An etiology of human modernity

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ABSTRACT: Following the refutation of the replacement hypothesis, which had proposed that a 'superior' hominin species arose in Africa and replaced all other humans existing at the time, the auto-domestication hypothesis remains the only viable explanation for the relatively abrupt change from robust to gracile humans in the Late Pleistocene. It invokes the incidental institution of the domestication syndrome in humans, most probably by newly introduced cultural practices. It also postulates that the induction of exograms compensated for the atrophy of the brain caused by domestication. This new explanation of the origins of modernity in humans elucidates practically all its many aspects, in stark contrast to the superseded replacement hypothesis, which explained virtually nothing. The first results of the domestication syndrome's genetic exploration have become available in recent years, and they endorse the human self-domestication hypothesis.

KEY WORDS: Self-domestication hypothesis; human evolution; human modernity; African Eve hypothesis; neotenization; genetics

Introduction

We are led to believe that the consensus view in the discipline is that an average of ~2% of the genomes of present humans everywhere, except Sub-Saharan Africa, are closely related to that of Neanderthals. The dominant model is reinforced by the belief that what is called 'anatomically modern humans' evolved exclusively in Sub-Saharan Africa. Presumably, evolving for 150 ka (or whatever) in their homeland, these AMHs are thought to have remained undiluted by 'primitive' robust genes. In its original, fundamentalist form, the replacement hypothesis demanded that AMHs emerged from a bottle-neck speciation event and were consequently unable to reproduce with any of the robust humans in much of the rest of the world (Protsch von Zieten 1973; Cann et al. 1987). The genetic hypothesis that they became a separate species, unable to breed with 'robusts', received a severe blow with the discovery that these 'Moderns' 'in-

terbred' 'occasionally' with both Neanderthals and Denisovans, and even with another, still undiscovered 'species'. This is not just because it refutes the hypothesis, but because it relegates it to the status of a version of multiregionalism. As Relethford (1999, 2001) contends, all modern origins stories other than the pure replacement version are merely variations of the multiregional theory proposing an inflow of African genes. These narratives, therefore, agree with Weidenreich's (1946) original trellis diagram (Wolpoff and Caspari 1996:200–1). This is a complete anathema to the African Eve advocates and the catastrophist scenario of the replacement hypothesis (the African Eve hoax (Bednarik 2008a)) thus stands falsified.

The 'modified replacement scenario' now being promoted assumes that breeding between its AMHs ('anatomically modern humans') and robusts, including Neanderthals and Denisovans, took place only rarely, and that the robust and gracile populations were essentially separate entities (peoples, tribes, populations, whatever). Ignoring for the moment that this contradicts a great deal of archaeological and paleoanthropological evidence (Bednarik 2008a, Bednarik 2007a), I wish to test this assumption by logic. There are three problems with the proposition that rare hybrids are responsible for the presence of up to 8% of Neanderthal DNA (Prüfer et al. 2014) in any one individual 'Modern'.

The first is one of arithmetic. Neanderthal-like DNA would be progressively reduced in each generation by recombination (Sankararaman et al. 2012). If we assume that a hybrid of one robust and one gracile parent received 50% robust DNA, and if subsequent generational unions were with 'graciles', the follow-ing generation would have 25% robust genes, the next 12.5% and after twenty generations that fraction would have reduced to a tiny 0.0000476%. However, we are dealing with thousands of generations, which means that the percentage of the residue of Neanderthal or Denisovan DNA would be so infinitesimally small that it approaches zero per cent. Therefore, the 'rare hybridization event' hypothesis seems to derive from an error in logic.

The second objection considers that the robust humans are so closely related to present-day humans that for about 90% of the genome, they fall within the present-day human variation. This means that for 90% of the genome, some of us are more closely related to Neanderthals and Denisovans than to our conspecifics today (Pääbo 2014). In thinking about the genetic differences between robust humans and us, it would "be useful to consider how present-day human groups differ genetically among themselves" (Pääbo 2014). To illustrate the point by example: some modern dog breeds resemble the dog's progenitor species, the wolf, reasonably closely, whereas others differ from it quite spectacularly. Nonetheless, the DNA of dogs and wolves, leaving aside the effects of the domestication syndrome (Hammer 1984; Sapolsky et al. 1992; Künzl et al. 1999; Brown et al. 2008; Wilkins et al. 2014), defines them as a single species. An appeal seeking to declare the comparison invalid because it invokes a domesticate has no standing: nobody has ever demonstrated that humans are not the product of domestication. Quite probably, nobody ever will.

These considerations bring us to the third problem faced by the consensus view. How do the African Eve advocates

propose to explain the magical number of ~2%, or in the case of Denisovans, ~5% (Reich et al. 2010; Reich et al. 2011)? Or, for that matter, the ~2% Neanderthals supposedly contributed to Denisovans (Prüfer et al. 2014)? First of all, it is entirely pointless to draw such comparisons between populations that are 50 ka or more apart in time; it is like comparing apples and oranges. We would need to know how similar or dissimilar the genomes were between Neanderthals and purported African Eve descendants *contemporary* with them, not those of the present day. Alternatively, we would have to provide information about where the robust DNA would be today if there had been no contact with 'other humans'. We completely lack such information, working in effect with isolated and incompatible data in a vacuum. Of course, genetic changes have taken place in the intervening time; that is to be expected. Nevertheless, they are not being factored in.

The alternative approach I advocate is much sounder. It is to ask: what proportion of initial robust gene input is required to arrive, through generational recombination for fifty millennia, at a modern result of ~2%? To arrive at a modern level of robust DNA of ~2% would need to involve tens of thousands of these postulated 'hybrids', and a prolonged process of recombination to maintain the required level of robust genes. Hawks (1997) has estimated that at least 25% of the ancestors of late Upper Paleolithic Europeans would need to be Neanderthals to account for the preservation of Neanderthal autapomorphies observed (see also Frayer 1993; 1994; 1998).

One of the most significant errors of the Eve advocates has been that they viewed Eurasia as a mostly empty con-tinent. They seem unaware that robusts occupied the Arctic Circle by at least 130 ka ago (Pavlov et al. 2001; Schulz 2002; Schulz et al. 2002) and lived in hypoxic high-altitude environments 160 ka ago (Chen et al. 2019). This implies that even the most marginal Eurasian environments must have been occupied by Neanderthals, Denisovans and other robusts long before any gracile remains can be detected. The Biblical belief of an Exodus into the wide-open spaces of Eurasia, there for the taking, is Biblically naive.

It is therefore odd that the percentages are about the same for Neanderthal / Denisovan and Neanderthal / gracile 'interbreeding'. The similarities seem more likely attributable to similar evolutionary dynamics, not to identical numbers or timing of rare introgressive hybridization events. Such events would have been geographically and temporally random, and the outcomes should, therefore, not be so similar. A systematic process would explain the outcome much better, and it agrees with both the paleoanthropological and archaeological record. The rather undeniable fact that there is no cultural, skeletal or genetic evidence for the African Eve scenario seems not to have bothered its advocates. It is very briefly revisited below.

Another fundamental error has been to think that there were two genetically isolated populations in Europe, Neanderthals and 'Cro-Magnons', the latter being the type fossils of the AMHs. In reality, we have numerous human fossils from the window from 50 ka to 25 ka in Eurasia that are skeletally intermediate between the two. The morphological change shows a distinct gradual decline of robusticity with time. For instance, one of the skeletal 'Neanderthal' features is the

shape of the mandibular nerve canal (foramen), accommodating the trigeminal nerve and the inferior alveolar vessels. A bony ridge surrounds it on the ramus in 53% of specimens of 'typical Neanderthals' (an arbitrary construct, conversely). Its occurrence declines to 44% during the said transition period and further still subsequently, but it is still present in 6% of today's Europeans (Lewin 2005: 196). This feature had demanded the presence of 'Neanderthal' genes in Europeans long before these were discovered.

Similarly, the process of gracilization has continued unabated to the present day: early Mesolithic skeletal and dental material, of the early Holocene, is still about 10% more robust than modern Europeans. In comparison, the supposedly modern humans of about 20 ka ago are 20% more robust. Gracilization, in Europe as well as elsewhere, was a gradual process. Indeed, the four adults and three or four juveniles from the Cro-Magnon shelter in France are considerably more robust than most present-day humans, and especially the very pronounced supraorbital torus, projecting occipital bone and other features of cranium 3 are Neanderthaloid rather than gracile. Nor, for that matter, is the Cro-Magnon sample of the Aurignacian, as frequently claimed; at only 27,760 carbon years (Henry-Gambier 2002) it is of the Gravettian technocomplex. We have, as Latour (1993) has long declared, "never been modern".

The African Eve hoax

The history of the wasteful diversion of the African Eve begins almost fifty years ago, with the proposal in Professor Reiner Protsch "von Zieten's" PhD thesis (1973) claiming that modern humans evolved exclusively in Sub-Saharan Africa. Protsch's replacement model was adopted by Bräuer (1980; 1981) and then developed into the 'African Eve' hypothesis (Cann et al. 1987). Protsch dated numerous hominin remains directly by radiocarbon analysis (Bednarik 2008a; 2011a) and it took the discipline almost three decades to discover that all of his datings (except one, that of the Mittlere Klause find from Bavaria) were false (Terberger and Street 2003). Protsch was dismissed in disgrace (Schulz 2004), but his replacement model had long captured the discipline and spawned numerous variations on the general theme (Cann et al. 1987; Bräuer 1984; Stringer and Andrews 1988; Mellars and Stringer 1989; Vigilant et al. 1991; Tattersall 1995; Krings et al. 1987; Pennisi 1999; Eswaran 2002; Templeton 2002; Smith et al. 2005). For the decades since this model was introduced, it has been impossible to publish any work challenging the dogma in one of the 'establishment journals'. Only one of them broke ranks (Bednarik 2008a) as the replacement hypothesis began to wane in the wake of genetic evidence contradicting it. Since the replacement model was replaced with the auto-domestication hypothesis (Bednarik 2011a; Bednarik 2008b), not one of its potential opponents, the Eve advocates, has ever addressed it or responded to any of the dozens of my publications addressing the issues. The Eve hoax is continuing with declarations that "we are still no multiregionalists" (Stringer 2014) and oblique references to my *Human condition* (Pääbo 2014). This can mean one of two things: that Eve's champions are bereft of counterarguments, or that they will not engage in a debate.

Since the five conditions required to sustain the African Eve hypothesis were listed (Bednarik 2011a:25), not one of

them has been addressed, but a great deal of new evidence has served the refutation of Eve:

1. Graciles and robusts would need to be sharply separated in the paleoanthropological record by distinguishing morphological features.
   There is no separation of robust and gracile skeletal remains, but there are hundreds of finds that are intermediate between the two forms, indicating a gradual change from archaic to modern morphology. That is precisely one of the significant issues the Eve model faces. Dating from between about 40 ka and the Bølling-Allerød interval, from Portugal to eastern China as well as in Africa and Australia, a catalogue of human remains has been found that present combinations of gracile and robust features. They include, for instance, specimens from Lagar Velho, Crete, Cro-Magnon, Miesslingtal, Mladeč Cave, Pavlov, Předmostí, Podbaba, Dolní Věstonice, Cioclovina, Peştera cu Oase, Peştera Muierii, Bacho Kiro levels 6/7, Starosel'e, Rozhok, Akhshtyr', Romankovo, Samara, Podkumok, Khvalynsk, Skhodnya, Omo Kibish, Herto, Hofmeyr, Qafzeh Cave, Skhul Shelter, Hathnora, Jinniushan Cave, Tianyuan Cave, Maludong, Longlin Cave and many of the numerous specimens lost in the Mikulov Castle fire of 1945 (Frayer et al. 2006). Eve advocates are either unaware of these finds or try to force them into one of the two pigeonholes their dogma demands.

2. The genetic signatures immediately before and after the claimed replacement would need to be sufficiently different to indicate separate species.

No such differences have ever been demonstrated. Let the Eve advocates nominate the earliest known human specimen they claim to be descendent of Eve and let them provide a genetic signature from it. Comparing modern DNA with that of so-called Neanderthals and Denisovans is simply irrelevant and demonstrates no replacement. Moreover, their dogma is formulated incorrectly: *Homo sapiens sapiens*, *Homo sapiens neanderthalensis* and *Homo sapiens denisova* are not separate species; they are subspecies. There appears to be much less interest in exploring the paleogenomics of populations supposedly ancestral to Eve's descendants than in robust populations, but until both are investigated with the same enthusiasm, the relevant genetic signatures cannot be compared. The reality is that only 'graciles' of less than 6000 years old have been found in a state that allows genome sequencing (Rasmussen et al. 2010; Keller et al. 2012). On the other hand, 'robusts' have only yielded small parts of mitochondrial DNA that could be sequenced, and in only a few cases.

3. The superior technological and intellectual capabilities of the 'victorious' 'graciles' would need to be demonstrated.
   An essential claim of Eve's advocates is that the introduction of paleoart and Upper Paleolithic (or Mode 4) technology co-occurred with the invasion of African Eve's progenies. This claim is a complete falsity, in every respect. The earliest European date for U.P. tools is from Senftenberg at >54 ka BP (Felgenhauer 1959), and there are various precedents in tool minia-

turization and bone technology tens of millennia earlier. In Australia, the Mode 3 technology continued up to mid-Holocene times, and in Tasmania up to the British invasion. In southern Siberia, Mode 4 and even Neolithic technologies are attributable to Denisovans. In Europe, not a single fully modern specimen has ever been demonstrated from an Early Upper Paleolithic context. The claim that the Aurignacian, Châtelperronian, Uluzzian, Proto-Aurignacian, Olschewian/ Alpine Paleolithic, Bachokirian, Bohunician, Streletsian, Gorodtsovian, Brynzenian, Spitzinian, Telmanian, Szeletian, Eastern Szeletian, Kostenkian, Jankovichian, Altmühlian, Lincombian or Jerzmanovician are all assemblages created by Neanderthaloid people (Bednarik 2011b) remains unfalsified. Moreover, some of these Mode 4 tool assemblages have yielded remains of 'robusts' of the kind called Neanderthals. These include the Châtelperronian of Saint Césaire (~36 ka) and Arcy-sur-Cure (~34 ka), which prompted White's (White 1993) and Hublin's (Hublin et al. 1996) convoluted explanations of how paleoart or Mode 4 artefacts could occur in occupation remains of Neanderthals. However, the Jankovichian or Trans-Danubian Szeletian (Allsworth-Jones 1986) has also yielded three mandibular 'Neanderthal' teeth from Máriaremete Upper Cave (~38 ka; (Gábori-Csánk 1993)); the Streletsian of Sungir' (~25 ka) produced a Neanderthal tibia (Bader 1978); the Aurignacian of Trou de l'Abîme (~33 ka) also yielded Neanderthal remains, as did the Olschewian of Vindija (~28–34 ka; (Smith et al. 2005; Smith and Ranyard 1980; Wolpoff et

al. 1981; Frayer et al. 1993; Smith et al. 1999; Wolpoff 1999; Ahern et al. 2004; Deviese et al. 2017); while R. Boy excavated a female Neanderthal maxilla in 1981 in the Alpine Paleolithic of the cave Cotencher. It is disconcerting that the African Eve advocates seem unaware of this abundant evidence that about one half of the Upper Paleolithic seems to be the work of Neanderthal-like hominins or their direct descendants.

4. Paleoart, i.e., apparently symbolic productions reminiscent of 'art', should only occur with the graciles.
The (testable) proposition that the paleoart of Chauvet Cave and several other Aurignacian contexts was created by Neanderthaloid people (Bednarik 2007b), which follows on from the considerations just stated, renders the Eve dogma severely challenged. Evidence that Neanderthals created rock art has been available at least since Peyrony reported the 18 cupules on a limestone block covering juvenile interment No. 6 in La Ferrassie (Capitan and Peyrony 1921; Peyrony 1934). Neanderthal petroglyphs have since been reported from Baume Latrone (Bednarik 1986), Zarzamora Cave and Gorham's Cave (>39 ka; (Rodríguez-Vidal et al. 2014)). The many proposals of Neanderthal rock paintings in Spain are perhaps less secure, as they refer to controversial U-Th minimum dates proposed for calcite speleothems (Tang and Bednarik 2021). Such claims come from Pondra Cave, Asturias La Peña, Abrigo de la Viña, El Conde Cave, Peña de Candama, El Sidrón, Maltravieso Cave, Tito Bustillo, Altamira, El Castillo, La Pasiega and Ardales. Be that

as it may, if it is correct that all Early Upper Paleolithic rock art was made either by Neanderthals or their direct descendants (Bednarik 2007b), numerous further corpora are the work of relatively robust people. Even the soundly reliable data show unambiguously that paleoart was produced long before the arrival of the hypothetical but not demonstrated gracile African invaders. The oldest known proto-figurines, portable engravings, petroglyphs, beads or pendants, curated manuports and evidence of pigment use are all several hundreds of millennia old, yet the African Eve advocates seem to be profoundly unaware of these thousands of instances of evidence of 'creative' or 'symbolic' activities (Bednarik 2017). Just as they are unaware that there is in fact more rock art of Mode 3 industries known in the world than of Mode 4. The question that needs to be asked is why the robusts need to be conceived as creatively inferior to the graciles, and this mindset appears to be politically/religiously motivated.

5. Since the graciles are claimed to have come from Sub-Saharan Africa and travelled via the Levant and south-eastern Europe, it would be expected that evidence of the graciles' presence needs to be found first in their homeland and later progressively along such a route, in the form of dramatically different technology as well as paleoart.
It is self-evident that no Paleolithic-style cave art has been reported from anywhere along the routes the mythical Moderns could have taken to reach south-western Europe from Sub-Saharan Africa (notwithstanding the controversial claim from Qurta). Absence of evidence does not indicate evidence of absence, but, significantly, there is a complete absence of Mode 4 technologies across all of northern Africa (Bednarik 2008a). The entire vast region was occupied by people with Middle Stone Age tools until about 20 ka ago, whereas the Mode 4 technologies can be first detected thirty millennia earlier in parts of Eurasia. While one might argue that there were no suitable sites or preservation conditions for cave art in northern Africa, or it is so rare that it has not been found so far, that argument cannot be applied to stone tools. Therefore, the African Eve advocates need to explain how their AMHs managed to tiptoe from Sub-Saharan Africa to Europe without leaving a trace.

The five conditions required to sustain the replacement hypothesis are all impossible to meet at present, and it can be anticipated that most will never be met. The hypothesis was presented without valid empirical evidence, *ex post facto*, and supporting evidence was then recruited selectively. However, none of it was sustainable from the beginning, be it skeletal, genetic or archaeological. For instance, the computer modelling applied by Cann et al. (1987) was botched, and its haplotype trees were irrelevant. It had arbitrarily selected one of 10^{267} alternative and equally credible haplotype trees (which are very much more than the number of elementary particles of the entire universe, about 10^{70}!). Maddison (1991) demonstrated that the Cann et al. model could produce 10,000 haplotype trees that are more parsimonious than the one randomly chosen by these authors. This pattern can be seen

in most endeavors to flesh out the skeleton replacement notion. It needs to be asked what rendered it so popular in the first place, particularly as it was initially based on Protsch's hoax. What was it that convinced its followers that, despite the many setbacks and contradictions encountered, they must be on the right track?

The answer, I contend, is quite simple. The politically correct intimation that it demonstrated how humanity is one single family in which all are interrelated was one factor. Another is the similarly shallow signal to the religious lobbies that it preserves the separation between those who can enter heaven and those who cannot. Now that the replacement hypothesis is unravelling, its supporters have taken the extraordinary step of limiting the term 'human' to *Homo sapiens sapiens*, denying human status to all other members of the genus *Homo*. It appears that the media, who coined the various Biblical references for aspects of the replacement hypothesis, were not too far off the mark: this is about preserving religion. The one overarching article of faith that reassured the Eve followers that they must be right was that after millions of years of slow and gradual evolution, there appeared to be an inexplicable quantum jump in this process. Within a geological instant of barely 20,000 years, gracile people 'suddenly' replaced the robust resident humans in Europe. Eve's supporters were confident that only an incursion of people from elsewhere could explain this, and Protsch's model provided the southern African homeland of these mythological invaders.

However, the most significant deficit of this model is that it fails to explain *how* we became 'modern'. It does not elucidate what could have caused the inherent laws of biological evolution to be suspended for humans during the last fifty millennia or so. The dramatic change from a dysteleological process (evolution) to a teleological one is not explained; nor is the question of why evolutionary natural selection apparently failed to select against thousands of deleterious genetic predispositions and defects (such as the 6328 Mendelian disorder phenotypes for which the molecular basis is known and 4017 genes with phenotype-causing mutations listed as of January 2019); or how to explain the significant atrophy experienced by the human brain (Henneberg 1988; Henneberg and Saniotis 2009; Bednarik 2014), not to mention the relentless neotenization of the species that led to Moderns. It fails to clarify why the etiologies of brain illnesses suggest that they involve mostly the same areas of the brain that are the phylogenetically most recent (Bednarik 2020); or why it should be that other extant primates are mainly if not wholly free of such pathologies. The Eve model does not attempt to clarify why evolutionary processes failed to select against the degenerative genetic predispositions of extant humans. The toleration of countless maladaptive traits, which range from somatic features to mental disorder susceptibility alleles, is not explored by it, nor is the question how humans coped with the loss of brain volume, why males have a universal preference for neotenous females, how exclusive homosexuality arose, the loss of estrus, the advent of menopause, of exograms, or indeed of any aspect of the present-day human condition (Bednarik 2011a). As a theory, this proselytizing program has no power of explanation whatsoever.

Science, however, is about causal relationships. Since we have a hypothesis

that can explain all these phenomena and many more and that has been available for well over a decade (Bednarik 2008b), it is incumbent upon the African Eve advocates to acknowledge it or, if they are so inclined, attempt its refutation.

The auto-domestication hypothesis

The self-domestication hypothesis or specific aspects of it have been published in numerous papers and two books since 2007, and readers seeking full details are referred to this literature (e.g., Bednarik 2011a; 2008b; 2020; 2007). Here I present just a concise introduction, before addressing its genetic basis. The Eve supporters are undoubtedly right in their belief that gracilization occurred too swiftly to have arisen by evolutionary developments. Although the neotenization or gracilization process that accounts for the change cannot be one of *natural* selection, *sexual* selection can lead to even more significant somatic changes in just a few millennia. It merely requires systematic selection for specific traits, which usually leads to a whole suite of other changes collectively defined as the domestication syndrome. These are well understood, and their genetic basis is currently being explored. Most of these changes can be described as detrimental in respect to Darwinian evolution, and yet they can render a domesticate highly successful for other reasons. Domesticates may thrive in vast numbers, forming symbiotic relationships with their domesticators (e.g., by mutualism or commensalism).

In investigating the skeletal and dental changes, especially cranial, from robust to gracile Europeans, I noticed that the fe-male specimens between 40 ka and 30 ka ago are consistently far more gracile than the males. Although both sexes become less robust with time, the females do so much more rapidly during the very same time when both rock art and portable art suggest a preoccupation with the female body. It occurred to me that modern humans are, as far as we know, the only species in which attractiveness in females seems more critical than in males, and in which the males select mating partners (in the natural world the females select, either actively or 'passively'). We are also the only subspecies exhibiting distinctive mating preferences concerning personality or anatomical traits, such as 'attractiveness', which is a purely cultural construct. Culturally governed mating imperatives undeniably dominate sexual choice in present-day humans (Buss and Barnes 1986) and as they exist in no other primate, it is inescapable that they must have been introduced at some point in time in the human journey.

Furthermore, no other animal shows in its mating behavior a preference for such attributes as youth, skin or hair color, body ratio, cephalofacial appearance, facial symmetry, or most especially neoteny in females, yet such characteristics powerfully condition us. Moreover, this trait is universal, found in all societies investigated, and independent of any cultural, social, or religious conditioning (Buss et al. 1990; Grammer and Thornhill 1994; Jones 1995; Jones 1996; Shackelford and Larsen 1996; Barkow 2001). Similarly, female attractiveness across the world is more important than male in all present-day humans (Ford and Beach 1951; Gregersen 1983). These trends are so universal that they cry out for a credible explanation, which to my mind, evolutionary psychology has never presented.

The characteristics that distinguish us from all other animals, and presumably from specific ancestral populations before us, are not upright walk, language, toolmaking, Theory of Mind, consciousness, self-awareness, culture or any of the other traits that have traditionally been trotted out in this context. All of them can be found in other animals, although symbol-based communication may be limited to hominins. Instead, they are a distinctive suite of attributes connected with domestication and neoteny. It was from this realization that the auto-domestication hypothesis was developed. The question was: what traits had been selected to introduce the domestication syndrome in humans? Since human females may have led the development to gracilization during Early Upper Paleolithic times, our contingent answer was the selection of features considered attractive in females in choosing mating partners.

Nevertheless, once even a small cultural bias had been introduced into what must traditionally have been a reasonably stochastic selection process, genetic biases developing over many generations would eventually invoke the changes dictated by the domestication syndrome. They are precisely the changes marking the conversion from robust to gracile *Homo sapiens* types. These mutations in a pleiotropic gene have effects on several traits simultaneously, and these tend to be mostly deleterious.

Once the etiology of the human gracilization in the final Pleistocene had been realistically elucidated, it became possible to rationally explain many other conundrums about the human condition as we know it. For example, the correlations of youth, neoteny, estrus and menopause become readily apparent in light of the domestication hypothesis; they are unfathomable in any other framework. The domestication theory also addresses the problem of having to explain how humans coped with the acute atrophy of the brain since the domestication syndrome triggered it. This particular conundrum is impossible to explain by any other model. So, because it contradicts every traditional explanation of hominin encephalization, which had become the exclusive mantra in paleoanthropology, it was ignored entirely (Bednarik 2014). Brain atrophy invalidates the most fundamental canon of human evolution: that the cultural, technological, cognitive and intellectual ascent of humans was underwritten by continuous enlargement of the brain. How, then, can this traditional interpretation account for the rapid reduction of brain volume since auto-domestication began—precisely during a time of unprecedented demands on the human brain? That reduction occurred at a rate 37 times greater than the previous long-term encephalization rate (Bednarik 2020). Most paleoanthropologists failed to consider this issue, and even less thought about explaining it. This example illustrates neatly the complete helplessness of the discipline in explaining anything realistically because brain size has fundamentally determined human sociology. It is the excessively large brain of the newborn that determined the social structures of hominin society because it rendered the frequently pregnant females dependent upon support. That dependency, in all probability, may well be responsible for the abolition of estrus. It never seemed to occur to the boffins of paleoanthropology that hominin societies paid an incredibly high price for brain enlargement: if there was no good reason for this abnormal organ enlargement—as

the final Pleistocene and Holocene brain atrophy seems to prove – how do they account for this 'blunder' of evolution? Or for the reduction of IQ with increased use of exograms? Conversely, considerations of relative body sizes are irrelevant here, because the issue is about absolute brain size vs birth canal size, not relative brain size.

The domestication hypothesis offers the most elegant solution for this enigma by recruiting yet another significant difference between us and other species. As the skilled use of exograms (Bednarik 2014) became an important natural selection factor, brain size was no longer crucial; interconnectedness with external memory devices was. In the same way, the hypothesis offers an explanation for the upright walk of hominins that renders the traditional version ('coming down from the trees') superfluous. More decisively, its solution of the Keller and Miller paradox (Keller and Miller 2006), which is impossible to solve in traditional frameworks, is so persuasive that it is almost certainly correct. In short, this one hypothesis is as effective in clarifying as many concerns in human origins as evolution is in biology. Ignoring it, as the relevant disciplines currently do, reflects upon their scientific credibility.

I am disappointed about the discipline's partisan reaction to my theory because, in science, the veracity of any hypothesis is tested by subjecting it to falsification attempts. A variety of approaches can readily test the auto-domestication theory, but this is not occurring. The most effective method would be by exploring how many genetic markers signaling the domestication syndrome are found in the genome of present-day humans. At the time of the theory's inception, these markers of domestication

had remained unknown. However, since then the science of genetics has made great strides in many respects, building on such earlier work as the Human Genome Project (1990–2003) that produced its 2.91-billion base pair consensus sequence of the euchromatic portion (making up 92.1% of the total) of the human genome (draft sequence Venter et al. (2001); cf. International Human Genome Sequencing Consortium (2004)). This was soon followed by the sequencing of the chimpanzee genome (Chimpanzee Sequencing and Analysis Consortium), and that of the genomes of the macaque (Gibbs et al. 2007), the orangutan (Locke et al. 2011), the gorilla (Scally et al. 2012) and the bonobo (Prüfer et al. 2012). More relevant here are the significant advances in establishing partial genomes for two robust forms of *Homo sapiens*, 'Neanderthals' (Prüfer et al. 2014; Green et al. 2010) and 'Denisovans' (Reich et al. 2010; Meyer et al. 2012). They permit limited comparisons with the present-day human genome.

Concerning the domestication syndrome (Hammer 1984; Brown et al. 2008; Wilkins et al. 2014), Darwin (1868) had already noticed that mammalian domestication yielded particular sets of behavioral and morphological traits. However, neither of Darwin's two potential explanations for this is accepted today: the traits are not caused by improved living conditions (as Leach (2003) and many others assumed), nor are they attributable to hybridization. It is well-established that feral domesticates preserve their traits for many generations (Bednarik 2011a), and domestication experiments with rats and foxes show that hybridization is not involved in the process (King and Donaldson 1929; Castle 1947; Belyaev 1969; Trut et al. 2009). Neural

crest cells (Wilkins et al. 2014) may influence embryological developments of tissues involved. The effects of the syndrome may derive from mild neural crest cell deficits (but see Sánchez-Villagra et al. 2016). One of the domestication genes shared by modern humans, dogs, and cattle, FAM172A, neighbors NR2FI on chromosome 5, which regulates neural crest specifier genes (Simões-Costa and Bronner 2015). A hypothesis alternative to the implication of neural crest cells, involving the thyroid gland instead, has also been proposed (Crockford 2000; 2002; 2009).

Testing the human auto-domestication hypothesis

The morphological traits defining the domestication syndrome in mammals are primarily general neoteny; reduction or abolition of estrus; reductions in general brain size or specific parts of the brain; changes to cranial and facial morphology (e.g., reduction in prognathism) and reduction of tooth sizes; alterations to the concentrations of neurotransmitters; and changes in adrenocorticotropic hormone levels.

In recent years, significant advances made in genomics have facilitated some preliminary understanding of the phenotypic traits underwriting mammalian domestication as a generic phenomenon (Morey 1994; O'Connor 1997; Zeder 2006; Zeder et al. 2006). Indeed, the term 'domestication' is being re-defined as it becomes better understood. Various species are now thought to have 'self-domesticated' rather than having been 'passive parties' in the process (Groves 1999; Marshall-Pescini et al., 2017). Such species have benefitted from the changes just

as has the human domesticator (Groves 1999; Budiansky 1992; Driscoll et al. 2009; Zeder 2012). Humans, of course, are only one of the hundreds of domesticators, and today it is better appreciated that many domesticator/domesticate relationships are symbiotic.

Selective sweeps in the genomes of modern humans and several domesticated species have recently identified dozens of genes overlapping among them (Prüfer et al. 2014; Prüfer et al. 2017; Racimo 2016; Peyrégne et al. 2017). The following domestication genes overlap in the domestic horse and human: AMBRA1, BRAF, CACNA1D, DLGAP1, NT-5DC2, NTM and STAB1. In cattle and humans, they are ERBB4, FAM172A, GRIK3, LRP1B, PLAC8L1, PVRL3, SNRPD1, TAS2R16 and ZNF521. The dog has yielded these 15 domestication genes shared with present humans: COA5, COL11A1, COQ10B, FAM172A, GGT7, GRIK3, HSPD1, HSPE1, LYST, MOB4, NCOA6, RFTN2, RNPC3, SF3B1 and SKA2. Finally, the cat shares with us BRAF, GRIA1, HSD3B7, ITGA9, MYLK3, NEK4, PLAC8L1, PPAP2A, PPAPDC1B, PRR11, RNPC3, SYTL1, TEX14, TP53BP1 and ZMYND10 (Theofanopoulou et al. 2017). These forty-one genes associated with loci under positive selection, both in present humans and in one or more of the four domesticates considered, do not prove that domestication in these five species necessarily proceeded analogously. The circumstances would have differed in the domestication of each species. However, these shared genes do suggest that humans were, in their relatively recent genetic history, subjected to changes that resemble those of domestication in other mammalian domesticates. Nevertheless, it must be cautioned, firstly, that few of the above

genes are shared across the five domesticates; and secondly, that numerous genes are under selection in various domesticates, but not in humans.

Just as important is the recent discovery that none of the 17,367 protein-coding genes identified in Neanderthals from Spain and Croatia (Prüfer et al. 2017; Castellano et al. 2014) are listed among the fifteen genes known to overlap between at least two domesticated species (ADAMTS13, ATXN7L1, BRAF, CLEC5A, DCC, FAM172A, GRIK3, NRG2, PLAC8L1, RNPC3, SEC24A, SMG6, STK10, TMEM132D and VEZT). While not providing finite proof, this circumstance does seem to confirm the 'pre-domestication' status of robust *Homo sapiens*. Other factors suggesting the same include the proposition that Neanderthals had a higher prenatal androgen exposure than present-day humans, based on the digit ratios D2:D4 (Nelson et al. 2011). The reduction of androgen levels and rise in estrogen levels (Cieri et al. 2014) is often associated with lower reactivity of the hypothalamus-pituitary-adrenal system in domesticates (Trut et al., 2009). Similarly, Neanderthals appear to have been free of such mental illnesses as schizophrenia: the NRG3 gene, associated with it, seems to be absent in them. Schizophrenia may well be a very recent condition that may have appeared only a few centuries ago (Jeste et al. 1985; Hare 1988; Bednarik and Helvenston 2012). Selective sweeps in regions associated in genome scans with psychosis, such as 1q21 (Voight et al., 2006), tend to yield relatively recent etiologies, of less than 20 ka, as predicted by the domestication hypothesis. Much the same applies to many other deleterious alleles in 'modern' humans, such as RUNX2 and CBRA1 (causing cleidocra-

nial dysplasia or delayed closure of cranial sutures, malformed clavicles and dental abnormalities), THADA (associated with type 2 diabetes), the microcephalin D allele (perhaps 14 ka old; (Evans et al., 2005)) and another contributor to microcephaly, the ASPM allele (5.8 ka old; (Mekel-Bobrov et al. 2005)).

FOXP2 (forkhead box protein P2; CAGH44, SPCH1, TNRC10) is a gene of considerable importance, located on chromosome 7 (7q31). Initially recognized as the genetic factor of speech disorder (Lai et al. 2001; Nudel and Newbury 2012), it is a transcription factor encoding for a regulatory protein. Involved in the regulation of gene expression, it is popularly known as the 'language gene', but there are also other genes involved in language development. In humans, FOXP2 has undergone changes significant to their evolution, in the form of two amino substitutions (Enard et al. 2002). It has been speculated that FOXP2 and SRGAP2 are part of a set of genes that changed function during hominin evolution. An amino-acid substitution in FOXP2 in humans relative to apes is shared with Denisovans and Neanderthals (Krause et al. 2007), giving rise to speculations about the emergence of language abilities before the divergence of robusts and graciles. I am perfectly comfortable with the notion that hominins possessed language a million years ago: they occupied cold regions, they colonized many islands by crossing the sea, and they used exograms (Bednarik 2014). However, the purported divergence, supposedly 300 to 700 ka ago, could not have taken place, because there is no evidence of gracile humans before the Late Pleistocene gracilization.

Genetics has provided the subject of hominin evolution with a wealth of useful information undreamt of a few de-

cades ago, but it has also produced some falsities. The most consequential seem to derive from the replacement model's gospel; geneticists have massaged their findings to render them compatible with that hoax, without realizing that there is a more realistic way to account for the differences between gracile humans and their immediate robust ancestors. It also needs to be remembered that genetic work is highly susceptible to contamination by present-day human DNA in both laboratories and reagents (Wall and Kim 2007). Other constraints are that the severely limited DNA surviving in ancient remains has meant that only mtDNA could be retrieved by PCR (polymerase chain reaction, used to make many copies of a specific DNA segment) and that we lack any knowledge of the genomes of the early 'anatomically modern humans'. Moreover, "our ability to identify functional variants in the genome is still very poor" (Pääbo 2014: 220).

To appreciate the inadequate and fragmentary nature of our understanding, it helps to consider the considerable gaps in our knowledge. Geneticists believe in having detected genetic traces of unknown types of hominins that would seem to have left no known skeletal remains. For instance, Mondal et al. (2016; 2019) have presented evidence that the Onge and Jarawa tribes of the Andaman Islands carried 2–3% genes from an unknown hominin source. They detected around 15 megabase pairs of unknown gene sequences attributed to a robust human that has not yet been identified (i.e., other than Neanderthal and Denisovan). This ancestry is considered absent from Europeans and east Asians and is in addition to Neanderthal genes also present in the Andaman population, as it is more widely in Asia. The presence

of Neanderthal and Denisovan genes in 'modern' humans is well-known (Green et al. 2010; Mondal et al. 2019; Wolf and Akey 2018). In sharp contrast, however, Wall et al. (2019), in searching for evidence of archaic admixture from a panel of 1667 individuals, report no presence of archaic genes in the Andaman Islanders. Nor did they find any in modern people of Flores, which challenges the status of the putative *Homo floresiensis* and demonstrates the effects of selection against introgressed genetic material. Some regions of the genome are believed to be resistant to introgression from robusts (Sankararaman et al. 2014; Vernot and Akey 2014).

Conclusion

This exploration of the origins or etiology of what is widely considered to be the modernity of humans has led to several useful insights. The soundly refuted replacement hypothesis, postulating the development of this modernity in one part of Africa and attributing the replacement of all other human groups to a 'superior' new species, has itself been replaced by the auto-domestication hypothesis. The superseded notion is based on a purported speciation event in Sub-Saharan Africa, but it has recently transpired that the robust humans supposedly replaced by the African über-humans were the same species, being just as inter-fertile with them as with each other. The five conditions that would have to be met to render the replacement or African Eve hypothesis viable, which I postulated in 2011, remain entirely without response.

Not only was that hypothesis bereft of any archaeological, paleoanthropological or genetic evidence in its favor; it was based on an academic hoax (Bednar-

ik 2008a), and its most significant deficit has always been that it failed to explain anything. Why should there have been a quantum jump in intelligence or cultural complexity? How did these Africans overpower the resident hominins of Eurasia? Why would it be that they arrived in Australia with a Middle Paleolithic toolkit after exporting the Upper Paleolithic from Africa? Of the hundreds of questions raised by the replacement scenario, not one has been answered credibly. Most of these were never even considered by the African Eve advocates: how to account for the neoteny of present-day humans or their brain atrophy, their genetic susceptibility to several thousand genetic impairments, or every other aspect of being 'modern'? A scientific theory is supposed to offer some kind of explanatory power, besides being meant to present evidence in its favor.

The alternative explanation of how humans became 'modern', the domestication hypothesis, is not only evidence-based, but it also offers a wealth of clarifications about the condition of human modernity, with all of its contradictions, flaws, and paradoxes. For instance, it explains the paradox of why natural selection failed to eliminate deleterious alleles, for which a logical rationalization had been lacking completely until 2008. It accounts fully for the reversal of encephalization and dozens of other developments accompanying this process of modernization in humans. Moreover, it is easily testable.

At the time of its proposal well over a decade ago, the genetic data needed to test the hypothesis was unavailable, but in the intervening years, there have been unprecedented developments in the studies of genomes of both human and other animals. The domestication syndrome, which largely explains the etiology of human modernity, has provided the first genetic explanations only recently. They confirm what has already been evident from archaeology and paleoanthropology: that the self-domestication hypothesis is correct, at least in its essentials. However, one more aspect that has never been contemplated, including by me, is the following consideration. The domestication syndrome is initiated by consistent selection of one specific characteristic, setting in train the modification of other, unrelated characteristics. However, in a more obscure way, the process of natural selection, also consistently selecting particular traits, should logically be assumed to lead to a similar effect. If that is the case then future scrutiny needs to review the distinction between Darwin and Mendel, or between natural selection and selective breeding. Rather than being two opposing potencies, they would more likely be the opposite ends of a continuum. That would mean that, realistically, both natural selection and selective breeding play a role in most genetic changes in a species. The sharp division is imaginary, and such changes simply lean more to one or the other direction. I would like to call this concept the *genetic fitness model*, in which both evolution and domestication contribute in some measure to genetic fitness. This demands a significant re-assessment of evolutionary theory to allow a more complicated interplay of the two purportedly antithetical processes of evolution and domestication. Instead of attributing genetic changes to one or the other, they would be the outcome of tensions deriving from both domestication syndrome and natural selection effects.

Thus, many details still need to be investigated, but the fundamentals of the

change from robust to gracile *Homo sapiens* were not those of a speciation event. The change was attributable mainly to the domestication syndrome, initiated by cultural or social practices hominin society introduced in the last part of the Late Pleistocene. That much can be regarded as certain, and to those who have buried their heads in the sand by ignoring the domestication hypothesis since 2008 I quote Boucher de Perthes: "They employed against me a weapon more potent than objections, than criticism, than satire or even persecution—the weapon of disdain. They did not discuss my facts; they did not even take the trouble to deny them. They disregarded them".

Conflict of interest

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