic drift: somehow a local population in sub-Saharan Africa must have become so isolated from the rest of the continent's human genome that rapid genetic change became possible, creating a new species that was no longer interfertile with other Africans. This would explain the postulated bottleneck, culminating in the notion of the single female all Holocene humans are related to. But when protagonists of the replacement hypothesis cite possible genetic bottlenecks to contrive explanations for inherent weaknesses of their model, they overlook that genetic bottlenecks tend to reduce fitness in the population (Bryant et al. 1986; Berger et al. 2008), rather than bring about the population's supremacy (cf. Hawks et al. 2000) as proposed for Eve's progeny. Already at this point the hypothesis begins to falter, because while the replacement model is untenable without a bottleneck, it implicitly rejects the tenets of genetic drift by creating the genetic trees its claims are based on. These unfalsifiable (and thus unscientific) constructs assume not only constant rates of genetic change; they even pretend to deliver divergence times, i.e. the dates when one species splits from another. This 'genetic clock' is without any scientific basis: none of the crucial variables can be known

(such as number of colonization events [Bednarik and Kuckenburg 1999], demographies or true base pair substitution rates), and this is borne out by the 'results' of these 'molecular archaeology' claims: the hypothetical split between 'Moderns' and other humans has been placed at times ranging from 17 to 889 ka bp. Contentions concerning mitochondrial DNA (African Eve) are as much afflicted by this lack of credibility as are those citing Y-chromosomes ('African Adam'; Hammer 1995). The divergence times projected from the diversity found in nuclear DNA, mtDNA, and DNA on the non-recombining part of the Y-chromosome differ so much that a time regression of any type is extremely problematic. Contamination of mtDNA with paternal DNA has been demonstrated in extant species (Gyllensten et al. 1991; Awadalla et al. 1999; Morris and Lightowlers 2000; Williams 2002), in one recorded case amounting to 90% (Schwartz and Vissing 2002). Not only was Cann et al.'s (1987) assumption about exclusive maternal transference of mitochondria without basis, the constancy of mutation rates affecting mtDNA was also a myth (Rodriguez-Trelles et al. 2001). Molecular time estimates are asymmetrically bounded random variables, constrained by a nonelastic boundary at the lower end, but not at the higher end of the distribution. This introduces a bias toward an overestimation of time since divergence, and Rodriguez-Trelles et al. (2002) have identified a fundamental flaw of molecular dating methods, rendering the mitochondrial 'genetic clock' ineffective.

Kidd et al. (1996) have shown that, outside Africa, the elements of which haplotypes are composed largely remain linked in a limited set. Gibbons (1998) observed that by using the new putative 'genetic clock', Eve would not be 200 ka old (Cann et al. 1987), but only 6000 years. By then the issue had become farcical: Cann et al. had not only been based on botched computer modeling, its haplotype trees were fantasies that could not be provided with time depth even if they were real. To render these issues even more ludicrous, the transfer of genetic information is not, as many seem to assume, limited to DNA. For instance ribonucleic acids associated with the brain's thrombospondin (THBS4 and THBS2) can carry such information (Christopherson et al. 2005; Cáceras et al. 2007), and epigenetic, behavioral and symbolic inheritance systems need to be considered as well (Jablonka and Lamb 2005).

The genetic picture in Africa as well as elsewhere has been found to be far more complicated than the Eve proponents ever envisaged. The much-promoted claims that 'Neanderthals' (a term used here only to comply with widespread usage, without endorsing it) were genetically different from modern Europeans, based on very fragmentary DNA sequences, were erroneous, Gutierrez et al. (2002) have shown. Their analysis suggests that the pair-wise genetic distance distributions of the two human groups overlap more than claimed, if the high substitution rate variation observed in the mitochondrial D-loop region (Walberg and Clayton 1981; Torrini et al. 1994; Zischler et al. 1995) and lack of an estimation of the parameters of the nucleotide substitution model are taken into account. Moreover, the results presented from museum specimens, especially 'Neanderthal' remains, are probably irrelevant. Pruvost et al. (2007) have recently shown that DNA deteriorates rapidly after excavation, up to fifty times as fast as in buried specimens. The various reported 'fragmentary DNA sequences' from 'Neanderthal' remains stored for up to 150 years need to be considered in that light. A large part, on average 85%, of the genetic material preserved in fossils is lost as a result of treatment by archaeologists and storage in museums, therefore the results disseminated from these specimens and their interpretations may be questioned. More reliable are genetic studies of living populations, which have shown that both Europeans and Africans have retained significant alleles from multiple populations of Robusts (Hardy et al.

2005; Garrigan et al. 2005; cf. Templeton 2005). In fact, the Neanderthal genome seems to include an excess of human-derived single nucleotide polymorphisms (Green et al. 2006). Recent genetic analyses confirm not only that 'Neanderthal' genes persist in recent Europeans, Asians and even Papuans (Green et al. 2010), but also that "it seems Neandertals interbred with the ancestors of Europeans and Asians, but not with the ancestors of Africans" (Gibbons 2010; cf. Krings et al. 1997). In Green et al.'s words, "[g]iven that the OOA alleles occur at a frequency of much less than 50% in non-Africans (average of 13%, and all less than 30%), the fact that the candidate regions match the Neandertals in 10 of 12 cases (P = 0.019) suggests that they largely derive from Neandertals". Thus the African Eve model has become an absurdity: it is precisely Africans who had the least contact with Europeans. Moreover, even the Green et al. pronouncements are incorrectly expressed: 'Neanderthals' did not interbreed with our ancestors; they *are* our ancestors. If Green et al. wanted to demonstrate that there were genetically very different populations around at the time, they would have to present *their* genomes' details, not only those of the Robusts.

The analysis and interpretation of paleogenetic, ancient DNA (Pääbo 1989), remains an experimental method and those who over-interpret its results tend to overlook its limitations. Initial results were obtained from a quagga (Higuchi et al. 1984), an Egyptian mummy (Pääbo et al. 1985), a moa (Cooper et al. 1992), and a cave bear (Noonan et al. 2005), before the genome of *Homo sapiens neanderthalensis* was tackled (Green et al. 2006). But paleogenetics poses challenges that differ significantly from *in vivo* studies, because DNA suffers both mechanical and chemical degradation through time and there are high sequencing error and template damage rates (Pääbo et al. 2004; Pruvost et al. 2005, 2007; Orlando and Hänni 2008). It is certainly easier to template modern DNA than ancient DNA. Results of the polymerase chain reaction (PCR) amplifications, performed by clonage, need to be repeated and three negative controls have to be added to safely detect contamination. Then there is the potential, particularly in moist conditions, of hydrolytic cleavage of phosphodiester bonds between phosphate and sugar (Jolivet and Henry 1994: 180). Similarly, sugars and amino groups in proteins and nucleic acids, caused by condensation, can react and lead to errors during PCR. Deamination of cytosine in xanthine, guanine and uracil, or adenine in hypoxanthene can occur, involving the incorporation of nucleotide in the process of PCR amplification. The issues of base substitution (Lindhal and Nyberg 1972) and fragmentation of DNA (Golenberg et al. 1996) have long been known, and the point is demonstrated, for instance, by the erroneous results obtained from the DNA of insects embedded in amber (Gutierrez and Marin 1998). Other problems with interpreting or conducting analyses of paleogenetic materials are alterations or distortions through the adsorption of DNA by a mineral matrix, its chemical rearrangement, microbial or lysosomal enzymes degradation, and lesions by free radicals and oxidation (Geigl 2002; Carlier et al. 2007). These scientific qualifications are generally unheeded in the archaeological folklore established around the 'authoritative' DNA data, in much the same way as archaeologists usually fail to heed the reservations of scientists concerning most archaeometric data (e.g. the dating of rock art; Bednarik 1996, 2002; Watchman 1999). Such results are always grossly simplified, misinterpreted and over-interpreted, and then embedded in the mythology of mainstream archaeology. In the case of paleogenetic data, they have been eagerly seized by one or another school of thought to support its case or discredit that of the opponents. Yet at no stage do most archaeologists make a concerted effort to appreciate the reservations scientists have.

For instance there are considerable complexities concerning the accumulation of base substitutions, or mutations, that are not even relevant to natural selection. The mechanisms governing DNA mutation rates, which are so central to the archaeological claims involving genetics, are not at all well understood. Those mutations that have no selection consequences, 'neutral' mutations, are also reflected in DNA mutation rates, which can be estimated by comparing neutrally evolving sequences in species that share a common ancestor. Sequences that are high in pairs of the bases C and G (CpGs) have been positively correlated with mutation rate. However, the chemical modification of CpGs makes them prone to mutation themselves, and with time they are eliminated from neutrally evolving sequences. Walser and Furano (2010) have taken advantage of this property to investigate the role of CpGs on the mutation rate of non-CpG DNA by comparing 'old' and 'young' sequences. They found that CpGs are not only promoting mutations, but they are also influencing how the non-CpG sequences around them are being mutated. In determining the neutral non-CpG mutation rate as a function of CpG content they compared sequence divergence of thousands of pairs of neutrally evolving chimpanzee and human orthologs that differ primarily in CpG content. Both mutation rate and mutational processes are contingent on the local CpG content.

In the absence of any reliability of the many proposed rates of nucleotide changes and the many variables to be accounted for effectively, the contentions by the replacement advocates were unsupported from the beginning of their campaign, and nucleotide recombination renders their views redundant (Strauss 1999). Instead of unambiguously showing that 'anatomically modern humans' (whatever that ethnocentric term is intended to mean) originate in one region, sub-Saharan Africa, all the available genetic data suggest that gene flow occurred in Old World hominins throughout much of human evolution (Templeton 1996, 2002), which is also strongly suggested by all available empirical evidence, both paleoanthropological and archaeological. For instance, the evidence that *Homo sapiens neanderthalensis* managed to live and subsist at the Arctic Circle, in temperatures that would at times have been below -40°C (Schulz 2002; Schulz et al. 2002; see also Pavlov et al. 2001), easily dispatches the notion that there were great expanses of habitable land in Europe by the beginning of the Late Pleistocene that remained unoccupied by humans. The Finnish evidence, dating back 135 ka BP, suggests that these innovative people coped with extreme climatic conditions then, and that the demographic modeling of Pleistocene archaeologists (e.g. Gamble 1999) must be largely false. If human groups on the margins were forced into regions of truly appalling living conditions the presence of largely continuous populations can safely be assumed in much of the Old World, and by 50 ka even in Australia.

Comparing the genome of Robusts with that of present-day people, as has been done, is futile; what would need to be compared are the genetic signatures of Robusts and the Graciles contemporary with them, and this has not been attempted. But there are many other unmet conditions to help support the replacement hypothesis. If the Graciles were cognitively and technologically superior to the Robusts, there would need to be distinctive differences in their toolkits, other artifacts and ecological strategies. None are apparent in any of the many regions where people of both somatic forms coexisted, often for very long periods of time. In all such cases, from Spain to Australia, the two populations used very similar or identical technologies, even ornaments. 'Neanderthals' produced beads and pendants, and very probably the earliest surviving cave art in Europe (Bednarik 2007), and significantly earlier expressions of symbolism occur in both Asia and Africa (Bednarik 1992, 1994, 2003). The advent of the Early Upper Paleolithic tool traditions of Europe is considered to indicate the

arrival of Eve's progeny there, but these traditions evolved locally and gradually in most parts of Eurasia. They first appear fairly simultaneously between 45 ka and 40 ka BP, or even earlier, at widely dispersed locations from Spain to Siberia (Makarovo 4/6, Kara Bom, Denisova Cave, Ust'-Karakol, Tolbaga, Kamenka, Khotyk, Podzvonkaya, Tolbor Dorolge; Bednarik 1994). At that time, only Robusts occupied Eurasia (see below). Senftenberg, a clearly Upper Paleolithic (Mode 4) blade industry in the middle of Europe has even been dated to 48,300 ± 2000 (GRO-1217), or a still earlier date, >54,000 years BP (GRO-1771) (Felgenhauer 1959: 60). The Aurignacian of El Castillo level 18, in Spain, seems to commence well before 40 ka ago (Cabrera Valdés and Bischoff 1989; carbon dates of 40,000 ± 2100, 38,500 ± 1800, 37,700 ± 1800 BP). At Abric Romani, the lowest AMS dates from the Aurignacian average 37 ka BP, but the probably more relevant uranium-series dates point to a sidereal age of 43 ka BP (Bischoff et al. 1994). At El Pendo, the Lower Périgordian (i.e. Châtelperronian) industry, attributed to 'Neanderthals' in France, overlies two Early Aurignacian levels (González Echegaray et al. 1980), a stratigraphic pattern also observed in France, e.g. at Roc de Combe (Bordes and Labrot 1967) and La Piage (Champagne and Espitalié 1981). The Châtelperronian at Morín Cave has been dated to about 36,950 carbon-years BP, an antiquity similar to that of the same tradition at French sites (generally 37–33 ka BP). The most recent Middle Paleolithic (Mode 3) occupation known in Spain, however, is at Abric Agut. According to both radiocarbon and U-series dating, it occurred only 13 to 8 ka BP, i.e. straddling the Pleistocene-Holocene interface (Vaquero et al. 2002). Like many other finds, it shows how illusory the separation of the Middle and Upper Paleolithic cultures is (Bednarik 1995a).

The Iberian pattern of a mosaic and gradually decreasing component of Mode 3 technology in regional EUP lithic industries applies through much of Europe. In southern Italy, variants such as the Uluzzian (Palma Di Cesnola 1976, 1989), the Uluzzo-Aurignacian, and the Proto-Aurignacian (43–33 ka BP) have been reported (Kuhn and Bietti 2000; Kuhn and Stiner 2001). The Olschewian of the Alpine region, another Aurignacoid tradition (42–35 ka BP), developed from the final Mousterian (Abel 1931; Bächler 1940; Bayer 1929; Bednarik 1993, 2007; Brodar 1957; Cramer 1941; Kyrle 1931; Malez 1959; Vértes 1959; Zotz 1951). Further east this mosaic includes the Bachokirian of the Pontic region (>43 ka BP), the Bohunician of east-central Europe (Svoboda 1990, 1993; 44–38 ka BP), and various traditions of the Russian Plains. The latter comprise major concentrations of sites in the Prut-Dniester basin and on the middle Don. Some of these industries, such as the Streletsian, Gorodtsovian, and Brynzenian derived clearly from Mousteroid technologies, whereas the Spitzinian or Telmanian are free of Mode 3 bifaces (Anikovich 2005). In parts of Russia, such as regions of the Don River, the Crimea and northern Caucasus, Mode 3 technologies (Mousterian and Eastern Micoquian) continue alongside intermediate and Mode 4 ones and the gradual development from one into the other can be observed at many individual sites. The coexistence of seven accepted tool traditions between 36 ka and 28 ka BP has been reported from the region: the Mousterian, Micoquian, Spitzinian, Streletsian, Gorodtsovian, Eastern Szeletian and Aurignacian (Krems-Dufour variant). The rich mosaic of early Mode 4 industries began before 40 ka BP on the Russian Plain and ended only 24–23 ka BP. In the Crimea, the Middle Paleolithic is thought to have ended only between 20–18 ka BP. Elsewhere in the region, the introduction of a first fully developed Upper Paleolithic tradition (the Kostenkian) appears about 24 ka at the major Kostenki-Borshevo site complex.

A succession of traditions connecting Middle Paleolithic biface technocomplexes, including the late Eastern Micoquian, with typical late Paleolithic ones, continue through the Szeletian of eastern Europe (Allsworth-Jones 1986; 43–35 ka BP), the Jankovician of Hungary; and the Altmühlian (c. 38 ka BP), Lincombian (38 ka bp) and Jerzmanovician (38–36 ka BP) further north. Similarly, the gradual development from the Middle Paleolithic at 48 ka BP (with 'Neanderthal' footprints of small children) to the Upper Paleolithic is clearly documented in Theopetra Cave, Greece (Kyparissi-Apostolika 2000; Facorellis et al. 2001). These and numerous other cases of 'intermediate' industries or gradual changes all demonstrate the continuity between Mode 3 and Mode 4 technocomplexes in many parts of Europe, but most especially in the east and southeast, the logical entry point of the presumed African invaders. A degree of regionalization precedes this period even in the late Mousterian (Kozłowski 1990; Stiner 1994; Kuhn 1995; Gamble 1999; Riel-Salvatore and Clark 2001), marked by both miniaturization and increasing use of blades, by improved hafting and the use of backed or blunted-back retouch, apparently heralding subsequent developments. German Mode 3 sites have produced backed microliths and evidence of the use of birch resin, and replication experiments suggest that the technology involved in preparing this resin are exceedingly complex. Even in France, there is gradual development, both from the Charentian to later Mousterian, and from the 'classic Neanderthals' of La Quina and La Chapelle to the more gracile Abri Peyrony specimen. Much the same pertains to western Asia, for instance the Aurignacoid Baradostian tradition of Iran clearly develops in situ from Middle Palaeolithic antecedents. The mousteroid traditions of the Levant also develop gradually into blade industries, e.g. at El Wad, Emireh, Ksar Akil, Abu Halka and Bileni Caves, and that region's Ahmarian is transitional. The artificial dichotomy between Middle and Upper Paleolithic materials (Bednarik 1995a) has thus only served to overemphasize differences that mark really gradual changes in technology (Fedele and Giaccio 2007). The specious separation of Mode 3 and Mode 4 technologies has even less currency in Africa (e.g. the Howieson's Poort tradition with its microliths, or the Amudian), India (Bednarik 1994; Bednarik et al. 2005) or China (Gao and Norton 2002). In Australia the Mode 3 traditions continue until well into the Holocene, and in Tasmania until the arrival of the British, just over two centuries ago.

Perhaps most pertinently, if the Graciles as claimed by the OoA advocates have come from sub-Saharan Africa, and arrived in Europe via the Levant and southeastern Europe, it would be expected that evidence of their presence can be found first in their homeland and later progressively along such a route, in the form of the arrival of a dramatically different technology. No such evidence has been reported, and African Eve advocates have cited none. Not one of the more than twenty perceived Early Upper Paleolithic stone tool traditions of Europe derives from Africa or the Levant. On the contrary, Aurignacoid or similar traditions arrived in the Levant long after they first arose elsewhere in Eurasia, so they were clearly not introduced through this presumed corridor. Moreover, right across northern Africa, the Mode 3 Middle Stone Age continued up to 20 ka ago, i.e. at 20 or 30 millennia after the advent of Mode 4 technologies across Eurasia. There is simply no Mode 4 tradition in sub-Saharan Africa until about 22 ka ago, a glaring inconsistency the advocates of the Eve model have habitually ignored. Nor have they ever explained where the African or Levantine precedents of the Upper Paleolithic art traditions are to be found, if these African invaders were their carriers as claimed. There is no trace of such evidence, nor any proven Pleistocene rock art other than typical Mode 3 productions known from Africa. Even the only demonstrated early

mobiliary art from Africa, found in Namibia, is not as claimed of a Mode 3 tradition (Beaumont and Bednarik 2010). The state of available information from the Levant or Arabia indicates much the same along the route the Africans are supposed to have taken to Europe.

Instead of a sudden change of technology in Europe at any time during the period from 50 ka to 25 ka ago, what can be observed is a complex mosaic of regional traditions which, in general, exhibit a gradual change of several variables, such as tool size, knapping method, retouch and reuse. This suggests in all cases *in-situ* evolution of cultures, rather than the effects of an intrusive tradition. It mirrors precisely the patterns documented in the development in human morphology, as shown next.

Gracilization of Humans

A fundamental error of the replacement advocates (e.g. Protsch 1973, 1975; Bräuer 1981, 1984a, 1984b, 1989: 136; Stringer 1984a, 1984b, 1985, 1989; Stringer and Andrews 1988; Mellars and Stringer 1989; Wainscoat et al. 1986; Wainscoat 1987; Cann et al. 1987) and even others, such as Churchill and Smith (2000a, 2000b), have been false datings (e.g. those by Protsch) of many European human skeletal remains of the time slot in question. In numerous cases specimens of relatively modern appearance were given ages well in excess of their true antiquities, thus claiming an early appearance of these 'modern' features. Examples are the four Stetten specimens from Vogelherd (in the Swabian Jura, southwestern Germany). Although it had always been perfectly transparent to more rigorous commentators that they derived from intrusive Neolithic interments (e.g. Czarnetzki 1983: 231; Gieseler 1974), the Eve folks had attributed them to the Aurignacian. Direct carbon isotope determinations, of samples taken from the mandible of Stetten 1, the cranium of Stetten 2, a humerus of Stetten 3 and a vertebra of Stetten 4, all agree, falling between 3980 ± 35 BP and 4995 ± 35 BP (Conard et al. 2004).

Similarly, the Cro-Magnon sample, frequently cited as the 'type fossil' of the first 'modern' Europeans and derived from four adults and three or four juveniles, had been subjected to so much pseudo-scientific spin that separating it from credible accounts is not readily possible (see Tobias 1995 for a most pertinent critique of the vacuous and blatantly anthropocentric term 'anatomically modern human'). The group is in reality quite robust, and especially the very pronounced supraorbital torus, projecting occipital bone and other features of cranium 3 are Neanderthaloid rather than gracile. Sonneville-Bordes (1959) placed the sample from the Cro-Magnon shelter, just outside Les Eyzies, in the late Aurignacian; Movius (1969) suggested an age of about 30 ka BP and preferred an attribution to the Aurignacian 2. Both opinions, and numerous others, including White's, are refuted by the direct dating to about 27,760 carbon years BP (Henry-Gambier 2002); it places the Cro-Magnon individuals in the Gravettian rather than the Aurignacian technocomplex.

The third set of human remains White (1995) cited to contradict Bednarik (1995b) when he proposed that there is no evidence of the humans of the Early Aurignacian being gracile are the Mladeč specimens from the Czech Republic, often also fielded by other Eve advocates. There is no clear evidence that Pleistocene humans ever entered this cave, partly excavated about 130 years ago (Szombathy 1925). Most of the macro-faunal remains in it apparently fell through the large shaft in the cave's roof, and Smyčka (1922: 118–9) proposed that the human remains had also dropped through this chimney, which is probably the case.

The literature on this site (Knies 1906; Smyčka 1907, 1922, 1925; Fürst 1922; 1923–24; Weiser 1928; Skutil 1938; Jelínek 1987; Svoboda et al. 2002; Bednarik 2006) presents no credible alternative evidence. The recently secured direct dates from some of the human remains (Wild et al. 2005), from specimens Mladeč 1, 2, 8, 9a and 25c, range from about 26,330 BP (the ulna of 25c) to 31,500 BP. They are therefore, at best, partly of the very final phase of the Aurignacian period with its duration of about 15,000 years. More likely, most or all of the series is of the Gravettian technocomplex. Moreover, there is considerable evidence that the Mladeč specimens were far from 'fully modern' (Smith 1982, 1985; Frayer 1986; Trinkaus and Le May 1982; and especially Jelínek et al. 2005). Notably, there appears to be pronounced sexual dimorphism, with male crania characterized by thick projecting supraorbital tori, Neanderthaloid posterior flattening, low brain cases and very thick cranial vaults—all typical robust features. As in 'Neanderthals', cranial capacities exceed those of Graciles (1650 cc for Mladeč 5), but there is a reduction in the difference between male and female brain size relative to Neanderthal data. The dimorphism is also expressed in the more inclined forehead in the males, their more angled occipital areas with lambdoidal flattening, broad superior nuchal planes and more prominent inion. The female specimens show similarities with, as well as differences from, accepted Neanderthal females, such as larger cranial vaults, greater prognathism, lack of maxillary notch, a very narrow nose and distinct canine fossa (Figure 1). However, the females are more gracile than the males, while still being more robust than males of later periods. The Mladeč population thus seems to occupy an intermediate position between late Neanderthaloid *Homo sapiens*, and *H. sapiens sapiens*, a position it shares with numerous human remains from other Czech sites.

Figure 1. Mladeč 1, 6 and 5, Czech Republic, showing the striking morphological differences between the two females on the left and the male on the right (to facilitate comparison, all specimens are shown facing the same direction).

This is an important issue to be revisited later in this chapter. Suffice it to note here that the material from Pavlov Hill, an important Czech site, is among the most robust available from the European Upper Paleolithic, sharing its approximate age of between 26 and 27 ka with yet another Moravian site of the Gravettian, Předmostí. The more gracile finds from Dolní Vestonice are around 25 ka old and still feature some archaic characteristics (particularly the Neanderthaloid specimen DV16). Another find that has been considered as very early European 'Modern' is the calotte from Podbaba, near Prague, variously described as sapienoid and Neanderthaloid, but undated; it probably belongs to the Mladeč-Předmostí-Pavlov-Dolní Vestonice spectrum. Morphologically similar specimens also come from

Cioclovina (Romania), Bacho Kiro levels 6/7 (Bulgaria) and Miesslingtal (Austria), so this is unlikely to be a local phenomenon. Indeed, it needs to be seen in the greater Eurasian context.

Besides the Neolithic human remains from Vogelherd, which the Eve advocates had been all too keen to place at 32 ka, nearly all of the German fossils claimed to be of the Upper Paleolithic are now thought to be of the Holocene. Of particular interest is the Hahnöfersand calvarium, described as so robust that it was judged to show typical Neanderthal features (Bräuer 1980) and hailed as the northernmost Neanderthal found. It was initially dated to the earliest Upper Paleolithic (Fra-24: 36,300 ± 600 BP; UCLA-2363: 35,000 ± 2000 BP, or 33,200 ± 2990 BP; Bräuer 1980), which conflicts sharply with results secured by Terberger and Street (2003): P-11493: 7470 ± 100 BP; OxA-10306: 7500 ± BP bp. The re-dating of the skull fragment from Paderborn-Sande yielded even more dramatic differences. Originally dated at 27,400 ± 600 BP (Fra-15; Henke and Protsch 1978), Terberger and Street (2003) report an age of only 238 ± 39 BP (OxA-9879). In fact the skull was so fresh that it emitted a putrid smell when Terberger and Street drilled it for sampling. Then there is the cranial fragment of Binshof near Speyer, dated by R. Protsch in the 1970s as Fra-40 to 21,300 ± 320 BP. According to Terberger and Street it is only 3090 ± 45 carbon years old (OxA-9880). These authors also analyzed two individuals from the Urdhöhle near Döbritz, which had been attributed to the Upper Paleolithic, and found them both to be about 8400 years old. Indeed, of all the German Upper Paleolithic human remains, only one remains safely dated to earlier than 13,000 BP: the interred specimen from Mittlere Klause in Bavaria. A carbon isotope date of 18,200 ± 200 bp (UCLA-1869) from a tibia fragment (Protsch and Glowatzki 1974) has been confirmed by Terberger and Street's date from a vertebra, of 18,590 ± 260 bp (OxA-9856). It has therefore become clear that there are currently no 'modern' remains from the first half, if not the first two thirds of the west-central European Upper Paleolithic. Nearly all the dates for German humans from the radiocarbon laboratory of the University of Frankfurt am Main appear to be substantially false, as do some of those from the University of California, Los Angeles. In addition, another German key specimen, the skull from Kelsterbach, has mysteriously disappeared from the safe of the Frankfurt institution. It had been dated to 31,200 ± 1600 BP (Fra-5) (Protsch and Semmel 1978; Henke and Rothe 1994), but is also believed to be of the Holocene, perhaps the Metal Ages (Terberger and Street 2003).

Then there are the robust but 'modern' hominin remains of the early Upper Paleolithic at Velika Pećina, Croatia, close to the Neanderthal site Vindija. This specimen, too, has been a principal support for the replacement advocates, but it has also joined the long list of European humans whose age was grossly overestimated. It is now considered to be only 5045 ± 40 radiocarbon years old (OxA-8294; Smith et al. 1999).

The currently earliest, liminal 'intermediate' (between robust and gracile) finds in Europe, the Peştera cu Oase mandible and face from southwestern Romania (found in different parts of the extensive cave; Trinkaus et al. 2003; Rougier et al. 2007), are perhaps about 35,000 radiocarbon years old, but they are without an archaeological context. Although in some aspects 'modern', the 'derived Neanderthal features' of the mandible include cross-sectional symphyseal orientation, exceptionally wide ramus, exceptionally large third molars and unilateral mandibular foramen lingular bridging (a distinctive 'Neanderthal' feature). The partially preserved facial remains, found in a different part of the extensive cave system and apparently from another individual, also combine robust and gracile features. Soficaru et al. (2006) have reported six human bones from another Romanian cave, Peştera Muierii, also

clearly intermediate between robust and gracile Europeans. Found in 1952, they have now been dated to about 30,000 carbon years, which might correspond to around 35,000 sidereal years, and combine a partly modern, partly archaic brain case with a suite of other intermediate features.

The loss of the only relevant Spanish remains, from El Castillo and apparently of the early Aurignacian technocomplex, renders it impossible to determine their anatomy. French contenders for EUP age present a mosaic of unreliable provenience or uncertain age, and direct dating is mostly not available. Like the Vogelherd and other specimens, those from Roche-Courbon (Geay 1957) and Combe-Capelle (originally attributed to the Châtelperronian levels; Klaatsch and Hauser 1910) are now thought to be of Holocene burials (Perpère 1971; Asmus 1964), and the former is now apparently lost. Similar considerations apply to the partial skeleton from Les Cottés, whose stratigraphical position could not be ascertained (Perpère 1973). Finds from La Quina, La Chaise de Vouthon and Les Roches are too fragmentary to provide diagnostic details. The *os frontale* and fragmentary right maxilla with four teeth from La Crouzade, the mandible fragment from Isturitz and the two juvenile mandibles from Les Rois, about 28 to 30 ka old (Ramirez Rozzi et al. 2009), range from robust to intermediate (e.g. Trinkaus 2007). Just as the Cro-Magnon human remains now appear to be of the Gravettian rather than the Aurignacian, so do those from La Rochette. The Fontéchevade parietal bone does lack prominent tori (as do many other intermediate specimens) but the site's juvenile mandibular fragment is robust.

This pattern of features intermediate between what paleoanthropologists regard as Neanderthals and Moderns is found in literally hundreds of specimens apparently in the order of 45 to 25 ka old (including the large Czech collection lost in the Mikulov Castle fire at the end of World War II). They occur in much of Europe, and intermediate forms between robust *Homo sapiens* and *Homo sapiens sapiens* existed also in Asia and Australia. They include examples from right across the breadth of Eurasia, such as those from Largo Velho, Crete, Starosel'e, Rozhok, Akhshtyr', Romankovo, Samara, Sungir', Podkumok, Khvalynsk, Skhodnya, as well as Chinese remains such as those from Jinniushan and Tianyuan Cave (Shang et al. 2007). Similarly, the African evidence does not, as is often claimed, present 'anatomically modern humans' at 150 ka or almost 200 ka. The skulls from Omo Kibish offer some relatively modern features as well as substantially archaic ones; especially Omo 2 is very robust indeed (McDougall et al. 2005). Their dating, also, is not secure at all, and Omo 2 is a surface find. The much more complete and better dated Herto skull, BOU-VP-16/1, is outside the range of all recent humans in several cranial measurements (White et al. 2003) and is clearly just as archaic as other specimens of the late Middle Pleistocene, in Africa or elsewhere. The lack of 'anatomically modern' humans from sub-Saharan Africa prior to the supposed Exodus is glaring: the Border Cave specimens have no stratigraphic context and are thought to be only around 80 ka old; Omo and Dar es Soltan are obviously not sub-Saharan (and the latter is undated), which leaves only the mandibles of Klasies River Mouth, lacking cranial and post-cranial remains. On the other hand, current Australians average a cranial capacity of only 1264 cc (males 1347 cc, females 1181 cc, i.e. well within the range of *Homo erectus*), while their molars average the size of those of Europeans several hundred millennia ago. And yet they are still considerably smaller than those of fossil Australians, such as the large Kow Swamp sample. So while diminution of molars did occur in Australia, supposedly also settled by Eve's progeny, it lags greatly behind that of the rest of the world.

With the lack of African fossils of the African Eve 'species', the Eve apostles turned to the Levant for help, and recruited the Mount Carmel finds from Qafzeh Cave and Skhul Shelter as supposed 'Moderns'. Yet all of these skulls present prominent tori and receding chins, even Qafzeh 9, claimed to be of the most modern appearance. The distinct prognathism of Skhul 9 matches that of 'classic Neanderthals', and the series of teeth from that cave has consistently larger dimensions than Neanderthaloid teeth. Even Chris Stringer, the principal protagonist for the Eve model, concedes that this material is 'transitional' or intermediate. Besides, supposedly much later 'Neanderthal' burials in nearby Tabun Cave as well as the Qafzeh and Skhul material are all associated with the same Mousterian tools, and the datings of all Mt Carmel sites are far from soundly established, with their many discrepancies. The TL dates from Qafzeh, for instance, clash severely with the amino racemization dates (ranging from 33 to 45 ka), and are in any case plagued by inversion: the lower layer (XXII) averages 87.7 ka, the middle layer (XIX) 90.5, while the uppermost (XVII) averages 95.5. Therefore the claims of 90-ka-old 'modern' humans from Mt Carmel, a cornerstone in the Eve notion, are in every respect unsound, and this population is best seen as transitional between robust and gracile forms, from a time when gracilization had commenced elsewhere as well.

This presents an overall picture that is very different from that which the replacement protagonists subscribe to. Their model cannot tolerate such intermediate forms, nor can it allow hybrids, yet in Europe there is a clear continuation of some Neanderthaloid features right up to and into the Holocene. This is demonstrated not only by the Hahnöfersand specimen, but also by others, such as the equally robust Mesolithic skull fragment from Drigge, also from northern Germany, which is about 6250 years old (Terberger 1998), and numerous other late specimens previously thought to be of the Early Upper Paleolithic. They range in age from the Magdalenian through the Neolithic, and even younger. One distinctive 'Neanderthal' feature is the shape of the mandibular nerve canal, surrounded by a bony ridge in 53% of specimens included in this designation. Its occurrence diminishes during the transition period to 44%, but it is still present in present-day Europeans, at 6% (Lewin 2005: 196). This feature alone demands the presence of Neanderthal genes in Europeans. The process of gracilization has in fact continued to the present time: even early Mesolithic material is about 10% more robust than modern Europeans. Indeed, Hawks (1997) has estimated that at least 25% of the ancestors of later Upper Paleolithic people would need to be Neanderthals to account for the preservation of Neanderthal autapomorphies observed (see also Frayer 1993, 1998; Frayer et al. 1994), and the genetic evidence for the Neanderthal ancestry of modern Europeans is overwhelming (Green et al. 2010).

This brief review suggests that there are now almost no supposedly modern specimens left as possible contenders for attribution to any Aurignacoid industries. The maxilla from Kent's Cavern, United Kingdom (~31 ^{14}C ka BP), and the Romanian remains from Peştera Cioclovina (~29 ^{14}C ka BP) lack secure and diagnostic archaeological association. There are, however, numerous 'Neanderthal' remains to fill this void. Of particular interest are the most recent, those from Saint Césaire (~36 ka), Arcy-sur-Cure (~34 ka), Zafarraya Cave (~33.4 ka), Máriaremete Upper Cave (~38 ka), Sungir' (~25 ka), Trou de l'Abîme (~33 ka), and Vindija Cave (~28 and ~29 ka). This state of affairs has prompted Bednarik (2007) to propose that the hypothesis of the Early Upper Paleolithic people being robust or intermediate is supported by empirical evidence, while the contrary view is without.

At the first of these sites, the 'Neanderthal' remains of a burial occur together with clear Châtelperronian artifacts, which until 1979 had been generally assumed to be the work of anatomically modern humans. Arcy-sur-Cure, also in France, yielded numerous ornaments and portable art objects, again from a Châtelperronian. This prompted various convoluted explanations of how these elaborate pendants could have possibly found their way into a 'Neanderthal' assemblage (e.g. White 1993; Hublin et al. 1996; a similar argument was used by Karavanic and Smith [1998] in explaining the bone points of Neanderthals in Vindija layer G1). It was contended that the primitive Neanderthals must have scavenged these objects from the camps of 'Moderns', as if people lacking the ability to use symbols would have any use for symbolic artifacts. The Jankovichian or Trans-Danubian Szeletian (Allsworth-Jones 1986) has yielded three mandibular 'Neanderthal' teeth from Máriaremete Upper Cave (Gábori-Csánk 1993). The Streletsian of Sungir' in Russia produced a Neanderthaloid tibia from a triple grave of Graciles, and the adult male exhibits pronounced supraorbital tori (Bader 1978); Trou de l'Abîme near Couvin in southern Belgium furnished 'Neanderthal' remains together with a typical Aurignacian industry; and there can be no question that the Vindija late 'Neanderthals' used EUP tools and technology. Not only has that site supplied some of the most recent 'Neanderthals' found so, these are more gracile than Neanderthals of much earlier periods, and they are seen as transitional by some (Smith and Raynard 1980; Wolpoff et al. 1981; Frayer et al. 1993; Wolpoff 1999; Smith et al. 2005). Vindija Vi-207 is a mandible of 29,080 ± 400 carbon years bp (OxA-8296), Vindija Vi-208 is a parietal of 28,020 ± 360 carbon years bp (OxA-8295) (Smith et al. 1999). These 'late Neanderthals' (or very robust Graciles) exhibit significant reduction in Neanderthaloid features, such as mid-facial prognathism and supraorbital tori. The related tool assemblage includes even apparent bone fabricators (Ahern et al. 2004).

Ignoring these many significant contradictions to their ideas, the replacement proponents have responded to the recent developments in Germany by contending that the new data bolster their model, because the 'Neanderthaloid' Hahnöfersand specimen had been suggested to be a hybrid (Bräuer 1980). Instead of admitting that they have been the victims of a hoax by Protsch, they have hailed each of the very late dates for Neanderthal remains as they appeared in recent years as a confirmation of their hypothesis, gradually painting themselves into a corner. Having strongly contended that a whole spectrum of radical cultural innovations appeared with the beginning of the Aurignacian, they effectively attributed these to their 'Neanderthals', contradicting themselves once again. According to them, the people of the Aurignacian are indistinguishable from us in terms of cognition, behavior and cultural potential. Perhaps they are right and the late Robusts were behaviorally modern, but that is certainly not what they hoped to show (d'Errico 1995). The period from 45 ka to 28 ka bp has produced dozens of 'Neanderthal' specimens, but no securely dated, unambiguously fully modern human remains anywhere in Europe. Hence the available evidence suggests that the people of the first half or even two thirds of the Upper Paleolithic were either robust or intermediate. The replacement hypothesis, obviously, cannot accommodate any intermediate forms, in fact it is decisively refuted by them. As, indeed, it is refuted by the genetic data that present-day non-Africans derive from Neanderthals (Green et al. 2010). This is not even needed to refute the Eve model, which is destroyed by just one single 'Neanderthal gene' in the genome of Eurasians. Although this model has now been refuted so resoundingly, some of the replacement advocates seem unable to grasp the effects of the new data on their embattled hypothesis (e.g. Mellars 2005). They seem incapable of appreciating that, in science,

exceptional claims such as their absurd model require exceptionally persuasive evidence, not the slipshod reasoning and methodological blunders characterizing all presentations of the Eve hypothesis—from Protsch to the present time.

Historically, Pleistocene archaeology has been a series of blunders, hoaxes and mistakes, beginning with the mistreatment of Boucher de Perthes, and the African Eve episode is simply one of the most recent examples of this susceptibility to erroneous consensus views. All present-day humans derive from robust *H. sapiens* types, who formed a largely continuous population across most of Africa and Eurasia, with the exception of regions that were simply not habitable. Introgression facilitated the travel of genes through this population, just as Weidenreich (1946) had predicted in his trellis model (Figure 2). The robust sapienoids were never replaced, they simply became gracile throughout the occupied world, including even in Australia, during the final part of the Late Pleistocene, beginning 40 or 50 ka ago. But what caused this universal gracilization? Since it involved numerous deleterious effects, as will be shown below, it is most unlikely to be the result of any form of natural selection. So how is the origin of anatomically modern humans to be explained, and how might genetic drift be implicated?

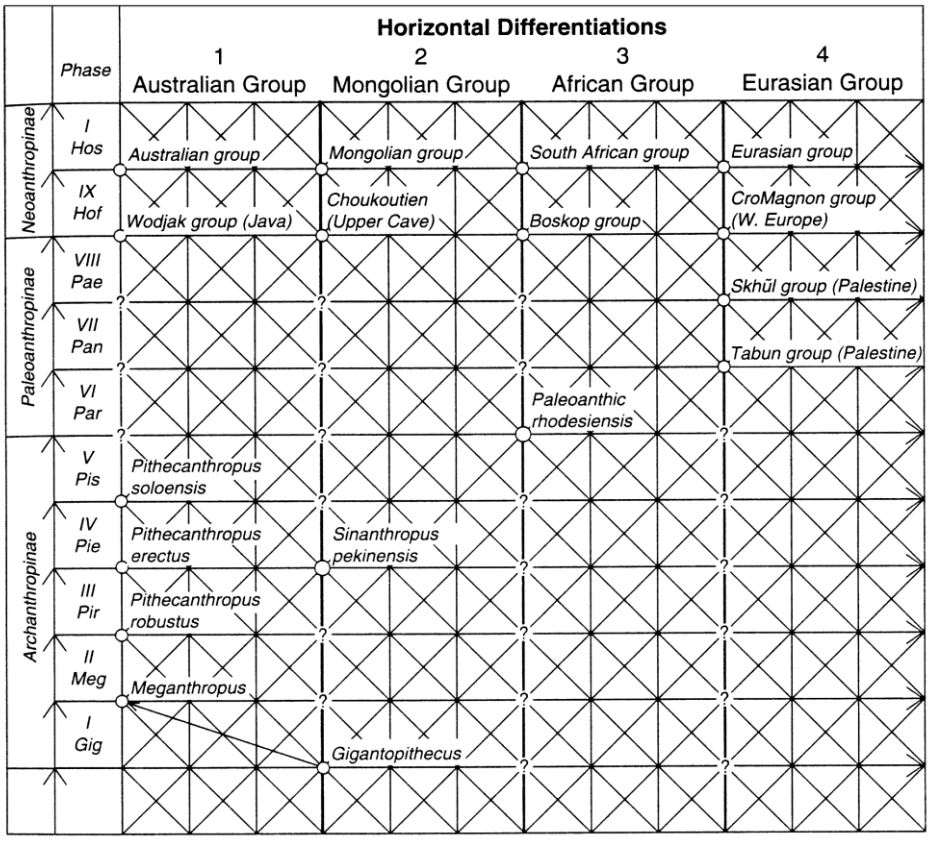

Figure 2. Weidenreich's trellis model of hominin evolution, the basis of multiregionalism.

Alternative Models

Evolutionary theory attributes evolutionary change essentially to two factors, natural selection and sexual selection. In the first, specific phenotypes representing aspects of morphology or behavior are preferentially reproduced across generations of a given population. In the second, phenotypes become over-represented either through mate choice or intra-sexual competition. The emphasis is on genetic inheritance, although the hard evidence for this is not particularly well established.

Over recent years several new directions of inquiry have evolved, challenging simplistic evolutionary theory. Developmental systems theory replaces the overly restrictive focus on the genes with a model of interacting systems (Oyama 2000; Oyama et al. 2001). While vague overall, it does raise some pertinent points, especially concerning the non-genetic inheritance of traits and the cybernetic feedback from organism-environment systems changing over time. Niche construction has been presented as another major force of evolution (Odling-Smee et al. 2003), operating similar to natural selection. In rather the same way as visual and mental taxonomizing processes and the inclusion of new neural structures becoming available for evolutionary selection in feedback systems (Bednarik 1990), niche construction also creates feedback within the evolutionary dynamic. Organisms engaged in it modify the evolutionary pressures acting on them, as well as on other but unrelated populations sharing the same space. Humans are rightly seen as the 'ultimate niche constructors', in which their increasingly complex cultures may play an important role. Laland et al. (2000) see much of niche construction as guided by socially learned knowledge and cultural inheritance (cf. Silk 2007), and Bickerton (2010) attributes language to niche construction.

Evolution has been suggested to encompass also other 'dimensions', termed epigenetic, behavioral and symbolic inheritance systems (Jablonka and Lamb 2005). All organisms are said to be subject to epigenetic inheritance, which refers to physiological/biological process above the level of DNA. Behavioral inheritance is found in most species, and defines the transference of information or behavior through learning rather than genetically. Symbolic inheritance is apparently found only in humans. The underlying contention of these new ways of thinking is that evolution is not a simple genetic process relying on the appearance of mutations. Evolution does not develop traits for selection; it has no foresight. The idea that human evolution simply cannot be assumed to have been a purely biological process is not at all new (Dobzhansky 1962: 18; 1972). It has recently received a new impetus from increasingly sophisticated work, and the notion of a progressive moderation of human evolution by culture is the central plank of the gene-culture co-evolutionary model (Boyd and Richerson 2005; Richerson and Boyd 2005). Most recently, Fuentes (2009) has sought to reconcile the pronounced duality of evolutionary biology and socio-cultural anthropology, pointing out that symbolic and other cultural processes influence behavior and potentially physiological and even genetic factors. His demand that behavioral plasticity has a specific role in human behavior runs again counter to neo-Darwinism, but upon reflection it seems impossible to explain hominin development, especially of the Late Pleistocene, without that factor.

These new developments are certainly useful, especially in that they reject the role of genetics in 'explaining everything' in hominin evolution. They also express considerable criticism for the self-confirming paradigms of recent decades, critique that is so crucial to a

sound epistemology. The debilitating, all-pervading appeal to authority governing archaeology does need to be severely challenged, and this has not occurred adequately. However, there are two significant shortcomings of these various strands of criticisms coming from the sciences. One is that they have not produced an alternative paradigm; they have merely illustrated problems that need to be attended to. The other concerns the lack of relevant empirical evidence, which the sciences simply have no access to because archaeology is either itself unaware of its existence (as far too often appears to be the case); or alternatively it has made great efforts, bordering on academic censorship, to discredit such evidence in order to uphold its dogma. Therefore the position of the behavioral, cognitive and semiotic sciences is essentially that they have detected the flaws in the dominant model of the emergence of human modernity, but they are not in a position to offer an alternative: archaeology dominates the discourse on hominin evolution, and it determines what may be published in this intellectually corrupt discipline.

The scenario remains that there is a significant change in the physiology of humans during the last 50,000 years in Europe, and modern Europeans differ genetically from robust Europeans 50 ka ago. The same change from Robusts to Graciles occurs in three other continents. Not only do these changes need to be explained, there is another issue which, again, the replacement advocates are completely silent on: the changes that did occur *contradict all canons of Darwinian evolution*. Without a significant change in their environmental mega-niche, these humans experienced numerous deleterious physiological changes to become gracile. The thickness of their skulls decreased radically, as did the general robusticity of their skeletons. The traces of muscle attachments indicate that physical strength declined markedly, perhaps by as much as 50%. On top of that, their brain shrank by around 200 cc (~13%), and that during a time when the demands on their mental abilities are thought to have increased exponentially. The susceptibility to neurodegenerative diseases developed apparently in this time, and mental illness may be a result of gracilization. These changes are certainly dramatic, occurring in fact over just a few tens of millennia. In the history of the human genus, there is no evidence of such rapid changes, and conventional wisdom has it that all previous changes were for the better of the species concerned. That certainly cannot be said about what happened in the most recent history of human evolution, which in many areas looks more like devolution, or evolution in reverse.

So what happened? If it was not a case of invasion by physically (and perhaps even intellectually) *inferior* Africans of evenly matched technology, what alternative is there? The answer is provided by a combination of two strands of determinants. One is the indisputably very major influence sexual selection has on who passes on their inheritance; the other is the rising power of cultural imperatives over natural. When breeding mate selection becomes moderated by cultural factors (such as cultural constructs of attractiveness, along with perhaps social position, communication ability, body adornment), the laws of evolutionary theory become suspended, and are supplanted by Mendelian laws of inheritance (Mendel 1866), the basis of the discipline of genetics: evolution by natural selection is replaced by breeding, or artificial selection, resulting in *domestication*. It was in studying artificial selection in pigeons that Darwin detected the similarity with natural selection, and here at last the deliberations seem to come full circle: modern humans are the result of incidental self-domestication. In their fetish of using the purported travel of genes to infer the movement of major populations, Pleistocene archaeologists have ignored that it is not evolutionary genetics that determines inheritance: in the end even Darwin has to defer to Mendel.

This revolutionary alternative has been outlined as a realistic option to the replacement hypothesis (Bednarik 2007, 2008a, 2008b, 2008c) and here it is explained in some more detail. The apparently most important question to be asked in this context is this: what could have caused the inherent laws of biological evolution to be suspended for humans during the last fifty millennia or so?

It is particularly important to note that the change seems to have occurred universally and roughly concurrently, in all four continents occupied by hominins by 50 ka BP. Since this enormous geographical range involved numerous climatically and environmentally different niches, from the tropics to the Arctic, it is impossible to explain such largely uniform change from robust to gracile as the result of natural selection. The same rejection of evolutionary dynamics may be implied by the relatively swift conversion, taking only a few tens of millennia. In southern and eastern Europe, one might argue that the Campagnian Ignimbrite Event and subsequent sharp climatic decline almost exactly 40 ka ago (Fedele and Giaccio 2007) may have precipitated demographic and cultural adjustments. Although this environmental bottleneck could have effected genetic or anatomical changes in some parts of Europe, there is no evidence that it did, and the universal human gracilization over the last 50 ka or so demands a universal explanation and precludes a local one. Occurring concurrently in the course of the second half of the Late Pleistocene, in all four continents occupied, this process needs to be explained if human origins are to be clarified.

In Europe it is best documented by human remains from the central region, particularly in the Czech Republic, from the crucial period of about 31 ka to 26 ka BP, which witnessed distinctive sexual dimorphism. Despite the lack of credible stratigraphic evidence from Mladeč Cave, the recent attempt to provide direct dates from some of its human remains suggests that they represent precisely this interval (Wild et al. 2005). As noted above, male crania are characterized by typical robust features. As in 'Neanderthals', cranial capacities exceed those of 'anatomically modern humans', but there is a reduction in the difference between male and female brain size relative to Neanderthal data (Figure 3). The female specimens show similarities with, as well as differences from, accepted Neanderthal females, but are far more gracile than the males, while still being more robust than males of later Pleistocene periods. The Mladeč population as well as contemporary others in central Europe (e.g. Pavlov Hill, Předmostí, Dolní Vestonice, Podbaba, Miesslingtal) thus seems to occupy an intermediate position between late Neanderthaloid *Homo sapiens* and *H. sapiens sapiens*.

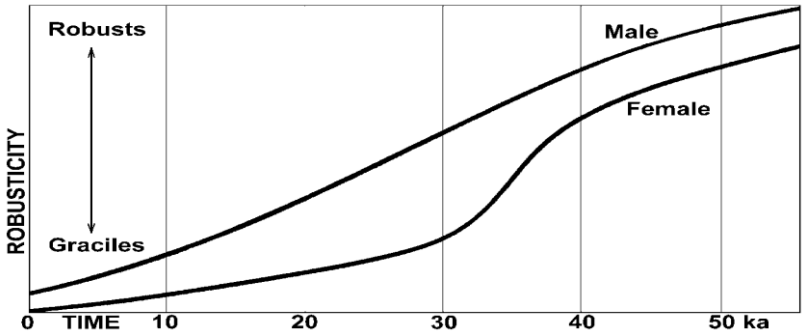

Figure 3. Schematic depiction of male and female relative cranial gracility in Europe through time, showing that the decline in robusticity is gradual in males, but accelerated in females between 40 and 30 ka.

Gracilization begins typically in females, with males lagging many millennia behind (Figure 3). The process has continued to the Holocene, and reduction in both dimorphism and robusticity is also still active in human evolution today. The face, jaw and teeth of European humans 10 ka ago are in general 10% more robust than those of today's Europeans and Asians, and those of 30 ka ago are 20–30% more robust. Some modern humans, as noted above, have retained tooth sizes typical of archaic *H. sapiens* and *H. erectus*, and other robust features are preserved in many populations or individuals. Neanderthaloid specimens occur in the Mesolithic, through to the Neolithic and even later.

Holocene gracilization could conceivably be explained as a response to changing food-processing techniques or less physically demanding lives. The smallest tooth sizes tend to be found in those areas where food-processing techniques have been used for the longest time. However, this explanation cannot be extended to universal gracilization during the Late Pleistocene. The life style of people 15 ka ago is not thought to have been significantly different from that of 35 ka ago, yet the overall rate of gracilization appears to be have been reasonably uniform over the past 50 ka (Figure 3). As a universal phenomenon it has not been explained, and indeed has been ignored due to the dominance of the replacement model.

Natural selection simply cannot account for a significant reduction in robusticity and reversal of encephalization without any apparent trade-off in evolutionary benefits for the organism in question. No such benefits are apparent, and yet this process seems to have been universal wherever humans existed during the Final Pleistocene. It is proposed here that the dimorphism observed during the crucial period of the last twenty or thirty millennia of the Pleistocene presents the key to the most parsimonious explanation. Dimorphism in mammals generally reflects one or both of two selection pressures: competition between males for access to females, or male-female differences in food procuring strategies, with males provisioning females (Aiello and Wheeler 1995; Biesele 1993; Deacon 1997). In the case of late hominins it has been suggested that physical competition among males may have been diminished radically with the introduction of accurate projectile weapons acting as 'equalizers' (Boehm 1993, 1999). This is, however, not a satisfactory explanation: effective distance weapons were in use long before the Upper Paleolithic (spears of the Lower Paleolithic were found at seven European sites), together with large game hunting. Thus the 'equalizers' had long been in use and they do not explain the gender-specific pattern of later gracilization, nor the extensive fetalization that took place in the Final Pleistocene.

The Fetalized Human

It is self-evident that practices such as deliberate breeding-mate choice determines procreational success today, so the obvious question to be asked is: at what point in time did it first appear? Other primates (indeed, all other animals) exhibit no preferences in mate selection of youth or specific body ratios, facial features, skin tone or hair; yet in present humans these are deeply entrenched, perhaps 'hardwired'. Facial symmetry, seen to imply high immunocompetence (Grammer and Thornhill 1994; Shackelford and Larsen 1997), is also of importance, and in female humans neotenous facial and other features are strongly preferred by males (Jones 1995, 1996). Since this applies undeniably today, the rational way to examine this issue is to consider at what point in human development the influence of non-evolutionary currents can be first detected. It is suggested that around 40 ka ago, cultural

practice had become such a determining force in human society that breeding mate selection became increasingly moderated by cultural factors, i.e. by factors attributable to learned behavior. These could have included the application of a variety of cultural constructs in such choices, such as social standing, communication skills, body decoration (which becomes notably prominent 40 ka ago, although existing earlier), and most especially *culturally negotiated constructs of physical attractiveness*.

In all animals, including all hominins, reproductive success determines phylogenetic direction. If one were to look for evidence of when deliberate sexual selection began to have detectable effects, two strategies spring to mind. One could look for signs that attributes of natural fitness were replaced by attributes that confer no Darwinian survival benefits, or one could look for indications of a culturally mediated preoccupation with female sexuality. One would note that, firstly, gracility, especially of females, develops strongly during the Aurignacian and Gravettian; and secondly, that this very same period is marked by a distinctive preoccupation with female sexual attributes. The latter is found in the common depictions of (mostly) isolated vulvae or pubic triangles (Delluc and Delluc 1978; Chiotti et al. 2007); at Abris Blanchard, Castanet, Cellier, Le Poisson, Pataud, and La Ferrassie, Laussel and in Chauvet Cave; and the creation of naturalistic female statuettes, often with pronounced sexual aspects, beginning with the Aurignacian (Bednarik 1989; Conard 2009; Mellars 2009). Therefore the question to be asked is: what cultural preferences could possibly have led to the gracilization of female humans during the second half of the Würm glacial in Europe?

Mating preferences and their genetic results in respect of personality and anatomical traits (Laland 1994), which could become cultural selection variables, can be modeled by methods of the gene-culture co-evolutionary model (Cavalli-Sforza and Feldman 1973; Feldman and Cavalli-Sforza 1989; Aoki and Feldman 1991; Durham 1991). It has been noted that traits selected for can include large female breasts, small feet or male macho behavior, and most certainly physical 'attractiveness'. The latter are necessarily informed by cultural constructs of attractiveness, because there is no objective measure of it. The question then becomes: if the recent gracilization of humans were related to fetalization, what would be its anatomical consequences?

Humans resemble chimpanzees anatomically most closely in the latter's fetal stage (Haldane 1932; De Beer 1940; Ashley-Montagu 1960). Both the fetal chimpanzee and the adult human have hair on the top of the head and on the chin, but are otherwise largely naked. In apes, this changes rapidly upon birth, in humans it remains for life. All male adult apes have a penis bone, but it is categorically absent in both fetal chimpanzees and all male humans, from the fetal stage and throughout life. In fact the penis bone of apes is one of the very last parts of the ape fetus to form, shortly before birth, and its atrophy in humans appears to have been compensated for by the significantly increased length and thickness of the penis, relative to apes (Badcock 1980: 47). Similarly, in female chimpanzees, the *labia majora* are an infantile feature; in humans they are retained for life. The hymen, too, is present only in the neonate ape, but is retained for life in human females in the absence of penetration. The organs of the lower abdomen, such as rectum, urethra and vagina, are typically aligned with the spine in most adult mammals, including apes; only in fetal apes and humans do they point forward relative to the spine (upright walking appears irrelevant, because fetal apes do not walk). The human ovary reaches full size at the age of five, which is the age of sexual maturity of the apes (De Beer 1940: 75). Most importantly, the skull of an unborn ape is thin-walled, globular and lacks the prominent tori of the adult ape, thus resembling the cranium of

a modern human. Upon birth its robust features develop rapidly. The slow closing of the cranial sutures in humans, on the other hand, is again clearly a neotenous feature, introduced by the recent genes RUNX2 and CBRA1. The face of the ape embryo forms an almost vertical plane, as it does in the modern human all the way through adulthood, which is certainly not the case in mature apes. Even the brains of fetal apes and adult humans are much more similar to each other, in terms of proportion and morphology, than they are to those of adult apes.

These and many other features define the anatomical relationship between ape and man as the latter's *neoteny*. The legs of fetal apes are relatively short, while the arms are about as long in relation to the body as in humans. In the apes, the arms become much longer after birth. Human hands and feet resemble those of embryonic apes closely, but differ significantly from both hands and feet of mature apes. In fact the human foot, especially, retains the general structure found in unborn apes, which rather contradicts the hypothesis that it is an adaptation to upright walking. Even the shape of the cartilage of the ear in humans is a neotenous feature.

In neoteny, sexual maturity is attained before full somatic development, and juvenile characteristics are retained for life. In an evolutionary perspective, it refers to species whose adults retain juvenile ancestral features. This has also been called fetalization, because in such phylogenic development, fetal characteristics remain into adulthood, and specific processes of anatomical maturation are retarded (de Beer 1940). Indeed, it is fascinating to note that in human fetalization, biological history seems to be repeating itself: all vertebrates appear to be the result of neoteny in chordates (species having a notochord) hundreds of millions of years ago (De Beer 1940: 76–78). The modern human has undergone so much selection in favor of neoteny that this retardation should be seen as rivaling in importance the distinguishing anatomical characteristic of the oversized brain. It therefore needs to be considered here. 'But neoteny does not only contribute to the production of large structural change; it is also the cause of the retention of plasticity' or 'morphological evolvability' (de Beer 1930: 93). Adaptively useful novelties supposedly become available as maturation genes are freed by pedomorphosis. This neotenous 'retention of plasticity', also noted by Fuentes (2009), could be a key factor in how humans became what they are today.

Encephalization and neoteny in hominin evolution are quite probably related, perhaps through supervenience. It is self-evident that, relative to the neonate ape, the newborn human is not remotely as far developed. For instance, it would find it impossible, for many months after birth, to cling to the fur of a mother for transport. Of course this is related to its excessive brain size, which has caused it to be expelled at a much earlier stage of fetal development. It can be regarded as highly probable that human mothers always had to carry their infants. Indeed, one of the first kinds of artifacts used by early humans was probably some kind of sling or baby carrying bag. The long period during which the human infant was entirely dependent upon the mother, not just for sustenance but also to move with the horde as well as for protection, extended the period for learning very significantly. This, obviously, coincided with the continued growth of the brain after birth, which in fact exceeds that of the fetus in man. In the first year after birth, our brain more than doubles in both volume and weight. It continues to grow, approaching adult size by the age of three, but goes on expanding slightly more up to adolescence and even beyond. If this extraordinary development, unheard of in the rest of the animal kingdom, is compared with that of other primates, in simians such as the rhesus monkey and in the gibbon, 70% of adult brain size is

achieved at the time of birth, the remaining 30% in the subsequent six months. In the larger apes, the size of the brain approaches adult size after the first year of life. These are very significant differences, and they are all connected with our neoteny.

Another marked difference between humans and most other animals is the abolition of estrus, or periodicity of libido in the female. This almost uniquely human feature has not been explained satisfactorily, but there is a good probability that it is also related to these factors—through one of two alternative scenarios. The excessively long period of infant dependency would have been mirrored in a similar dependency of mothers on the horde, most especially for the meat protein needed for the brain tissue of their unborn (Aiello and Wheeler 1995; Leonard 2002; Leonard and Robertson 1992, 1994, 1997). It is thought probable that there was strong selection favoring female mutations allowing long periods of sexual receptivity, leading to the abandonment of estrus altogether: those females who were longer or always receptive were favored in the distribution of meat from kills (Biesele 1993; Deacon 1997), in a feedback system facilitating fetal encephalization through better access to animal protein. It has been noted that on occasion, female chimpanzees are only given meat after they have copulated with a successful hunter, and it is logical that such a behavior trait would select in favor of continuously receptive females.

The second alternative explanation for the loss of estrus in humans is simpler and would favor a very late introduction, but may seem no more than a stab into the dark. Domesticated mammalian species lack the seasonal reproduction of their wild ancestors and most can reproduce themselves at almost any time of the year. It is possible that the same effect in humans is the result of their self-domestication.

Be that as it may, the numerous physiological features of human neoteny should suffice to demonstrate that humans are anatomically best defined as a fetalized form of ape. Although the process of selecting in favor of infantile physiology appears to mark much of human history, during the Final Pleistocene it suddenly accelerated to an unprecedented rate and resulted in markedly unfavorable mutations, from the perspective of natural selection. Domesticated species and laboratory experiments indicate that strong selection leads to maladaptive consequences, attributed to antagonistic pleiotropy in populations out of equilibrium (Andolfatto 2001; Lu et al. 2006). Worldwide, wherever humans existed 40 or 50 ka ago, possessing as they did Mode 3 technological traditions, they shed all of their robust features in just a few tens of millennia. Their brain size decreased, despite the rapidly growing demands made on their brains. Their muscle bulk waned until their physical strength was perhaps halved, in tandem with significant reductions in bone strength and thickness. The decrease in skull thickness is particularly prominent, as well as the relatively rapid reduction in cranial robusticity. This process occurred so fast that it can be tracked through the millennia. At about 35 ka, partially gracile female specimens are encountered from Europe to Australia. The subsequent skeletal evidence presents a distinctive sexual dimorphism: the female crania, though still much more robust than male crania were towards the end of the Pleistocene, show distinctive gracilization (development of globular crania, reduction or absence of supraorbital tori and occipital projection, significant loss in bone thickness, reduction in prognathism, and several other features bringing humans closer to the fetal ape's morphology). The males, however, remain almost as robust as typical 'Neanderthals'. Ten thousand years later, the females have become markedly more gracile, and the robust features of the males have also begun to wane. Towards the end of the Pleistocene, the males begin to catch up with the females, and from there on the loss of robusticity continues right to the

present time. These relatively rapid changes *are not attributable to genetic drift via a bottleneck*, but are the result of selective breeding—unintentional self-domestication.

Susceptibility of the Human Brain to Illness

The deleterious effects of human domestication are not limited to the gracilization and neotenization of Final Pleistocene humans; there is another significant factor to be considered. Extant non-human primates appear to be largely free of the neurodegenerative diseases as well as numerous genetic defects that are so prominent among modern man (Rubinsztein et al. 1994; Walker and Cork 1999; Olson and Varki 2003; Bailey 2006). A review of the relevant brain illnesses and their etiologies also suggests that they involve largely the very same areas of the brain that are the phylogenetically most recent, in that they differ most from those of other extant primates (Bednarik and Helvenston 2011). It is these areas that support the much-vaunted perceived advanced cognitive and intellectual characteristics of 'modern humans'. It appears that *Homo sapiens sapiens* is paying a price for the extraordinary abilities acquired. What made us human, especially the neural system supporting language and social cognition (Horrobin 1998), has also led to psychosis, as predicted by Badcock (1980).

Not only have the mental and cognitive developments in our brain rendered humans vulnerable to neurodegenerative diseases as well as frontal lobe connectivity problems—such as those causing autism, schizophrenia, bipolar illness, myelenization—which significantly other primates seem to be free of. They have apparently also facilitated the rise of quite specific personality disorders, such as obsessive compulsive disorder and sociopathic or antisocial personality disorders. Like Rett and Down syndromes and dozens of other known genetic impairments endemic to humans, they could be expected to have been vigorously selected against by natural evolution (Gangestad and Yeo 1997; Keller and Miller 2006; Keller 2008). The same applies to such conditions as chronic fatigue syndrome, which, although of unknown etiology, is often related to psychiatric disorders (Brown et al. 2010). Here, however, the focus is on neurodegenerative pathologies, of which a considerable variety is being distinguished. Among the better known are Alzheimer's, Huntington's and Parkinson's diseases, frontotemporal dementia and behavioral variant FTD; but amyotrophic lateral and diffuse myelinoclastic sclerosis, AIDS dementia, Batten disease and neuronal ceroid lipofuscinosis, Creutzfeldt-Jakob disease and many others also pertain. The first listed are briefly reviewed, as well as several further common human brain illnesses posing evolutionary selection issues.

Alzheimer's disease (AD) can be diagnosed in people from the 30s onwards, but is primarily a disease of aging. It results from extracellular plaque deposition of beta amyloid and intracellular accumulation of tau, a protein. Tau is the component of intracellular neurofibrillary tangles. These plaques and tangles, clearly visible with MRI, are initially found primarily in the hippocampus and entorhinal cortex, later in some areas of the frontal cortex and temporal (medial temporal lobe) and parietal association cortex. AD targets the limbic structures (Hyman et al. 1984), including the amygdala, the locus coeruleus and the cholinergic neurons of the nucleus basalis of Meynert. As a result of the plaque deposition neurons and synapses die, axons degenerate and connections are lost; general atrophy of the cortex and brain shrinkage occur (Smith 2002). VENs (von Economo neurons, see below) are

particularly vulnerable to AD, and about 60% of them may be lost in the anterior cingulate cortex (Seeley et al. 2006).

VENs are also highly implicated in *frontotemporal dementia* (FTD, also known as Pick's disease) (Mayo Clinic 2010). This group of relatively rare disorders affects primarily the frontal and temporal lobes, associated with personality, behavior, and language. In one variant of frontotemporal dementia known as behavioral variant bvFTD the anterior cingulate cortex and the orbital frontoinsula both show marked signs of focal degeneration, which is prominent in the right hemisphere (Seeley et al. 2007).

Huntington's disease derives from cell loss in the basal ganglia and cortex (Revilla and Grutzendler 2008). This movement, cognitive, and behavioral disorder can affect most age groups and occurs in the neostriatum, where marked atrophy of the caudate and putamen is accompanied by selective neuronal loss and astrogliosis. Degrees of atrophy in other regions, including the globus pallidus, thalamus, subthalamic nucleus, substantia nigra, and cerebellum, depend upon the progress of the disease. Its genetic basis involves the expansion of a cysteine-adenosine-guanine (CAG) repeat encoding, a polyglutamine tract in the N-terminus of the protein product called Huntingtin—the function of which remains unknown.

Parkinson's disease (PD) is associated with a loss of dopaminergic nigrostriatal neurons, which are located in the substantia nigra of the midbrain. By the time a patient is diagnosed with PD, usually at stage three of six defined stages, about 60–70% of the substantia nigra dopamine cells are already lost. By that time the substantia nigra, basal ganglia, amygdala, part of the limbic system, nucleus basalis of Meynert and part of the extended amygdala have all been affected.

Obsessive compulsive disorder (OCD) involves persistent thoughts, feelings and impulses that are attributable to an overactive inferior prefrontal cortex. Appearing first in childhood to early adulthood, this anxiety disorder affects areas of the brain called the 'worry circuit' and is connected with an imbalance of the neurotransmitter serotonin (Schwartz and Begley 2002). Excessive activity in the inferior prefrontal cortex leads to the development of obsessive stereotypical behaviors. The striatum (caudate nucleus and putamen) is also over-activated in OCD sufferers. Projecting to the striatum, the inferior prefrontal cortex, orbitofrontal cortex and the cingulate cortex cause the caudate to be overactive in the striosome area, thus bringing emotional tones and valences into the experience via the amygdala because it also projects into this same striosome area. Between the matrisome and the striosome areas are the tonically active neurons (TANs), which integrate the input from the inferior orbital frontal cortex via the strisomes with the input from the amygdala and orbitalfrontal region, also via the striosomes. The TANs thus function as a gating mechanism between the matrisome and the striosome regions.

Bipolar or manic-depressive disorder (BD) is characterized by extreme mood swings between alternatively euphoric and depressed states. Cyclothymic disorder is a milder form of this illness (Goodwin and Jamison 1990). Several genetic regions have been implicated in these conditions, including six specific chromosomes (Craddock and Jones 1999). Since Schildkraut (1965) suggested the involvement of the neurotransmitters norephinephrine and serotonin and with the advent of neuroimaging a number of brain areas have been implicated. This includes the observation of reduced gray matter in the left subgenual prefrontal cortex and amygdala enlargement (Vawter et al. 2000), and decreased neuronal and glial density in association with glial hypertrophy (Rajkowska 2009). Significant shape differences have also

been observed in caudate and putamen, thus implicating the basal ganglia (Hwang et al. 2006). One of the genes implicated in BD is MAOA (Preisig et al. 2005).

Schizophrenia afflicts the frontal lobes with connectivity problems, contributing to the appearance of atrophy, and the cingulate cortex, temporal lobes and hippocampus are all adversely affected. The illness involves volumetric changes of gray matter in the right and left middle and inferior temporal gyrus, worsening with chronicity (Kuroki et al. 2006a, 2006b). Hippocampal volume is also reduced in schizophrenia and there is lateral ventricular enlargement (Harrison 1999). The condition is associated with frontal lobe dysfunction and disconnectivity (Mathalon and Ford 2008). These morphometric changes are suggestive of alterations in synaptic, dendritic and axonal organization, a view supported by immunocytochemical and ultrastructural findings. Numerous rare alleles are thought to be involved (McClellan et al. 2007). Pathology in subcortical structures is not well established apart from the dorsal thalamic nuclei, which are interconnected with the dorsolateral prefrontal cortex (which possesses VENs). The anterior cingulate cortex containing large numbers of VENs is also involved. Reductions in the number of small neurons in layer II and reduced cerebral blood flow in the anterior cingulate have been noted in schizophrenia (Tamminga et al. 1992), which has been linked with the genes SLC6A4 (Cho et al. 2005), NRG1 (Li et al. 2006) and NRG3.

Multiple sclerosis (MS) is apparently but not conclusively an autoimmune inflammatory disease of the central nervous system, causing demyelination of axons (Sailor et al. 2003). It is characterized by multifocal lesions, the MS plaques. Activated mononuclear cells destroy myelin and to some degree oligodendrocytes, the glial cells that produce the myelin in which axons are wrapped. Remaining oligodendrocytes attempt to produce new myelin, but in most cases this pattern of inflammatory reaction subsides only to appear at another location or at another time. The pattern of progression suggests a relative hierarchy of changes over time, involving first frontal and temporal regions (Lumsden 1970) and later the pre-central gyrus (Wegner and Mathews 2003). MS can impact on any area in the central nervous system although visual areas are commonly affected.

Autism spectrum disorders manifest themselves in early childhood and their etiology remains unknown. Abnormalities have been detected in the frontal and temporal lobes, the cerebellum, the amygdala, and the hippocampus. VENs have been implicated in autism (Allman et al. 2005: 367; but see Kennedy et al. 2007). Underconnectivity in the brains of children with autism (Hughes et al. 1997) offers a basis for further investigation of this and other pervasive developmental disorders (Brasic 2009). In some subgroups, cerebellar dysfunction may occur, in others there is dysfunction of the prefrontal cortex and of connections to the parietal lobe. Reduced activation in the fusiform gyrus, the portion of the brain associated with facial recognition, and increased activation of adjacent portions of the brain associated with recognition of objects have been observed. The amygdalas of patients with autism have fewer nerve cells, especially in a subdivision called the lateral nucleus of the amygdala (Balter 2007).

Asperger's syndrome differs from autism in that it lacks the aberrations or delays in language development or cognitive development that are typical of autism. Sufferers may also have normal or even superior intelligence, in contrast to the low IQ associated with autism. However, they share social insensitivity and other characteristics with autism patients. Asperger's also develops in early childhood, generally after the age of three.

Temporal lobe epilepsy involves the limbic system and may originate in several locations within the temporal lobe, the hippocampus, parahippocampal gyrus, amygdala, etc. (Benson and Blumer 1975). This epileptic condition is included here because of its effects on the limbic system (Volle and Heron-Helvenston 1979), which it shares with many of the other pathologies listed.

Middle cerebral artery stroke, although not related to neurodegenerative conditions, is considered here because it is the leading neurological illness, and evolution would have strongly selected against this susceptibility. Stroke derives from thromboemboli lodged in a cerebral blood vessel; from platelet emboli; or from carotid or vertebral stenosis. The middle cerebral artery is the largest cerebral artery and also the most commonly affected by cerebrovascular incidents. Since it supplies large areas of the brain (most of the outer convex brain surface, nearly all the basal ganglia, and the posterior and anterior internal capsules), infarcts can lead to diverse conditions. These include apraxia (inability to perform previously learned physical task) and dyspraxia (inability to perform a physical task), and Broca's and Wernicke's aphasia (expressive and receptive language deficits).

This brief list of brain disorders should suffice to show not only that specific brain regions are selectively affected by them, but also that these are in most cases those very same regions facilitating what are generally defined as the 'higher cognitive functions' of the human brain (Damasio et al. 1990). There is every possible indication that this neurological susceptibility is directly linked to the complexity of the ever-burgeoning brain. Expressed in simplistic terms, it has given us both the genius of our greatest thinkers and artists, and the despair of 'losing our mind'. This immediately raises a fascinating question: did the human ancestors of early parts of the Pleistocene suffer from the neurodegenerative curse? If the two extreme conditions of the human mind are in some measure correlated, the answer might be, these afflictions appeared only as hominin cognition became overly complex, perhaps as if it placed excessive demands on new neural structures. To investigate the origins of mental illnesses involves three closely related issues that have not been investigated in any depth: (1) how did these pathologies initially develop; (2) at what time in our evolution did they appear; and (3) why did evolutionary processes apparently fail to select against the relevant genetic predispositions (the Keller and Miller 2006 paradox)? Without some appreciation of these issues the diseases concerned have no causal context or explanation; one is merely trying to make sense of end effects at specific loci without an appreciation of how they came about. Science, however, expects some level of causal reasoning from us.

In seeking to determine how humans became human, and how they acquired the neuropathologies this involves, our search would benefit from an initial focus on those rather few characteristics that appear to be uniquely and quintessentially human. Preoccupied with inconclusive word games, the social sciences have not produced much sound empirical data. Neuroscience, on the other hand, has, but that wealth remains largely untapped by those examining hominin cognitive evolution. For instance, one of the major differences between humans and other extant primates is found in Brodmann's area 10 (Brodmann 1912) in the pre-frontal lobe, apparently much more developed in humans than in chimpanzees (Semendeferi 2001). This cortical region supports higher cognitive functions, including the extraction of meaning from experience; the organization of mental contents that control creative thinking and language; artistic creation; initiation of, expression of, and planning for future action (Damasio 1985). Hodgson and Helvenston (2006) suggest that area 10 is one of the most likely substrates for the expansion of complex, sustained and focused human

consciousness, which is one of the major differences between humans and other extant primates (the other being speech). Details of their neurological disparities suggest that distinctive changes must have taken place during the course of hominin evolution, since the phylogenetic split in the Miocene period. Differences between the brains of humans and members of the pongid clade are essentially in respect of *structure* and *size*. The structural dissimilarities are considered first.

VENs (von Economo neurons), occur in both apes (and other mammals) and humans (Nimchimsky et al. 1999; Watson et al. 2006), but they are larger and far more numerous in the latter, occurring in humans in the anterior cingulate cortex (Allman et al. 2002; Hayashi et al. 2006) and the frontoinsular cortex (Sridharan et al. 2008). These structures are thought to be involved in complex social emotion and cognition. Nerve cells in humans, e.g. in the primary visual cortex, are arranged in far more complex patterns than in apes (Preuss and Coleman 2002). The minicolumn, the mammalian brain's basic information processing structure, in the left planum temporale, is significantly enlarged in the human, relative to the chimpanzee or rhesus monkey (Buxhoeveden and Casanova 2002), containing the axons, dendrites, and synapses that make neural connections (Sherwood et al. 2009). Significantly, the planum temporale is involved in language production. Ullian et al. (2001) found that synapses form between neurons only in the presence of astrocytes, neuroglial cells constituting almost half the cells in a human brain (see also Ullian et al. 2004; Barres 2008). These cells secrete the protein thrombospondin, which triggers synapse formation (Christopherson et al. 2005) and of which the human brain produces about six times as much as that of chimpanzees or macaques (Cáceras et al. 2007). It also produces about twice as much of THBS4 and THBS2 messenger RNA (mRNA), respectively, in the human cerebral cortex. (RNAs are ribonucleic acids that, like DNA, can carry genetic information.) Thrombospondin expression differences were observed in the forebrain (cortex and caudate), whereas the cerebellum and most non-brain tissues exhibit similar levels of the two mRNAs in humans and chimpanzees. Increased expression of thrombospondins in human brain evolution could result in changes in synaptic organization and plasticity, and contribute to the distinctive cognitive abilities of humans, as well as to the vulnerability to neurodegenerative disease that seems unique to humans (Walker and Cork 1999; Olson and Varki 2003).

VENs are considered to participate in rapid signal transmissions and are relatively newly evolved in mammals, being present in humans, pongids, sperm and beluga whales, bottlenosed and Risso's dolphins, and in African and Asian elephants (Coghlan 2006; Hof and Van der Gucht 2007; Butti et al. 2009; Hakeem et al. 2009; Seeley et al. 2006). This list suggests that VENs may be restricted to relatively large animals with large brains and extensive social networks.

Those areas of the anterior cingulate cortex that contain VENs have been proposed to be a phylogenetically new specialization of the neocortex (Allman et al. 2001) rather than a more primitive state of cortical evolution, as most other areas of the cingulate cortex are (Nimchinsky et al. 1995). The anterior cingulate is an area involved with a variety of emotions, both positive and negative, and its VENs are believed to project to Brodmann's area 10 (Allman et al. 2002). While the human frontal lobes are not relatively oversized, parts such as areas 10 and 13 may be enlarged relative to what would be expected from a primate of human body size. The increase in area 10, used in retrieving memories from the individual's past experience and in planning future action, has been suggested to begin with *Homo habilis* (Semendeferi 1994). Area 13 is part of the limbic system (Heimer et al. 2007)

and involved in emotional, motivational and social behavior via its interconnections with other limbic and cortical structures. The cingulate gyrus, a significant part of the limbic lobe, is of substantial size in humans. It subsumes viscero-motor, cognitive-effector, instant emotional experiences, adaptive motor responses, and sensory processing areas (Mega and Cummings 1997). The extended and in some ways unique human limbic system (Heimer et al. 2007) includes the hippocampus and the amygdala, the septum, olfactory nucleus, entorhinal cortex, bed nucleus of the stria terminalis, and the nucleus basalis of Meynert. The amygdala is implicated in a spectrum of social attributions, such as appraisal of the emotional state of others (Adolphs et al. 1994), value judgments such as trustworthiness (Adolphs et al. 1999), and the emotional tone of memory consolidation and restructuring. The hippocampus receives its input from the entorhinal cortex, which derives its inputs from the associative neocortex—the most recent cortical development and involved in spatial orientation (Frank et al. 2000). The entorhinal cortex, hippocampus and amygdala are implicated in memory functioning (Gloor 1990, 1992). Since there are few conditions that involve almost exclusively the amygdala (e.g. Urbach-Weithe disease) its now accepted neuroanatomical extension includes the subpallidal region and the bed nucleus of the stria terminalis.

The prefrontal cortex as well as portions of the posterior association areas have in humans become enlarged beyond what would be expected in comparison to primary sensorimotor structures (Preuss 2001). Preuss and Kaas (1999) report that the human Brodmann's area 17, comprising the primary visual areas, differs from both apes and monkeys in the way information is segregated from the magnocellular and parvocellular layers of the lateral geniculate nucleus. These authors attribute to humans an improved ability of evaluating moving stimuli. Holloway (1995, 1996) notes that the visual striate cortex and lateral geniculate are significantly smaller in a human than expected for an ape of human size and suggests that the variation in the former area began with australopithecines (Holloway 2001). Another distinctive difference is in the pyramidal motor system, the most recently evolved part of the motor cortex. In particular, the rostral section of the motor cortex is phylogenetically recent. In contrast to apes, where the motor cortex is located on both banks of the central sulcus, it is in humans located in front of the central sulcus. The caudal primary motor area is mediated by corticospinal efferents in the extrapyramidal system, which includes the caudate and putamen, i.e. the striatum. The latter and the globus pallidus form the basal ganglia, thought to integrate emotion and reason for us, generating motor neuron activity and motor output (Rathelot and Strick 2009).

Another difference between pongid and human brains concerns the cerebellum, which is smaller in humans than would be expected in an ape of human body size, but larger than expected in the gorilla (Semendeferi 2001). It serves fine motor tuning, balance and some aspects of cognition (Leiner et al. 1995), in the routinization of complex cognitive procedures, error detection and language. The ability to predict the actions of others and the preparation for behavioral responses have also been attributed to cerebellar learning of sequences (Mueller and Courchesne 1998).

The parietal association area is larger in humans than in apes, at the expense of the occipital cortices. The planum temporale, presenting a left-right asymmetry favoring the left (Geschwind and Levitsky 1968), has been related to language reception, but it is also present in apes (Gannon et al. 1998, 2001). This challenges the often-perceived simple relationship between this asymmetry and language. These similarities are perhaps merely homologous in apes and humans, as suggested by the work of Stepniewska et al. (1993) with owl monkeys. It

showed that when the homologue of Broca's area is stimulated in that species it produces oral and laryngeal responses. The insula in the anterior Sylvian fissure of the temporal lobe has also been suggested to be large in humans, constituting part of the extended limbic system (Heimer et al. 2007). The nucleus subputaminalis in the basal forebrain is unique in humans, providing cholinergic innervation to the inferior frontal gyrus where Broca's area (crucial for speech) is located. Wernicke's area is specialized in humans for the reception of sounds, especially language comprehension. Located in the posterior temporal lobe, this area has six layers, in contrast to the three-layered allocortex (hippocampus and olfactory cortex) (Buxhoeveden et al. 1996).

Having thus considered *structural* differences between human and ape brains, the question of their respective *sizes* is reviewed next. Encephalization is one of the two most distinguishing characteristics of humans, the other being neotenization (as discussed above). At 1350 cc, the human brain is significantly larger than that of any other species, relative to body size. This is perhaps best expressed by the encephalization quotient (EQ), introduced by Jerison (1973). It expresses the ratio of actual brain volume to 'expected brain volume', the latter being based on average sizes of living mammals (Kolb and Whishaw 2008: 41). It predicts an increase of 0.75 in brain size for every unit of body size increase (Martin 1996). Based on the cat having an EQ of 1.0, the quotient thus reflects the increase in brain size over and beyond that demanded by body size. The rhesus monkey's EQ of 2.09 (200 cc brain volume) is not spectacularly smaller than the EQ of the chimpanzee of 2.48, with more than double the brain volume (440 cc). The chimpanzee is our closest living relative, genetically much closer to us than the gorilla, but when it comes to the EQ, it is decidedly dwarfed by our EQ of 7.30.

Since the cell bodies of large brains are more scattered, there is more room in them for interconnections between areas (Semendeferi 2001). It is precisely the expansion of association cortices that has made the human brain disproportionately large (Preuss 2000). The human cortex is ten times larger than that of the macaque and three to four times larger than any ape's (Semendeferi 2001: 108). It had long been assumed that the frontal lobes in humans were much larger than would be expected for a primate of human body size (Brodmann 1912; Blinkov and Glezer 1968), but recent evidence suggests that they are just about what should be expected (Semendeferi 1997, 2001). However, as noted above, specific areas (e.g. expanded limbic system, Brodmann's areas 10 and 13) are larger than would be predicted.

In humans, adult brain size is partly determined by the number of neurons produced and retained during an individual's ontogeny. Different neural areas differ in the length of the embryonic period of neuronal cytogenesis of precursor cells. The longest periods of cytogenesis apply to the areas of greatest degree of enlargement (cortex), and the shortest apply to the least enlarged brain areas (medulla). This suggests that brain size as well as relative size of specific structures could be the result of developmental timing (Kaskan and Finley 2001). A decrease in rates of apoptosis could also account for increased brain size. Rakic and Kornack (2001) have suggested that in encephalization, cortical neurons are formed from precursor cells lining the ventricles and migrate radially along glial fascicles to reach their cortical destination. Thus the neurons that are formed first make up the deepest layers of the neocortex, and those formed last are its most superficial. Since the neocortical thickness of the macaque brain is similar to the human brain, it is significant that the surface area of the human cortex is ten times as large as that of the macaque. Surface area is

determined by the number of these radial columns, while the number of cells in each column determines cortex thickness. It is suggested, from comparing macaques and mice, that the process is regulated by the numbers of mitotic cell divisions involved in the cytogenesis of neurons prior to or during the early stages of the initial formation of radial columns.

CONCLUSION

The ventromedial or orbital prefrontal cortex has thus been implicated in human cognitive evolution as well as in the attendant pathologies, and the involvement of forebrain-neuroanatomy and neurophysiology of frontal and prefrontal structures in mental illness has been demonstrated (e.g. Heimer et al. 2007). This nexus between emerging advanced cognitive abilities and neurodegenerative susceptibility (Bednarik and Helvenston 2011) has considerable implications for the question of the involvement of genetic drift in recent human evolution. On the strength of the evidence presented here, natural selection as such had very limited influence in the most recent direction of this process. That is to be expected, but the timing of the change remains to be established: is this a very recent development, related perhaps to urbanization or the 'Neolithic revolution', or did the change from natural to cultural genetic selection already commence in the Final Pleistocene? The strongest evidence points to culture favoring deleterious somatic aspects over the last 50 ka, and it also demands some mechanism preventing natural selection acting upon neuropathologies.

The evolution of mental and cognitive faculties in hominins should be assumed to have also involved a gradual change from impulsive towards the obsessive range of a spectrum of behavior (cf. Ochse 1990; Bednarik 2008d). The apparent absence of neurodegenerative and other mental illnesses in extant non-human primates seems to point in the same direction. Based on judicious archaeological reasoning, a rudimentary sense of perfection appears to have been developed by the Middle Pleistocene, and it can apparently be traced back to Mode 1 technocomplexes (Bednarik 1992, 1995a, *et passim*). The neuroscientific information seems to imply that these ancestors, late *H. erectus* and early *H. sapiens*, had developed specific brain structures and tissues that facilitated advanced mental and cognitive performance. As the mental faculties of hominins increased with the rise to the top of the food-chain, individual reliance was delegated to society and to objects, the latter ranging from tools to objects of externally storing symbolic information ('exograms'). But to what extent were our ancestors at the same time rendered progressively more susceptible to neurodegenerative and neurological pathologies?

In some cases first genetic indications are already available that such predisposition may have been limited to 'modern' humans. For instance, the DYRK1A gene, implicated in causing Down syndrome, seems absent in robust *Homo sapiens*. The genes CADPS2 and AUTS2, responsible for autism, also appear to be limited to modern Graciles. Perhaps more dramatic is the proposal that schizophrenia is of late historical origin and might have been introduced by a virus as recently as 200 or 300 years ago (Hare 1988). Indeed, there appears to be no earlier mention of the disease, in contrast to other conditions such as bipolar illness (Bednarik and Helvenston 2011). Be that as it may, the NRG3 gene, associated with schizophrenia, also seems to be absent in so-called Neanderthals. Using the human haplotype map to test for selective sweeps in regions associated in genome scans with psychosis, such as

1q21, is promising (Voight et al. 2006). Again, such selective sweeps tend to yield relatively recent etiologies, of less than 20 ka, as predicted by the domestication hypothesis. Continuing research is likely to locate more evidence that neurodegenerative illnesses are the burden specifically of 'modern' sapienoids, just as other 'modern' human genes such as RUNX2 and CBRA1 (causing cleidocranial dysplasia or delayed closure of cranial sutures, malformed clavicles and dental abnormalities) and THADA (associated with type 2 diabetes) are certainly deleterious and would not be expected in robust populations. Allele frequencies may have come to be out of equilibrium, therefore equilibrium-based population-genetic models for explaining standing levels of variation, based on antagonistic pleiotropy or related mechanisms, are irrelevant. In a species fully subject to the canons of natural selection the disadvantageous mutations of *Homo sapiens sapiens* would tend to be suppressed.

The concept of perfectionism, which can be traced to several Lower Paleolithic features (beads, cupules, hand-axes; Bednarik 2001) certainly has adaptive value in a cultural system, but it does require a level of obsessiveness. There is no sense of perfection apparent in anything extant non-human primates make. Their sleeping nests or tools reveal no compulsion to go beyond the purely functional, and have very probably remained completely unchanged for a long time: no desire to improve is evident. Nor is any such obsession apparent from the tools of australopithecines or early *Homo* (up to *H. erectus*). Evidence for these impulses seems to appear roughly mid-way through the Acheulian technocomplex, or close to a million years ago. OCD seems to illustrate that obsessive and neurotic behavior is the price humans pay for their rapid cognitive evolution; they are rather like an unwelcome side effect of it. The argument can be extended to most cultural behavior, which, when viewed pragmatically, is frequently irrational. Seen in a realistic perspective, it is often overwrought and involves countless obsessive aspects, e.g. our regimented behavioral routines or our relentless acquisition of excessive surpluses as an insurance against the loss of another insurance, which surely would qualify as an obsessive behavior symptom. Our access to 'objective reality' (should such a state exist) is severely limited by the residues of irrational ideologies, baseless ontologies and metaphysical straightjackets, the baggage of many millennia of cultural development. Other primates do not share our hankering for something to believe in. Our reliance on 'specialists' (shamans, prophets, scientists, medical doctors) ignores that *déformation professionnelle* is also a distortion in the way the world is perceived. Professional training involves obsessive behavior traits that may be neurophysiologically relatable to compulsive behavior. Indeed, it is almost a tautology to say that without obsessions humans would not have reached the level of cultural sophistication they have.

By the same token, as that very process appears to be implicated also in the rise of neurodegenerative diseases, it needs to be assumed that these, too, developed during the last million years or so. The advantages of the development of the prefrontal cortex must have significantly outweighed its detrimental effects, which might suggest that the latter were negligible initially, otherwise they could have selected against the changes giving rise to cognitive sophistication. The question of when and why natural selection apparently failed to select against unfavorable traits is central to these considerations (the paradox of Keller and Miller 2006), but cannot be answered empirically. However, the hypothesis attributing Final Pleistocene human neoteny to cultural selection offers a realistic explanation. Just as evolutionary determinants could not prevent the deleterious changes from robust to gracile forms, because they were overruled by cultural determinants, the mental diseases arising from burgeoning prefrontal cortex complexity may have escaped natural selection in much the

same way. The development and persistence of these diseases seems to signal that selection against them was somehow muted. It could also be taken as an indicator that the selective benefits of the Late Pleistocene development of cognition and symboling were of such outstanding effects (Deacon 1997) that the 'byproduct' of neuropathologies was tolerated—or rather, not significantly selected against. Perhaps the level of tolerance of these consequences expanded in proportion to the selective benefits of developing cognition.

The principal effect of the rise of symbol-based culture, then, has been its facilitation of changes not dictated by natural evolution, but determined by cultural evolution. This is not to suggest natural selection has been abolished for humans; rather that cultural factors have begun to co-determine changes to our genome. The gene-culture co-evolutionary model predicts such a development, and some of the evidence and propositions presented in this chapter document it. The gracilization marking human development over the past fifty millennia was not an evolutionary process; it was determined by cultural selection. Selection for specific traits results in changes in numerous other traits—changes that are usually deleterious—be they physiological or a range of others. The resulting loss of robusticity involved several reductions in evolutionary fitness, e.g. the size of the brain decreased at a time when demands made of it are thought to have increased dramatically. This development was, however, offset by the increased use of exograms, which eventually reached such extraordinary proportions that today most of our symbolic information resides outside our brain.

While the role natural selection played in recent human development has decreased at an exponential rate, the effects of the alternative, genetic drift, may have also become progressively marginalized. Population sizes and densities have increased markedly since the mid-Late Pleistocene, and especially since the advent of agriculture in the early Holocene. Susceptibility to genetic drift is a direct function of population size, and with today's world population of billions of interbreeding organisms must be assumed to be negligible. However, the Final Pleistocene deserves closer scrutiny. To the extent that bottlenecks are the result of genetic drift within very small and isolated populations, it can reasonably be assumed that these have played major roles on many occasions, ranging from the Campagnian Ignimbrite Event to relatively recent maritime colonization events (Wallacea, Polynesia, New Zealand, to mention a few). There are, however, other processes that either resemble genetic drift or involve it as an underlying factor. One is niche construction, which can take on many forms, but essentially refers to an organism's alteration of its environment and the resulting ecological inhertitance. As the population adapts to these niches, relevant alleles are preferred, and the changes are neither natural selection derived nor genetic drift derived, but rather somewhere between the two. Humans, obviously, are the ultimate niche constructors, especially through their culturally determined faculties. Human language, which probably appeared around the beginning of the Pleistocene, has been defined as a niche, and like niche construction, it is an autocatalytic process (Bickerton 2010: 231). A much more recent human niche is based on the acquired genetic tolerance to milk sugar. Lactose intolerance beyond weaning is required to ensure that the mammalian mother can feed a new infant. Human lactose tolerance can only be a Holocene development, developing after milk-providing species had become domesticated. A rare mutation on chromosome 2, which in the Pleistocene would have been dysfunctional, gained rapid dominance once animal milk became widely available. Not surprisingly lactose tolerance is greatest among people who have long been milk-consuming herders (>85%), while Chinese are only 7% tolerant, and

Native Americans not at all. Again, this is not natural selection in any Darwinian sense, nor is it a stochastic process such as genetic drift. It is, however, highly effective and relatively swift.

In the case of hominins, the most glaring challenge to natural selection derives from the recently developed toleration of maladaptive traits, which range from somatic features universally related to neotenization, to mental disorder susceptibility alleles, and to almost countless other detrimental susceptibilities. Disorder susceptibility alleles have not either fixated, if adaptive, or gone extinct, if maladaptive. Those that are rare, the single-gene Mendelian disorders, may escape selection precisely because they are rare, and the molecular bases of over 1700 of them have now been identified. However, the preservation of the mutations deriving from multiple mutant alleles at different genetic loci involved in the major deleterious etiologies has remained entirely unexplained until now (Keller and Miller 2006). Not only that, Pleistocene archaeology and paleoanthropology have instead conjured up a fantasy of how humans became 'modern' through the complete global replacement of all other hominins by a species mysteriously arising by genetic drift (bottleneck or founder effect)—a veritable Biblical explanation provided by disciplines of Biblical naivety. There can be no doubt that genetic bottlenecks occurred throughout hominin history, and that they had extensive effects on the human genome. But the momentous and rapid changes of the last fifty millennia are largely the result of self-domestication and of cultural ability to tolerate maladaptive susceptibilities.

Not natural selection, *not genetic drift*, but ultimately cultural selection and niche construction account for the human condition.

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