

Genetics of domestication by *Homo sapiens* and of *Homo sapiens*

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Abstract

Biological human evolution has an irreducible cultural dimension. It is through adaptations that humans dealt with their own evolutionary genetic challenges for achieving and sustaining biological fitness. One salient strategy was sexual selection in human groups. This was further on strengthened through the domestication of other species, a process that led to the establishment of a close behavioral bond between the domesticated and the domesticator. As a corollary to this bonding process, bilateral behavioral and genetic adaptations ensued that today makes independent life for both domesticator and the domesticated nigh impossible. After plants, animals, and other organisms humans attempted to domesticate each other through enslavement; a failed experiment with devastating consequences that still resonate today, particularly in slaveholding societies like the United States. Lastly, the process of establishing organized and stratified societies during the Holocene became also a process of human “self-domestication”, and the product of that process is the modern “civilized” human with a genetic and cultural makeup strikingly different from the one held in the Pleistocene environment of evolutionary adaptation.

Key words: Human evolution, domestication, genetics, adaptation, slavery, self-domestication

Resumen

La evolución biológica humana tiene una dimensión cultural irreducible. Fue mediante la adaptación que los humanos lidiaron con los retos genético-evolutivos para lograr alcanzar y retener adecuación biológica. Selección sexual constituyó el mecanismo inicial que permitió alcanzar y mantener dicha adecuación. En segundo lugar, y con posterioridad, la estrategia para su alcance fue la domesticación de otras especies, un proceso que creó un intrincado entramado conductual y biológico entre el domesticador y el domesticado. Como corolario a este enlace emergieron adaptaciones genéticas de parte del domesticador como del domesticado que hacen la vida independiente de las partes virtualmente imposible. Luego de la domesticación de plantas, animales y otros organismos surgió un esfuerzo de domesticación del ser humano por sus congéneres mediante la esclavitud. Fue este un experimento fallido cuyas consecuencias repercuten en la historia de las sociedades esclavistas, particularmente la de los Estados Unidos. Finalmente el proceso que dio paso al desarrollo durante el

Holoceno de sociedades estratificadas sirvió de mecanismo de auto-domesticación, proceso este que dio paso al llamado “humano civilizado” poseedor de una acervo genético y cultural que le aparta marcadamente del poseído en el ambiente de adaptación evolutiva del Pleistoceno.

Palabras clave: evolución humana, domesticación, genéticas, adaptación, esclavitud, auto-domesticación

Fitness or power

The objective of this narrative is to analyze the genetic effects of processes operating in tandem and partly in parallel in the attainment by humans of the maximum possible level of biological fitness: the processes of sexual selection, guided by biology and later by culture, followed by the development of domestication, since the days of the use of the domestication of fire to the present. Genetics began in an as yet undetermined manner about 3.5 to 3.8 billion years ago, a period as yet unfathomable save to theoretical speculation grounded on the laws of physics and chemistry. Gradually, as the message of the genes was being written the rules of syntax of its language were also evolving. Eventually, after a lengthy incubation through a unicellular and perhaps viral phase complex organisms arose with all sharing the same fundamental message as well as its syntactic rules. The message, perhaps first encoded in ribonucleic acid (RNA) eventually gelled into the more stable form of deoxyribonucleic acid (DNA) (Walker & Davies, 2013). Although DNA contains most of the instructions for the assembly, development and evolution of organized living structures it is helpless without a decoding apparatus and its translation into material products or regulatory sequences; an apparatus that permits life and its evolution while at the same time shapes and produces the very letters with which the message is written. Through this creative tautology the interacting constituents of the cell, the fundamental and minimal unit of life, moved along a path leading to increasing complexity. Eventually our genus, Homo, can be recognized emerging about 2.3 to 2.4 million years ago (mya). The species sapiens is discernible half a million years into the past, and our modern version of that species emerges in Africa approximately 200,000 years ago (Hall & Hallgrímsson, 2008). Our genus in its various anatomical guises explored the planet, except for the Americas, more than once. It was H. sapiens who drifted into a new world upon crossing Beringia (Stanford & Bradley, 2012). For all that time until just 12,000 years before present we lived as hunter-gatherers in communal bands bereft of dominance or specializations other than those nature dictated for a sexually differentiated (dimorphic) species.

Coeval with the development of the genus is the emergence of the first domesticate: fire, an ideal form of undifferentiated energy. A notable trait of fire is that its use is exclusively human (Gouldsblom, 1989). At the same time, the domestication of fire brought about profound genetic adjustments in *Homo sapiens* whereas, in contrast to the domesticates to come, the properties inherent to fire are not modified by humans. Early indications of possible fire-use are documented in Africa from about 1.5 mya, during the Lower Pleistocene (Beaumont & Vogel, 2006). The presence of clusters of ancient hearths evidences the controlled use of fire by *Homo erectus* ca. 1.5–1.0 mya (James, S. R., 1989). During the Early-Middle Pleistocene (0.79 mya), when *Homo erectus* had already crossed through the Near East into Eurasia, evidence of Out-of-Africa controlled use of fire was uncovered at the Acheulian site of Gesher Benot Ya'akov, Israel (Goren-Inbar, Alperson, Kislev, Simchoni, Melamed, Ben-Nun, & Werker, E. (2004)). The knowledge of fire making enabled them to set fire at will and in different ecological settings thus effecting by this means niche modification. Aside from niche modification a signal use of fire was for cooking. The act of cooking simplified the chewing and digestion of food leading to a reduction in the size of teeth and supporting masticatory structures (Emes, Aybar & Yalcin, 2011), a reduction of gut length and an expansion of food sources (Burton, Fire & Us, 2010). It possibly enabled advanced encephalization and socialization (Aiello & Wheeler, 1995). It also lead to the first known diet-related pathology: the use of fire for cooking starchy tubers led to the emergence of caries prior to the development of established agriculture (Humphrey, De Groote, Morales, Barton, Colcutt, Ramsey, & Bouzouggar, 2014). The anatomical and functional modifications accumulated had to have a genetic underpinning, thus the use of fire reverberated widely along our genome.

A marked encephalization opened the door to increasing brain complexity which made cultural evolution possible (Sakai, Matsui, Mikami, Malkova, Hamada, Tomonaga, ... & Matsuzawa 2013). The changes that would lead to the eventual sedentarization of humans in large enclaves took its first steps during the Mesolithic (ca. 22,000 to 11,500 before present –BP–) when the number of humans increased to a point that impelled a wave of new hunting and foraging technology. How predator-prey systems evolve is a function of population density. The concept of prey applies equally to plants as to animals as predation includes all interactions in which one organism consumes all or part of another. In this context humans are primarily omnivorous predators although they can also be prey for others either through pathogenicity or

carnivory. Archeology reveals that, after the Last Glacial Maximum (25,000–15,000 BP), as the density of humans increased in relation to the abundance of habitual foodstuffs an expansion of their diet to include plants and small animals hitherto disregarded occurred (Richards, Pettitt, Stiner, & Trinkaus, 2001). To extract nutrients from large recalcitrant nuts and seeds requires adequate technology to minimize the effort expended for otherwise to harvest them would entail a net caloric loss; a similar accounting applies to small game as an effort in capture may exceed the caloric value of the prey. However, archeological evidence points in the direction of a Mesolithic demographic expansion accompanied by a dietetic enlargement to include new, smaller or difficult to acquire resources (Stiner, Munro, Surovell, Tchernov & Bar-Yosef, 1999). This pre-agricultural mode of hunting and gathering has been termed the “Broad Spectrum Revolution.” It is the period that just precedes the emergence of the Neolithic in western Asia and is characterized by a broadening of the subsistence base of Late Pleistocene hunter-gatherers in the Near East (Stutz, Munro & Bar-Oz, 2009). During this period, it appears that the increasing population numbers led to a phase-change in which the nuclear and extended family assembled into more complex groupings that have been termed clans. This social arrangement now opened new avenues for exogamy and since acceptance into the clan is social, not filial, ceremonial methods arose to signal the transfer of a person from one clan to another. As the social aggregates became larger –clan, tribe, etc.– controlled mating with emphasis on out-of-group pairing broadened the genetic exogamic landscape (Flannery, 2012).

Throughout this period social phase-changes linked to demographic expansions saw the emergence of larger and more complex groupings of foragers (Baum, 2004). This period of social restructuring due to demographic pressures preceded and helped pave the way for plant and animal domestication and the emergence of agriculture. When humans realized that certain plants and animals could be made to reproduce and provide nourishment in a controlled manner they performed the first major human-directed genetic feat: selection for the domestication syndrome (Gepts, & Papa, 2003). Initially, this process was rustic, as one would expect given the absence of a theoretical underpinning. When humans began to practice plant and animal domestication through agriculture by artificial selection of useful varieties they created a completely new niche; a novel way of life that transformed every facet of human existence (Durham, 1991). Humanity had crossed into the Holocene. In the process of domestication *Homo sapiens* too became not only domesticated but underwent identifiable

genetic modifications. It went from the forager mode of life to the farmer and pastoralist one with its attendant sedentism or transhumance with the actions to be executed being dictated by the needs of the crops or flocks (Vigne, 2011). As a result of an agricultural-surplus driven demographic explosion and waves of niche construction different modes of living emerged as well as new modalities of social interaction for coexistence and reproduction: the 'Neolithic revolution'(Childe, 1949).

For all but the last few decades knowledge of the fundamentals of heredity was phenomenological and artisanal. One aspect of it –the search for a mate with which to reproduce– has a genetic basis of its own: the propagation of selfish genes (Dawkins, 2006). This is the root of the first great genetic experiment of Homo sapiens: how to secure the best possible mate so that reproduction would yield the fittest possible progeny. Natural and sexual selection guided the process as the participants were unaware of anything other than the drive to reproduce. One of the cardinal issues that had been resolved by evolution eons before the advent of humans was not the fact that mating is mandated genetically, for the survival of any species is predicated upon it, but that homozygosis should be avoided. The ultimate objective is to achieve maximum evolutionary fitness, an accomplishment predicated upon the survival of offspring that go on to reproduce. A corollary to this concept is that of inclusive fitness. (Lehmann, & Rousset, 2014). This concept states that altruism among organisms who share genes heightens the possibility of shared genes being passed on to subsequent generations. In this way, an altruistic act that supports the survival of a relative theoretically enhances the genetic fitness of both the recipient of the act as well as that of the altruist. In other words, a mother's inclusive fitness arises through the combined contributions of her current infant, other offspring, and matrilineal relatives (Haig, 2014). In humans, the biology of the offspring requires enormous investments, prior to birth and postnatally, to maximize evolutionary fitness. The parents share the cost of achieving evolutionary fitness, but the highest burden falls upon the female. Males would assist by providing and protecting the female during gestation and during the infant's childhood. The breeding system underpinning reproductive success, whether monogamy, polyandry (whereby a woman acquires two or more husbands simultaneously), polygyny (one male with several females) or promiscuity, determined the degree of certainty a male could have concerning the paternity of the child being reared. One of the putative reasons monogamy emerged among higher primates is because it gave the male the closest to

reasonable certainty that the effort expended on an offspring was done on behalf of its own genes (Opie, Atkinson, Dunbar, & Shultz, 2013).

The search for human evolutionary fitness via sexual selection.

The quest for maximum fitness requires a balance be achieved between disassortative mating, i.e., the coupling of individuals for reproductive purposes that possess traits more divergent than would otherwise be the case had the mating been random (Sandro Carvalho Santos, Augusto Schinemann, Gabardo, & da Graça Bicalho, 2005) and assortative mating, i.e., the mating of individuals sharing more traits than expected had the mating been random (Thiessen, & Gregg, 1980). There is evidence in humans that some aspects of mate selection are under genetic constraints such as mating between individuals with disparate Major Histocompatibility Complex (MHC) antigens so as to maximize the progeny's protection against pathogens (Chaix, Cao, & Donnelly, 2008). Indeed, the MHC, the major regulator of immune responses to exogenous pathogens, contains the maximal genetic heterogeneity of all gene complexes in humans (Beck, & Trowsdale, 2000). There is an evolutionary vector leading to avoidance of homozygosity to escape the resultant inbreeding depression, caused by the accumulation of deleterious genes, through curtailing mating between genetically similar individuals such as the members of nuclear families. On the other hand, there is a contrary, selective force that operates to increase genetic homology between mates as well as between parents and progeny because this fluidizes communication and altruism thus enhancing inclusive fitness without additional energy and resource expenditure in reproduction. Outbreeding has an implicit deleterious genetic effect in that it brings about the break-up of coadapted gene complexes or favorable intergenic (epistatic) relations (Lynch, 1991) and enhances the incidence of maternal-fetal incompatibilities: outbreeding depression (Raghupathy, 1997). The result of these opposing evolutionary vectors is that individuals gravitate toward those with proximate to, but not with, identical phenotypic (and genetic) traits. By this mechanism individuals can maximize genetic homogamy without incurring in deleterious inbreeding (Berezkei, Gyuris, Koves, & Bernath, 2002).

Other than selecting mates for reproduction humans prior to the Holocene did not engage in much genetic reconnoitering. Late Pleistocene population densities were too low to enable sufficient choice in mate selection (Frost, 2006) and worked against enhancing cultural

complexity (Barnosky, Koch, Feranec, Wing, & Shabel, 2004). Nevertheless the demands of natural selection can only be met through genetic variability, so population admixing was biologically required and along with the process of social interaction for reproduction came the development of rituals and ceremonials for selection and bonding. It is noteworthy that recent DNA sequencing of Neanderthal, as well as Denisovan genetic material, revealed that the genetic diversity in these archaic hominins was extremely low. This paucity of diversity is indicative of a striking level of inbreeding thus pointing to their low population densities over the vast Eurasian ecological landscape. (Meyer, Kircher, Gansauge, Li, Racimo, Mallick,... & Pääbo, 2012); (Prüfer, Racimo, Patterson, Jay, Sankararaman, Sawyer, ... & Pääbo, 2014).

Mating is required for continuity of the species; marriage is not, for the latter addresses primarily economic, social, and kinship networking. Marriage potentiates reproductive prowess but is not a sine-qua-non requirement for evolutionary fitness: mating is. Like many other organisms, humans evolved a series of biological and cultural adaptations aimed at inbreeding avoidance because of the adverse costs to fitness of inbreeding depression. As discussed below (vide infra) this includes forms of socially prescribed norms grounded on selection being dictated or influenced by parents or elders. Nevertheless, intra-family coupling and reproduction is not proscribed, as some form of such close kin breeding remained in the background (Khlát, 1986). The persistence of this low-level trait can contribute to overall biological fitness through the mechanism of inclusive fitness (Zaoui, & Biémont, 2002). Some human groups unwittingly reduce their gene pool in order to retain power, as power flows through kinship paths. *This reduction opens the door for artificial selection through cultural evolution (Darwin, 1883)*. The nature of this reproductive strategy is exemplified by a variety of monarchical regimes where endogamy projecting into incest is sanctioned: *Royal Incest*. This mating strategy is the product of the collision between our reproductive imperative, which is guided by the need to maximize offspring fitness, and our cultural evolution. It became incumbent upon genes to accommodate culture. This created a dichotomy between biological fitness and cultural fitness. Biological fitness is defined by the number of fruitful progeny; cultural fitness is here defined as the acquisition and retention of power within the human social group.

Incest, and particularly the royal version, –Royal Incest– is a form of artificial selection that emerged as a mechanism for obtaining and retaining power. This mating scheme has left its

historical imprint, and geographically it spans the globe, as can be seen by the following examples. *This form of selection* has been documented among the *Ancient Egyptians* (Shaw, 1992) as well as among the *Incas of Peru* (Bixler, 1982). A trait of Polynesian societies was the preference for intra-status marriages (Valentine, 1963). In the case of Hawaii's ruling elites this trait encompassed sibling marriage (Carando, 2002). Analogous to the Hawaiians, both the Thai, as well as the Laotian ruling classes, practiced Royal Incest until early in the 20th century when it became taboo (Evans, 2010). The practice of *mia noi* (second wife) mitigated the genetic shortcomings accrued via sibling endogamy (Bao, 2008). Among African kingdoms several institutionalized endogamous brother-sister marriage, but reserved it for royalty or other high status groups. Salient among these are the ruling elites of *three of the four traditional kingdoms of Uganda*, viz., *Ankole* (Berghe, & Mesher, 1980), *Buganda and Bunyoro* (Lumsden, & Wilson, 1980). Royal Incest was also practiced among the *monarchical families of the Monomotapa (Mutapa) kingdom*, located between the Zambezi and Limpopo rivers straddling Mozambique and Zimbabwe (Chaplin, 1957). Another kingdom where incestuous pairing was a prerogative of the ruling castes was Shilluk, a Nilotic kingdom in Southern Sudan (although, in their case, it has been labeled "symbolic incest") (Howell, 1952). The kingdom or land of the Zande, located along the Kotto River, a tributary of the Ubangi, and extending to the foothills of the Bahr-al-Ghazal watershed and the Uele River (Larken, 1923), and *Dahomey in Western Africa* is another Sudanese Nilotic kingdom known for the practice of Royal Incest. Endogamy was noted among the European Hapsburgs (Ceballos, & Álvarez, 2013) and there is the case of Queen Victoria transmitting hemophilia to members of the European royal families, a disease that percolated through the royal families of Germany, Russia and Spain because of royal endogamy. Endogamy certainly contributes to maintaining a monopoly on power in certain societies but at a significant biological cost (Ager, 2006). Loss of biological fitness is a bane that accrues the pursuit of the monopoly of power via mating strategies.

Incest carries with it the risk of homozygosity that underpins inbreeding depression. Inbreeding depression stands out as one of the dominant selective forces steering the evolution of mating systems, favoring breeding among dissimilar individuals through dispersion and kin recognition. Early pastoral animal breeders, as well as agriculturalists, observed inbreeding depression; information that antedated by millennia any knowledge of genetics. However, unlike royal families that formed close communities of consanguinity by choice, there are pockets of

humanity in which population numbers are low, either by geography or ideology, and exogamy is impossible or actively discouraged as happens when religion is the stricture to marriage across cultural boundaries (Heaton, 1990). When endogamy is caused by small populations and, therefore, small gene pools, the operations of natural selection will extinguish such small groups. There is little, if any, available data for assessing how often this has happened in the past, but inbreeding depression reduces the biological fitness of the individuals and hence their capacity to leave fruitful progeny (Hedrick, 1994). This genetic outcome leads, among other things, to a dearth of births and an excess of hereditary anomalies (Frankham, 1995). Such can be observed among certain extant groups where as a result of reduced gene pools inbreeding depression has been documented. Among these populations are found the American Hutterites, an Anabaptist sect (Ober, Hyslop, & Hauck, 1999); pre-industrial Canadian populations (Robert, Toupance, Tremblay, & Heyer, 2008); migrant Brazilians of northwestern rural origin (Barbosa, & Krieger, 1979); endogamous Muslim groups from Delhi and Lucknow in India (Basu, 1975); the Telaga from Kharagpur, West Bengal (Kanti, 2005); Tamil Nadu of South India (Rao, & Inbaraj, 1977); also in Lahore, India, (Shami, & Zahida, 1982) and among Punjabi Sheikhpurans. Similar observations have been made among the Fukuoka of Japan (Yamaguchi, Yanase, Nagano, & Nakamoto, 1970), and Fadetchi, Kenuzi and other Arabs living in the valley of Kom Ombo, north of Aswan (Badr, 1972) where small mating groups have forced close kin pairing and also among the small (between 500 and 700 inhabitants) and isolated villages of Caverigno and Bignascoino located in the southern part of the Swiss Alps (Postma, Martini, & Martini, 2010). Nevertheless, despite the evident emergence of inbreeding depression among humans, in North and South Saharan Africa, the Middle East, Turkey, Central and South Asia consanguineous marriages are observed in between 20% and 50% of all unions, with a prevalence of first cousin unions (Bittles, 2010), especially patrilineal parallel-cousin marriages (Sueyoshi, & Ohtsuka, 2003). It is evident that operant in these populations, in addition to their small population numbers, is also an element of a cultural mandate – inevitable due to the pervasiveness and potency of culture as a factor- because for causes such as religious beliefs or ethnicity the pool of partners is limited. To mitigate this trend, which is a product of cultural evolution, humans have evolved a fairly sizable number of mating strategies that favor evolutionarily more efficient reproduction. Polygyny is quite prevalent and legal in most of the African continent north of the Equator, and southern Asia except the Indian

subcontinent but including the Philippines and Indonesian archipelagos. From 30 to 50% of males practice it (Goody, 1976). It is practiced clandestinely in other geographic regions. Exogamous polygyny serves the function of mitigating the inbreeding depression that would otherwise be expected were endogamous pairings the most prevalent (Thornhill, 1991).

One can safely state that ancestrally human reproduction was subject exclusively to natural and sexual selection with little on the way of cultural influence. Such is supported by the fact that *H. sapiens* even interbred with sister species such as *Homo sapiens neanderthalensis* (Wall, Yang, Jay, Kim, Durand, Stevison, ... & Slatkin 2013) and the Denisovan people (Pennisi, 2013). The genetic imprint of these hybridizations is still detectable by genome sequencing (Whiten, 2011). Possibly since the emergence of archaic *Homo sapiens*, by which time encephalization would have reached near-present values, the increasing brain size and the attendant complex circuitry would have supported an emerging culture relevant to mating. Indeed, even among modern bonobos -formerly called the pygmy chimpanzee- (*Pan paniscus*) there is clear evidence of discrete cultures that impinge upon differential behavior though not necessarily on reproduction (Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, ... & Boesch, 1999). But in the case of *Homo sapiens* there is evidence supporting the concept that, among early modern humans, there was some form of polygyny and retribution for bride services. Phylogenetic studies support the existence of a practice of arranged marriage to about the time of human migrations out of Africa (Walker, Hill, Flinn, Ellsworth, 2011). It is noted that, among contemporary hunter-gatherers, a pattern of paternally arranged marriage is the chief mode of marriage in 85% of groups whereas polygyny is observed in less than 20% (Apostolou, 2007). If some bride price and bride service payment were indeed in evidence that far back in human history then this inevitably brings to the fore a parental role in mating decisions (Apostolou, 2013). Of course, there are always exceptions, and among the Hazda of Tanzania marriage ceremonies are non-existent, marriage is not arranged, divorce is easy; however, the levirate (where the brother of a deceased man is obliged to marry his brother's widow) is the norm (Marlowe, 1999).

Band societies have inhabited and continue to live in widely varying ecosystems ranging from equatorial rainforest, habitat of the Mbuti Pygmies net hunters (Hart, 1978), to boreal landscapes inhabited by Skolt Saami *sii'das* of northern Fennoscandinavia (Olsen, 1987).

Extant groups are known for the variety of social rules and mores, the richness of pair breeding strategies as well as the myths they hold dear. At the most basic males may choose to enhance their own individual fitness even at the cost of evolutionary fitness. For example, they may choose to enhance mating fitness by having multiple partners but at the expense of reduced certainty concerning the paternity the offspring. Conversely, they may opt for maximized investment on high value offspring to enhance evolutionary fitness via enhanced certainty of paternity (Hewlett, 1992). Within the scope of these general alternatives the reproductive norms followed are quite varied. Doubtless, keeping the incest taboo is the norm in most social contexts with the exception of those that culturally choose to ignore it, or because they have little choice due to population imperatives, as discussed above (Wolf, Durham, 2004). Numerous theories have been posited to explain the evident reluctance, even among members of small groups, to breed with close kin. These vary from the strictly biological or evolutionary (Miller 1994) to socioeconomic ones where the role of raw unconscious evolutionary biology is minimized. Among humans, as among all sexual species, natural selection interweaves with sexual selection within an evolutionary phase-space to obtain the best possible mix of in- and out-breeding to maximize fitness (Buss, 1989). One invariant fact remains: the well-nigh universal interdiction of incest in nearly all extant societies.

Humans recognize their close relatives (kin recognition), either to prevent incestuous mating or to recognize the most suitable beneficiaries of nepotistic behavior (kin discrimination) (Pusey, 2005). Some mammals such as lemurs (*Lemur catta*) (Charpentier, Crawford, Boulet, & Drea, 2010) and mandrills (*Mandrillus sphinx*, Cercopithecinae) (Setchell, Vaglio, Abbott, Moggi-Cecchi, Boscaro, Pieraccini, & Knapp, 2011) have even evolved olfactory signaling to aid in the process. The genus *Pan* and the genus *Homo* diverged ca. 6 million years ago. Today just as humans evidence inbreeding avoidance, so do common chimpanzees (*P. troglodytes*) (Pusey, 1980) as well as bonobo (*P. paniscus*), the latter despite their well-known opportunistic and promiscuous mating (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999). Similar observations have been made concerning humans in close-knit environments such as the kibbutzniks of Israel (Shapher, 1971). As detailed above, very close-knit groups do make accommodations for incestuous pairing, but at the cost of sacrificing fitness due to inbreeding. The proximate mechanism of human inbreeding avoidance seems to predate the predominance of cultural over biological evolution, and to involve the interaction of genetic predispositions subject to

positive selection and environmental circumstances, particularly those dictated by the carrying capacity of the environment (Glassow, 1978). Environmental situations characterized by sparse resources would have led to dispersal thus bringing about low population densities and a concomitant paucity of opportunities for exogamy as happened to Denisovans and Neanderthals. Eventually, humans would develop a method for the sustainment of larger populations for effective outbreeding: agriculture. But agriculture, the domestication of plants and animals for the benefit of humans, often requires that traits that made them successful in the wild, like ease of seed dispersal, be genetically expunged. During the process agriculturalists became aware that domestication exacted a price from domesticates: loss of fitness and vigor through inbreeding depression (Charlesworth, & Willis, 2009). They also learned to palliate for it via selective hybridization (heterosis) (Schnable, & Springer, 2013). But what was lost in the quest for more productive domesticates humans would have to substitute for because human became domesticates of the domesticated.

The domestication of plants

Thus, *Homo sapiens*' genetic assessments extended beyond itself to encompass other organisms. That was perhaps the most transcendental step the species took as its history was irretrievably changed: the food surpluses generated by plant cultivation lead to increase population size, augmented social complexity and thus further cultural evolution became a new and pervasive selective force in addition to –and sometimes overcoming– natural and sexual selective forces. Nevertheless natural and sexual selection are presently active and exerting their influence in 100 and perhaps more human genes (Courtiol, Pettay, Jokela, Rotkirch, & Lummaa, 2012). Following the involvement of humans in their own genetic history via cultural manipulation of mating strategies came the genetic manipulation of other species. It began with the cultivation and domestication of plants, saliently cereals. Agriculture not only arose in the old world, marking the beginning of the Holocene, but it also emerged independently in the Americas. Humans came out of Africa approximately 70,000 years ago (95,000 to 62,000) via serial expansions for niche exploitation and exploration. This led to a cascade of bottleneck-driven founder effects. This process is demonstrated by extant human genetic and linguistic evidence. The geographic point of emergence was at the junction Africa with the Eurasian mass: the Middle East. The rate of travel for the spreading waves of humans was of approximately of 5 Km per year. During that migration some groups remained hunting and

foraging in Africa and the Middle East region and other groups continued on. The earliest group traversed skirting the southern Asian coast to Australia ca. 65,000 (62-75kya) years ago, and the dispersal from which modern Asians emerged occurred 25,000 to 38,000 years ago. (Rasmussen, Guo, Wang, Lohmueller, Rasmussen, Albrechtsen,... & Krogh, 2011). Travel was not linear and several recursions occurred leading to varying levels of genetic admixture effacing any semblance of local discontinuities and by extension any suggestion of “races” (Serre, & Pääbo, 2004). By 17,000 years ago humans were crossing Beringia and entering North America. There have been several proposed migratory scenarios to explain the peopling of the Americas. The most recent data suggests that an early differentiation from Asian populations ended with a modest genetic bottleneck that occurred in Beringia during the last glacial maximum (Fagundes NJ, Kanitz R, Eckert R, Valls AC, Bogø MR, et al. 2008). This stopover was followed by a notable population expansion concomitant with speedy settlement along the North American Pacific coastal route, a process dated to about 18 to 15 kya. This dispersion was nearly coeval with the emergence and dissemination of the Clovis culture. Recent genetic studies support the existence of a second migratory path geographically delimited by the Laurentide and Cordilleran ice sheets. (Kashani, B. H., Perego, U. A., Olivieri, A., Angerhofer, N., Gandini, F., Carossa, V., ... & Torroni, A. 2012). This migration, near parallel in time to the migration along the Pacific coast, probably occurred between 17 to 15 kya. (Coutinho, A., Valverde, G., Fehren-Schmitz, L., Cooper, A., Romero, M. I. B., Espinoza, I. F., ... & Haak, W. (2014). Archeological evidence points to the peopling of South America occurring no later than 15 to 14 kya, judging by the archeological findings in Monte Verde in Chile dated to ca.15 kya. (Dillehay TD, Ramírez C, Pino M, Collins MB, Rossen J, et al. (2008). Mesoamerica appears to have received the first migratory waves that continued on towards South America. This Mesoamerican stopover was followed by a swift southward expansion via the Pacific coast and into the Andean region. (Battaglia, V., Grugni, V., Perego, U. A., Angerhofer, N., Gomez-Palmieri, J. E., Woodward, S. R., ... & Semino, O. (2013). They continued south and it is estimated that divergence between central and south Amerindian populations occurred between 13,000 and 19,000 years before present. The post-Pleistocene global temperature increase following the ice age provoked marked ecologic changes that led to the expansion of heat-loving (thermophilous) plants (Walther, Post, Convey, Menzel, Parmesan, Beebee,... & Bairlein, 2002). Their evolution made them amenable to foraging and

then to cultivation, a trait which in turn promoted the change from a world of hunter–gatherer societies to more complex foraging bands followed by complex plant-cultivating societies and eventually stratified full-fledged sedentarized agriculturalists and transhumant pastoralists (Staubwasser, & Weiss, 2006). Plant domestication revolutionized human cultural evolution, paved the way for animal evolution –with new animal domesticate species arising from feral precursors– and is primarily responsible for the advances that have occurred in our civilization. This effort had its beginnings about 12,000 years ago and dates the beginning of the Holocene. As the precursors of modern humans went about their breeding and evolving in Africa, plants located in the region of the Zagros Mountains of the Fertile Crescent were engaged in their own genetic interactions (Assadi, & Runemark, 1995). Geography and climate would bring the two together and for the first time humans would extend their instinctive and artisanal genetic explorations to those involving plant and animal species. This is the next chapter in the history of genetics. Operating through artificial selection the hunter-gatherers would become the seeder, grower, harvester and often pollinator of plants that would feed humans as well as animals. However, in order for *H. sapiens* to avail itself of wild cereals and grains as a source of concentrated energy through facilitated growth and collection a price had to be paid: sedentism (Bar-Yosef, & Belfer-Cohen, 1989). These transformations occurred at varying time periods during the early Holocene, and at disparate sites on the planet, eventually providing the impetus for the development of the great ancient fluvial civilizations, including those of the Euphrates and Tigris, of the Nile and the Indus. Agriculture also emerged in the Americas in four different regions and a time not too distant from the emergence in the Fertile Crescent. The experience of Neolithic agriculture in the Levant and in Mesoamerica serves to illustrate the process of reciprocal domestication that now ensued.

Plant agriculture predated animal husbandry by about a thousand years. Of the vegetation native to the Zagros piedmont region hunter-gatherers selected eight wild plants which upon initial domestication constituted the founder crops (Riehl, Zeidi, & Conard, 2013). Of these three were cereals, namely, einkorn wheat (*Triticum monococcum*), emmer wheat (*Triticum turgidum* subsp. *Dicoccum*), and barley (*Hordeum vulgare*). Four pulses became amenable to cultivation: lentils (*Lens culinaris*), peas (*Pisum sativum*), chickpeas (*Cicer arietinum*), and the grain legume bitter vetch (*Vicia ervilia*). The remaining crops provided oil (*Olea europaea*) and fiber (*Linum usitatissimum*). These particular plants all happen to be annuals and require no assisted

pollination (Zohary, Hopf, & Weiss, 2012). I shall focus on the cereals.

Domestication of three cereals, all self-fertilizing —einkorn, emmer, and barley— marked the beginning of the process of cereal domestication in the Levant and Taurus regions. Wild emmer wheat was initially foraged for by transitional sedentarists in the southern Levant around the Pre-Pottery Neolithic A period (ca. 10,300-9,500 BP) (Asouti, & Fuller, 2012). Domesticated emmer appeared ca. 500 years later during the early Pre-Pottery Neolithic B period (9,500-9,000 BP) (Özkan, Willcox, Graner, Salamini, & Kilian, 2011). As the agriculturalist life style expanded south into the Levantine region the cultivated and the wild varieties grew in close proximity over the primordial Levantine agricultural sites. Domesticated emmer came in contact with the resident subpopulation of wild emmer. Gene exchanges between the two variants occurred as these plants have a propensity to undergo spontaneous hybridizations so following early cultivation there were subsequent hybridization and introgression of genes from the wild into the domesticated varieties (Peng, Sun, & Nevo, 2011). The einkorn and emmer wheat as well as spelt are now relic crops. Thus the various versions of the ancestors of today's types of wheat underwent a variety of genetic exchanges with contemporaneous other grasses native to the Zagros region. These precursor varieties arose as a result of hybridizations in the wild between two and three different species, respectively (Wendel, 2000). These exchanges and combinations led to the emergence, and selection for, by humans, of the varieties of plants known as emmer, durum and common wheat. The domesticated wheat, bearing twice the usual number of chromosomes (tetraploid), did not evolve as a single genotype but instead developed in a polymorphic manner. One of the results of these genomic exchanges was an increase in seed volume. There is a strong positive correlation between genome size and seed mass (Beaulieu, Moles, Leitch, Bennett, Dickie, & Knight, 2007). Increasing ploidy, a measure of the number of chromosomes, causes seeds to be larger, plumper, and causes the cells comprising the seed to increase in size, thus enhancing their nutritional and agricultural value (Smith, McFarlane, Croft, Trigg, & Kearney, 2003). Seed mass, a factor which varies over nearly 12 orders of magnitude, carries significant nutritional importance for the larger the seed the greater its estimation by early agriculturalists. A larger seed that does not disperse easily with the wind were traits of great value to early agriculturalists as they made harvesting (with crude scythes) and seed collection by threshing possible. Throughout cereal and maize agriculture, large seed mass has been selected for by growers (Meyer, DuVal, & Jensen, 2012).

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As agriculturalists expanded northward into the corridor stretching from Armenia to the southwestern coastal area of the Caspian Sea enlargement of domesticated emmer cultivation resulted in sympatry with Tausch's goatgrass (*Aegilops tauschii*), as in keeping with sympatric speciation, they inhabited the same geographic region. This relation lead to the emergence of hexaploid common wheat (*T. aestivum*) (Dvorak, Luo, Yang, & Zhang, 1998). All of these developments appear to have multiple originating sites across the Levant rather than one circumscribed site (Riehl et.al., 2013). The genetic changes that ensued were responsible for the loss of spike shattering, preventing the grains from scattering by wind and enabling

harvesting by threshing. The emergence of these traits differentiates domesticated plants from their wild ancestors and conform part of what we referred to above as the domestication syndrome (Jantasuriyarat, Vales, Watson, & Riera-Lizarazu, 2004).

The domestication of plants in the Americas took place near simultaneously at four distinct geographic regions: Eastern North America, Mesoamerica, the Andean region and tropical lowland South America in a period between 7,000 and 1,000 years before present. Thus the first efforts at agriculture in the Americas were near coeval with those in China. The most likely reason for this coincidence lies in climatology: agriculture follows on the heels of the Younger Dryas (Munro, 2003). The last glacial climates were not hospitable to agriculture because of the low CO₂ concentrations, generally dry atmosphere and variable to erratic weather regimes on short time scales. Agriculture was impossible under last-glacial conditions because the energy consumed in cultivation could not be paired with the energy derived from the foodstuffs harvested. Foraging was energetically the most efficient regime. With the end of the last glaciation came an abrupt change to a pattern more stable and hospitable and CO₂ levels rose from 180 to 270 ppm (Monnin, Indermühle, Dällenbach, Flückiger, Stauffer, Stocker, ... & Barnola, 2001). This change made agriculture possible and it began developing nearly synchronously from the Fertile Crescent to the Americas. The idea of plant cultivation eventually emerged independently across the planet. Of the numerous plants domesticated in the Americas *Zea mays* stands out as one of the earliest and most important with its cultivation being carried out about 8,700 years before present in the region of Mesoamerica. Cultivation proceeded from landraces from lowland West Mexico, with the Guilá Naquitz Cave in Oaxaca, Mexico being the putative maize center of origin. The teosintes, a group of primarily outcrossing species of wild grasses in the genus *Zea* and comprised by five species endemic to a region stretching from northern Mexico to Central America, are the original plants from which modern corn eventually arose through artificial selection. A noteworthy aspect of the development of domesticates in various regions of the planet, and of Mesoamerica in particular, is the fact that by the time of the end of the last glaciation they grew under a very different climatic regime. The present climate is quite different from the late Pleistocene-early Holocene one, particularly as it pertains to temperature and atmospheric CO₂ contents (Marchal, Stocker, Joos, Indermühle, Blunier, & Tschumi, 1999). Mesoamericans gathered and then cultivated maize's wild ancestor *Zea mays* ssp. *parviglumis*. This original domesticate differed markedly from the domesticated

version that arose from it due to the effect of environmental factors as, for example, the reduced CO₂ levels present at the end of the Pleistocene (Piperno, Holst, Winter, & McMillan, 2014). As a result of the notable genomic plasticity of the teosintes the numerous large and relatively undisturbed natural populations of teosinte species that still exist inhabit a wide span of environmental gradients. Genetic studies have definitively identified *Zea mays* ssp. *parviglumis*, known as Balsas teosinte, native to the Balsas River valley in Mexico's southwestern highlands as the teosinte genetically most proximate to domesticated maize. The conclusion that teosinte *parviglumis* is the definitive precursor of maize is subtended by microsatellite and allozyme genetic analysis (Matsuoka, Vigouroux, Goodman, Sanchez, Buckler, & Doebley, 2002). The trait selected for appears to have been a reduction in branching through coalescence of the *parviglumis* spikes, for maize has one dominant axis of growth, whereas teosinte is highly branched. This change most likely involved a few genes with large effects to account for the rapid domestication of the grass (Tian, Stevens, & Buckler, 2009). The domestication trail goes from *parviglumis*, with its 2 interleaved rows bearing 6 to 12 kernels, to landraces, to today's maize (*Z. mays* ssp. *mays*), a primary world food source, with a cob consisting 20 rows or more with numerous exposed kernels.

Agriculture brought with it the emergence of sedentarism, the construction of permanent lodgings and the creation of the support infrastructure needed for plant cultivation. Furthermore it led to larger groups living together and sharing genes as well as pathogens. Coexistence between animals and humans also led to exchange of pathogens. However, it also had a more direct genetic impact on man. Previous major dietary changes had a profound impact on the evolution of our ancestors (Klein, 2000). The shift from herbivory and frugivory to carnivory led to simplification of the gut as well as important modifications of the dental apparatus and its support structures (Diamond, 2002). Following raw meat carnivory the next major dietary event preceding agriculture was cooking which simplifies the chemical composition of foodstuffs making them more digestible (Wrangham, Jones, Laden, Pilbeam, & Conklin-Brittain, 1999). These two signposts in human evolution are accompanied by anatomical, metabolic as well as behavioral changes. So it is not surprising that the change to a diet derived primarily from domesticates would also bring about transformations that affect the nature and culture of humans. Starch is a macroconstituent present in many plant foods including the cultivated varieties of wheat and other plant domesticates. The digestion of wheat starch requires the

action of amylase, an enzyme present in saliva as well as the pancreatic exocrine secretions. Amylases perform the initial step in the digestion of dietary starch and glycogen. The human genome has a cluster of several amylase genes that are expressed at high levels in the salivary gland and pancreas (Stam, Danchin, Rancurel, Coutinho, & Henrissat, 2006). Of these the gene AMY1 encodes for the salivary version of amylase. Indeed, in the case of agriculturalists that consume large amounts of starch there are multiple copies of the amylase gene. It is therefore evident that the trait of an augmented number of copies of the AMY1 gene has been subject to positive or directional selection in populations that consume large amounts of starch be they agriculturalists (Pickrell, Coop, Novembre, Kudaravalli, Li, Absher,... & Pritchard, 2009) or modern hunter-gatherers like the Khoisan (Schuster, Miller, Ratan, Tomsho, Giardine, Kasson,... & Hayes, 2010). In the case of non-starch consuming populations evolutionary changes in the AMY1 gene are the result of genetic drift. Salivary amylase would be expected to confer a fitness advantage to individuals with a high-starch diet for it hastens energy extraction from the nutrient (Perry, Dominy, Claw, Lee, Fiegler, Redon, ... & Stone, 2007). But we made one of our domesticates, the dog, partake of the starch rich diets. This exposure led to novel adaptations allowing the ancestors of current dogs to flourish on a starch-rich diet relative to the carnivorous diet of wolves. This may have facilitated the domestication process of dogs. It is noteworthy that a process of parallel evolution in dogs and humans emerged as a result of the agricultural revolution (Axelsson, Ratnakumar, Arendt, Maqbool, Webster, Perloski, ... & Lindblad-Toh, 2013). The fact that exposure to natural foodstuffs can modify us genetically raises concerns regarding artificially genetically modified crops (Uzogara, 2000).

The domestication of animals

A thousand years after the domestication of plants came the domestication of animals, interestingly, occurring in the same region where plants were first domesticated. It is an accident of geography that the Fertile Crescent harbored the principal domesticable plants and animals (Diamond, 1998). Dogs became the first known domesticates, and the development of their domestication syndrome has been the subject of numerous studies.

The earliest detected domesticates –other than dogs– are from the Levant and arose from feral versions. These were the Oriental mouflon (*Ovis orientalis*; 11-9000 BP) (Pedrosa, Uzun, Arranz, Gutiérrez-Gil, San Primitivo, & Bayón, 2005). which evolved into domestic sheep, (*O.*

aries); the bezoar goat (*Capra aegagrus*; 10,500 BP) (Ducos, 1968) from which arose the domestic goat (*Capra hircus*); the now extinct aurochs (*Bos primigenius*; 8,500 BP) (Troy, MacHugh, Bailey, Magee, Loftus, Cunningham,... & Bradley, 2001) which evolved into domestic cattle (*Bos Taurus*); and the wild boar (*Sus scrofa*; 13,000BP) (Larson, Albarella, Dobney, Rowley-Conwy, Schibler, Tresset, ... & Cooper, 2007) which gave rise to the pig (*Sus domesticus*). Following this initial domestication phase subsequent domestications occurred in the Eurasian mainland and Africa. From the point of view of human genetic transformations the most important aspect of this wave of domestication is that all the domesticates are mammals and three of the domesticates are sources of plentiful milk. The first humans to exit Africa through the Middle Eastern corridor likely numbered in the range of 17,500 to or 9,000 (Harpending, Batzer, Gurven, Jorde, Rogers, & Sherry, 1998). Just as present humans are derived from a few original travelers, a similar small number of animals gave rise to the domesticated cattle herds of the early Agricultural Revolution. It is estimated that around 80 female aurochs were initially domesticated 10,500 years ago and that this event occurred at *Dja'de el Mughara* in the Middle Euphrates (Helmer, Gourichon, Monchot, Peters, Saña-Segui, 2005) and Çayönü in southern Turkey located forty kilometers north-west of Diyarbakır, at the foot of the Taurus Mountains (Bollongino, Burger, Powell, Mashkour, Vigne, & Thomas, 2012).

As humans began domesticating the various dairy bovids, these reciprocated by altering – domesticating– humans. The newly minted agriculturalists, particularly the pastoralists, now lived with the care of their flocks or herds as their primary concern. Animals had to be penned, sheltered and protected from environmental inclemencies, provided with fodder and water, or herded to appropriate feeding grounds. Furthermore, as their feral defensive traits waned they had to be protected from predators because the principal behavioral trait common to domesticated species is a dulling of the manifestation of important forms of aggressive behavior required for survival, particularly offensive and defensive aggression (Hare, Wobber, & Wrangham, 2012). This reduction was mediated by a dampening of the activity of the hypothalamic-pituitary-adrenal (HPA) axis (Kunzl, & Sachser, 1999). Seasonality of reproduction, molting and similar circum-annual events in the life of domestic animals required human cultural adaptation. The free ranging, unfettered life-style that characterized hunter-gatherers was now circumscribed and hemmed in by the domesticate's biological as well as the herder's cultural imperatives: humans became constrained by the domesticate's ecology.

Animals acquired a new and vital presence in human culture. They were celebrated in religious festivals as well as employed in worship and as mortuary offerings, (Eliade, 1959) and some were even sacralized (Dodson, 2005). Moreover, animals became symbols of social status as well as exchange currency. Not that hunter-gatherers were complete strangers to the cyclical rhythms of nature. Their pre-agricultural lifestyle was already imposed upon them by the annual cycle of animal and plant availability. Once fully domesticated, selected animals became almost entirely dependent on humans for their survival. The great nutritional, commercial and cultural value of these animals ensured that their human domesticators now were inextricably entangled and bound to them for their joint survival.

In the case of sheep this would eventually lead to political adaptations, such as the establishment of guilds of sheep owners and the shepherds that attended to their flocks. For example, in the case of Spain Alphonse X, the Wise, created an organization, the Honrado Concejo de la *Mesta*, that regulated the transhumant transfer of herds between feeding grounds along designated cañadas reales (right-of-way) into assigned pasturage. In addition to the control of paths, the Mesta became a powerful economic and political force particularly since exportation of Merino sheep wool was the primary source of revenue for the Spanish crown. The conquest of the New World was paid for with the proceeds from sheep wool. Domesticated bactrian camels (*Camelus bactrianus*), (Ji, Cui, Ding, Geng, Gao, Zhang, ... & Meng, 2009) the instrument that for intercontinental bulk transfer of goods between China and Europe, propelled the pacification of the Asian steppe and the stabilization of the Great Silk Road (Kuz'mina, 2008). Transfer between pasturage fields was employed with a variety of other herbivores, but other than sheep the animals that best thrive under this regime are camels, horses and yak (*Bos grunniens* & *Bos mutus*), although in some regions several other herbivores, like cattle, are also managed in this way.

However herbivorous mammals transformed humans in a much subtler way: they transformed our genome thus becoming a selective force in their own right. Humans, being mammals, lactate. Milk constituents –such as casein and other milk proteins– emerged around the Jurassic or Cretaceous period, as they are present in monotremes (e.g., platypus, spiny anteaters), marsupials (e.g. Kangaroo) and eutherians (e.g., cows and humans). This deep lineage indicates that the production of milk constituents was already present in mammalian

precursors (Ofstedal, 2013). Human milk, like the milk of all domesticated mammals contains the sugar lactose, a disaccharide sugar composed of galactose and glucose. Infants up to the age of three can digest lactose because they produce in their digestive tract the enzyme –lactase– needed for cleaving it into its individual sugar moieties. After age three the gene encoding for the enzyme is repressed and continued milk consumption leads to signs and symptoms of lactose intolerance due to bacterial fermentation of the sugar in the gut. By this time a child’s diet has shifted to regular foods. Occasionally, in any population there are individuals that persist in producing lactase –standing variation– (Barrett, & Schluter, 2008) and thus retain the ability to cleave lactose throughout life because the gene coding for lactase is not repressed. For them milk is a lifelong nutrient. Thus 5,000 years ago lactase persistence was expressed sporadically among herders. Extant populations in which lactase prevalence is greater than 60 percent are those descended from the original pastoralists. Extensive positive selection and recurrent waves of migration fueled this development, which took place in a period of a mere 3,000 years; quite brief in evolutionary terms. In a display of genetic plasticity the lactase persistence phenotype emerged via several different mutations and underwent selective sweeps (Fu, & Akey, 2013) being now present in Africa, the Middle East, Northern Europe and regions of India, all areas of cultural acceptance of milk-animal herding and milk consumption as a way of life. Lactase persistence in a population, therefore, is strongly correlated with its dairying history (Hollox, 2004). Today cow byproducts other than edible components are indispensable for a variety of industries. Domestic animals are a vast industry spanning the globe and contributing not merely foodstuffs, but also contributing to disease transmission (Scott, Will, Ironside, Nguyen, Tremblay, DeArmond, & Prusiner, 1999), land degradation (Lange, Barnes, & Motinga, 1997) and global warming (Moss, Jouany, & Newbold, 2000) .

The domestication of single-celled organisms

This process of domestication will not only encompass multicellular organisms but also unicellular ones. Such organisms would be harvested for their capacity to ferment certain foodstuffs so it is not unexpected that it marches in tandem with the domestication of crops and animals. However, pre-agricultural nomadic pastoralist may have discovered fermentation before the onset of the agricultural revolution. Prior to or coeval with the domestication of cattle milk was being obtained from other domestic mammals such as the mare, goat, camel, etc., it was discovered that milk would be transformed into a reduced lactose product, yogurt, by the

fermenting action of bacterial species such as *Lactobacillus delbrueckii* subsp. *bulgaricus* and *Streptococcus thermophilus* bacteria (Kolars, Levitt, Aouji, & Savaiano, 1984). Perhaps coeval or further along in this process would come the production of cheeses (Salque, Bogucki, Pyzel, Sobkowiak-Tabaka, Grygiel, Szmyt, & Evershed, 2012). In them mesophilic bacteria of the genera *Lactobacilli* and *Streptococci* are employed for the fermentation of lactose. Some regional cheeses are produced with specialized bacteria discovered serendipitously, like [Propionibacter shermani](#), essential in the production of Swiss cheese. In any case the reduction of lactose through fermentation would have made milk products palatable to lactose non-tolerant individuals –the vast majority– until such time as genes regulating lactase persistence became widespread among pastoralists and their descendants (Tishkoff, Reed, Ranciaro, Voight, Babbitt, Silverman, ... & Deloukas, 2006). This is a clear example of gene-culture coevolution between a variety of microorganisms and domesticated mammals (mostly ungulates or hoofed animals) led by human evolution (Beja-Pereira, Luikart, England, Bradley, Jann, Bertorelle,... & Erhardt, 2003). It was the beginning of the Neolithic dairy industry which ushered in the Secondary Products Revolution (Chapman, 1982).

Another microorganism domesticate was the yeast *Saccharomyces cerevisiae*. Found on the surface of ripe fruits –such as grapes– it has been employed since prehistory for fermentation in the making of breads, wines and beers from various grains and fruits (Cavaliere, McGovern, Hartl, Mortimer, Polsinelli, 2003). Fermentation helps preserve and enhances the nutritive value of foodstuffs (McGovern, Zhang, Tang, Zhang, Hall, Moreau, ... & Wang, 2004). However one of the byproducts of fermentation is alcohol and it is not surprising that the presence of such a powerful psychotropic agent left its imprint in the human genome. Around 10,000 years ago rice agriculture took root in Southern China (Zong, Wang, Innes, & Chen, 2012). One of the uses rice was put to early on was preparing fermented beverages (Wang, Ding, Shu, & Chen, 2010). Like in the case of milk and starch, genes involved in the ethanol metabolic pathway became the target of selection from the moment ethanol-containing foodstuffs became a regular part of the diet. There is a linkage between the ability of humans to metabolize alcohol, the development of agriculture and the fermentation industries.

Alcohol dehydrogenase (ADH) and aldehyde dehydrogenase (ALDH) are the major enzymes responsible for ethanol metabolism in humans. Ethanol is oxidized to acetaldehyde mainly via

the liver enzyme alcohol dehydrogenase IB (class I), beta polypeptide (ADH1B). After absorption the first step in ethanol metabolism is its oxidation to acetaldehyde by the enzyme (ADH). Acetaldehyde is then oxidized to acetic acid by aldehyde dehydrogenase (ALDH). Specific alleles at the loci ADH1B, ADH1C and ALDH2 can increase the blood level of acetaldehyde. Several populations, most notably the southeastern Chinese, evidence a reaction to alcohol ingestion consisting of skin “flushing” and marked gastrointestinal discomfort, particularly vomiting. Individuals who flush are protected by its unpleasantness from heavy drinking. Over 10% of Chinese are estimated to respond to a small amount of alcohol with this “flushing” reaction (Cochrane, Chen, Conigrave, & Hao, 2003). The reaction is due to variations in the metabolism of ethanol due to genetic variations in the ADH and ALDH genes among them the evolutionarily derived ADH1B*47His. ADH1B*47His- increases alcohol metabolism by a factor four- to ten-fold (Peng, & Yin, 2009). The global distribution of ADH1B*47His- reveals that this allele reaches high frequencies (often exceeding 80%) among east Asians but is nigh absent in sub-Saharan, European, and Native American populations. However, it is also present in western Asia; the highest frequencies appear in the Persians, Turks, Samaritans, and Jews from a variety of regions (Li, Mukherjee, Soundararajan, Tárnok, Barta, Khaliq, ... & Kidd, 2007). It is important to note that the emergence of this allele (7000~10,000 years ago) is coeval with the emergence of rice cultivation in East Asia thus there is a strong correlation between ADH1B*47His- frequency and the age of rice domestication (Ye, & Gu, 2011). It is also linked in West Asians with the emergence of cultivation in the Fertile Crescent. Thus, it was proposed that the rise of ADH1B*47His- frequency was an adaptation to rice domestication in the east as well as cereal domestication in the west and the subsequent production and consumption of fermented food and beverages. ADH1B*47His-induced “flushing” reaction is thought to have a protective role in preventing alcohol overconsumption, a relation consistently demonstrated (Li, Zhao, & Gelernter, 2012). Conversely low frequencies of ADH1B*47His- have been identified in European, North African, and Middle Eastern populations and an association between alcohol dependence and reduced enzyme levels has been established (Whitfield, Nightingale, Bucholz, Madden, Heath, & Martin, 1998). Through conjoint effort yeast and their fermentable substrates generated an addictive substance that assures them a continued existence. They also, through selective forces, modified the human genome enough to insure the continued existence of at least some of their

protectors.

Domesticated microorganisms are not identical to wild ones. Domesticates evidence growth and metabolic traits that are different from the ones expressed by their wild counterparts. Several indicators reveal that environmental circumstances have a significant influence on the properties of microbial communities, a feature that becomes predominantly manifest in colonies of bacteria and yeast (Landry, Townsend, Hartl, & Cavalieri, 2006). Wild microorganisms tend to assemble in complex communities comprised of several different species. On the other hand, under domestication they do not form the same type of communities nor do their colonies have the same morphology as in the wild (Váchová, & Palková, 2005). Furthermore, it is clear that the strains of *S. cerevisiae* specialized for the production of alcoholic beverages were originally derived from natural populations unassociated with alcoholic beverage production, and not the opposite (Fay, & Benavides, 2005). It was inevitable that humans would come in contact with these microorganisms as they are ubiquitous. Now both are intertwined and dependent on each other.

Slavery as failed domestication

With the advent of agriculture the capacity of the egalitarian social glue to hold hunter-gatherers together as communal nomadic bands of up to 50 individuals was exceeded (Whitelaw, 1991). Once this occurred social stratification appeared and was quickly followed by the emergence of dominance structures. Dominance in turn had as a corollary enslavement. Originating in antiquity as an outcome of defeat in war it evolved so that ultimately, in modernity, it led to its darkest expression: slave commoditization, i.e., they became simple commodities in the eyes of the market, (Fleischman, R. & Tyson, 2004) coupled to the factorage business (Conrad, & Meyer, 1958), whereby sellers operated via allowances paid in their role as a factor: the slave as an item for exchange. Therefore slaves, aside from doing forced labor, were used as “investments (purchased and then rented out as laborers), credit (for securing loans), property, commodities and capital making them an odd mix of abstract and concrete values” (Grandin, 2014). They therefore differed little from animals and their valorization (Bailey, 2005). Domestication, the process already described whereby animals and plants are rendered dependent on humans for survival and propagation could be applied to humans. In non-human organisms domestication involves the use of artificial selection to alter the physical and

behavioral phenotype of an organism. Humans partake of a dual, imbricated, evolutionary process: biological as well as cultural evolution. The attempted domestication of man by man – slavery- required a modification of the cultural phenotype towards tameness or at least tractability. Humans were quite successful with some plant and animal species, but plants do not exhibit cultural evolution discernible to us, and some of the higher primates do evidence cultural qualities (vide supra) but they are not as dominant a trait as it is in humans where cultural evolution can overpower biological evolution. In the case of humans, since they have cultural and social as well as biological evolution, the concept would apply to cultural domestication as well as biological domestication (Davis, 1988). Slavery was an ancient scourge, and those enslaved generally came from the ranks of the defeated in battle. The slavery of modernity –of the recent Holocene– was primordially an African catastrophe. During the European expansion and domination of the last half millennium Africans became the overwhelming majority of the world’s slaves. At the height of the slave trade about 90% of slaves coming out of Africa were bought by western Europeans. Since the Middle Ages slaves were also exported towards Muslim lands, however this trade remained relatively constant and represented between five to ten thousand persons exported per year. The other major civilizations of Eurasia, India and China did not participate in the African slave trade at all (Austen, 1988).

There does not seem to be a process whereby humans were successfully domesticated biologically by other humans. Failing the selection for a domestication syndrome phenotype another process was required for enslavement: deracination and cultural deprivation. Enslavement viewed within the reference frame of historical slavery entails a process of dehumanization and a parallel process of bestialization (Fielding, 2012.) These elements could be taken to be, therefore, part of a process of cultural domestication, or at least attempted domestication. The only society for which contemporary information is available concerning the management of humans, specifically breeding, as if they were part of the farm commercial fauna, is antebellum southern United States. But this is an accident of history given that slave breeding was present in earlier slave-holding societies but we lack details as to its efficacy. Indeed, it was an important component of the slavery industry of Rome during imperial times (Jones, 1956). In early Rome, unlike the modern West, the primary source of slaves was prisoners captured in battle. During the latter part of the Western Roman Empire, as its military

power waned, slave breeding was the dominant method of expanding the slave population.

The domestication syndrome among animals entails that they become neotenuous, i.e., retention of childhood traits into adulthood, which equates with submissiveness and tameness not observed in their wild mature counterparts. These behavioral traits were accompanied by morphological equivalents such as shortening of the mandible and a decrease in size of the teeth: a parallel phenotypic language that signaled domesticity. Selection against aggression in mammals can have multiple effects on their morphology, physiology, behavior and psychology, and these results are the traits that characterize the domestication syndrome observed in domestic animals. The most recent experimental domesticate, the silver fox, exhibits just such traits (Gogoleva, Volodin, Volodina, Kharlamova, & Trut, 2013). The changes in anatomy and behavior defining the domestication syndrome were closely tied to human needs, especially in farming. Physiologic modifications such as those due to castration of males or to the modification of breeding patterns were adjuncts in the domestication process. Animal control also required the invention of suitable collars, restraints, prods, lashes, and branding tools. Such instruments would in due course become part and parcel of the slave-owners paraphernalia. Humans also assumed the role of herd leader –a paternal role– as they expunged dominance traits from animals and took over that role for themselves. Humans seem not to have effected such obvious phenotypic transformations on other humans. For example, there is no evidence of neotenization in slave populations. However phenotypic after-effects of slavery and the slavery experience are biologically detectable today: the effect of trans-generational epigenetics (Sullivan, 2013). The average birth weight in the contemporary African-American population is about 250 g lower than the average birth weight of European Americans. It has been proposed that this difference is a product of fetal programming brought about by generations of matrilineal malnourished ancestors (Jasienska, 2009) driven by a thrifty genotype (Goldstein, & Segars, 2013). A trans-generational effect can also be detected on the side of cultural evolution. An inverse causal relation has been demonstrated between the intensity of slave raids to which ancestors were subjected and firmness of social trust relations among descendants. Individuals whose ancestors were heavily raided during the slave trade today exhibit less trust in neighbors, relatives, and their local government (Nunn, & Wantchekon, 2009). To establish this relation investigators have regressed self-reported trust from the 2005 Afrobarometer surveys (Afrobarometer, 2005) on ethnicity-specific historic slave

exports. Further studies by other authorities employing different research strategies confirms that individuals from ethnic groups that experienced high levels of slave exports are less trusting.(Deconinck, & Verpoorten, 2013). Today cultural mistrust persists as a social force on both sides of the Middle Passage and has a significant impact on the attitudes and behaviors of native Africans as well as on African Americans (Whaley, 2001a). Among the latter group it is extensively in display as a coping behavior to deal with racism and prejudice (Whaley, 2001b). Social rejection or marginalization as a result of their ancestors slavery experience has introduced added elements that operate in tandem with epigenetic factors causing underweight pre-term deliveries,(Rich-Edwards, & Grizzard, 2005) and other disproportionately high rates of adverse birth outcomes among African Americans (Giscombé, & Lobel, 2005) which appear to be caused by altered levels of adrenocorticotrophic hormone, cortisol and corticotropin-releasing hormone as well as placental dysfunction during pregnancy (Glynn, Schetter, Chicz-DeMet, Hobel, & Sandman, 2007). These reproductive dysfunctionalities are traceable not only to the slavery experience as a cultural stressor, but also to the rendering of otherwise adaptive metabolic traits suitable for life in Africa into maladaptive ones in the New World environment, particularly in its contemporary version. The environment of evolutionary adaptedness of native Africans was one of salt, sugar and fat scarcity. The survival adaptations to these important dietary traits are a variety of metabolic or behavioral traits that mediate avidity for energy storage as well as frugality in energy expenditure nested into the “thrifty phenotype theory” (Zhou, Wang, & Yu, 2014). The trans-Atlantic trade funneled Africans, primarily from the west coast, with high prevalence of malaria and trypanosomiasis, through a genetic bottleneck. This led to the reduction in genetic variability inherent to bottlenecks as evidenced by the problem arising from homozygosis for ApoL1 (Ko, Rajan, Gomez, Scheinfeldt, An, Winkler, ... & Tishkoff, 2013) and sickle cell trait (Gong, Parikh, Rosenthal, & Greenhouse, 2013).

To forcibly dominate a person in the way slave labor demanded required a profound emotional as well as physical deracination. 'Natal alienation,' -the sundering of a person's social and ecologic ties with the natal socio-biologic ecosystem- leads to profound existential disorientation (Patterson, 1982). One can add the “seasoning” of slaves during their transport to plantations whereby they were robbed in transit of moral agency and autonomy: brutalizing the captives (Holdren, 2013). A sociobiological effect akin to taming could be obtained via the mechanism explicating the Stockholm syndrome (Sar, & Ozturk, 2013). In addition, once ashore, slaves

were frequently housed with or in proximity to domestic animals. This accentuates the “animalization” or “bestialization” of slaves that was central to the bondage experience. It has been argued that the domestication of the various herbivores during the early Holocene paved the way for the enslavement of humans (Jacoby, 1994). Slaves were treated in a manner analogous to farm machinery: machinery that could transform chemical into mechanical energy as well as reproduce, but that required precious food to do so. Bringing slaves into the set of attempted domesticates brought in individuals that, unlike all other domesticates, had to be fed processed food in order to be able to extract maximum value without having to consume them: the slave and the master competed for the same food. So it is not unexpected that slaveholders would readily recognize the value of female slaves of reproductive age. Through them they could increase their wealth and thus cancel the cost incurred in keeping slaves. But southern slaveholders did not embark in the careful artificial selection of humans that had hitherto been deployed to obtain the best breeds of farm animals or plants. It was cheaper to buy a slave than to breed one and this equation held until the African source of slaves dried up. Now, as in Imperial Rome’s latter years, it made sense to breed slaves. Furthermore, the westward expansion of the United States created a market for slaves once the Atlantic slave trade had been closed by the West Africa Squadron after the British Parliament passed the Slave Trade Act of 1807 (Sutch, 1972). This naval interdiction dried up the supply of slaves to the United States and propelled the breeding activity. This activity explains that though the United States received far fewer slaves than were imported into Brazil or the West Indies by the end of the slave era the United States had a comparable enslaved African population. It is evident that the source of United States slaves was internal breeding. There is a notable difference in the breeding rates between African slaves of the West Indies and the rate of those in the mainland. Among hunter-gatherers in Africa, like the San of the Kalahari, the traditional weaning age was about the fourth year whereas other groups like the Ache or the Hadza children are usually completely weaned by age three and nursed at low frequency by age two years (Konner, 2005). This led to an inter-birth interval of at least three to four years. Among slaves in the southern United States the weaning age among slaves was at the end of the first year, whereas among slaves in the West Indies it was the end of the second year. Inter-birth interval is a function of lactation as breast feeding is the naturally evolved method of ensuring an adequate inter-birth interval through its contraceptive effect (Howie, & McNeilly, 1982). Therefore the shortened

lactation period in the mainland led to a faster reproductive rate. This, as well as control of female slave reproduction by favoring early childbearing, the maximizing the number of breeding females, and the high age at last birth, is the reason why despite the unavailability of slave imports breeding increased the slave population in the United States to the size of that of Brazil or the West Indies (Klein, & Engerman, 1978). In this manner, by manipulation of the biology of reproduction and its cultural traits, southern slave-breeding was accomplished.

A further cultural adaptation was to tie the status of the newborn to that of the mother. Because of the fluid status of the slave as a human, and the extant laws delineating lines of succession and inheritance an old Roman law was called to the fore: *partus sequitur ventrem*, that is, the parental lineage presumption adopted in 1662 by American courts that "all children borne in this country shall be held in bond or free only according to the condition of the mother." (Bush, 2013). Because of this legal doctrine it did not matter whether the father was African or European. The offspring of a female slave was a slave, and thus belonged to the master. Available evidence informs us that the direction of the artificial selection force employed by slaveholders operated through female fecundity and fertility (Morgan, 2011).

Aggravating the disease load provoked by the genetic bottleneck of the Atlantic trade, as well as the transfer to a new ecosystem, it is in slaves that we have the first glimpses of post-traumatic stress disorder. In the text *Reflexiones Histórico Físico Naturales Médico Quirúrgicas*, written between February of 1797 and July of 1798, Francisco Barrera y Domingo, a Spanish surgeon, wrote an 894-page manuscript account of eighteen years of his medical observations in Cuban sugar plantations on slave medicine in the Caribbean. It gives a startling account of what today would be diagnosed as Post Traumatic Stress Disorder: "[Es] una tristeza melancólica que les acomete repentinamente, sin delirio, furor ni calentura, nacida de una tenaz abersión a quantas cosas puedan substraerlos de su imaginatiba, como no sea la vuelta a su amada patria" (Barrera y Domingo, 1798/1953). This condition was also encountered in Brazil where it went by the name of *banzo* (Oda, 2008). Suicide was a tragic denouement to this disorder (Oliveira, & Oda, 2008). Herein lays the etiology of the aforementioned stress-mediated diseases that plague slave descendants. However just as with the reciprocal domestication –the first biological; the second cultural and biological– between humans and their domesticates, the residue of slavery affected the slaveholder as well as the slave. Is the

transformation of forager to farmer and then to city dweller a form of self-domestication? The rapid gracilization of humans of the recent Pleistocene can be ascribed to the interruption of natural evolutionary developments by culturally mediated breeding patterns favoring skeletal gracility. Thus despite our best efforts to domesticate each other that task has been best performed by nature itself. The most pernicious effect of slavery was the bestialization of human by human. Neither the slave nor the slaveholder escaped bestialization. Charles Darwin, a committed abolitionist, witnessed the effects of slavery first hand as he narrates that a slave misconstrued a hand motion of his as an act of impending violence and the slave “Instantly, with a frightened look and half-shut eyes he dropped his hands. I shall never forget my feelings of surprise, disgust, and shame, at seeing a great powerful man afraid even to ward off a blow, directed, as he thought, at his face. The man had been trained to a degradation lower than the slavery of the most helpless animal” He also describes the effects of slavery upon the slaveholder as he accompanied one on a trip to his plantation in Brazil: “The Brazilians, as far as I am able to judge, possess but a small share of those qualities that give dignity to humankind. Being surrounded by slaves, they become habituated to the harsh tones of command & the sneer of reproach” (Darwin, 1909). Slave and master entwined in the bestial degradation inherent to slavery.

Self domestication?

Was the transformation of foraging to farmer and then to city dweller a form of self-domestication? The rapid gracilization of humans of the recent Pleistocene can be ascribed to the interruption of natural evolutionary developments by culturally mediated breeding patterns favoring skeletal gracility (Ruff, 2006). Despite our best efforts to domesticate each other that task has been best performed by nature itself. Perhaps the most central development in the history of Homo sapiens—and one having among the most profound impacts on the terrestrial ecosystem and its human and non-human inhabitants—was the domestication of a source of energy (fire), plants and animals. In addition to modifying landscapes globally from the terminal Pleistocene and early Holocene, the transformation from foragers to farmers has impacted in negative and multiple manners human health. Studies contrasting human skeletal remains from pre-agricultural and Neolithic periods reveal that the introduction of grains and other cultigens led to a dietary transformation that has resulted in a decline in health and deleterious alterations in physical activity and lifestyle. Although agriculture afforded the economic basis for the

emergence of and the development of civilizations, the resultant surplus has changed not only our diet but the very nature of our social organization: civilization as a pathogen. During the last 12,000 years humans have not only domesticated nature; we have ensnared ourselves in our own ecologic transformations. The diseases of modernity such as cancer, (Jordá, 2006) metabolic syndrome, hypertension, obesity (Attie, Brooks-Gunn, & Petersen, 1990), diabetes type 2 (Hossain, Kowar, & El Nahas, 2007), chronic inflammatory and degenerative diseases of the axial and appendicular skeleton (Yun, & Lee, 2004) as well as brain (Walach, & Loef, 2013) and newly emerging transmissible conditions are the product of the collision between our cultural evolution and our biological evolution (Wiedman, 2010). Niche modification in the form of ecologic degradation and the creation of colossal cities has brought deficient diets and the emergence of social suffering (Hidaka, 2012). Furthermore we have now pseudo-diseases that are the creation of the pharmaceutical industry, (Moynihan, Heath, & Henry, 2002) the pathology of cultural evolution in modernity. We are our own domesticates and that process has taken and is taking a severe toll upon humans as a biological and as a cultural species.

Conclusions

Humans throughout their evolution first attended almost exclusively to their own reproduction and genetic enrichment of the evolutionary fitness. Complex interpersonal strategies ensured that such was the case. With the advent of surplus and wealth derived from the agricultural revolution unusual power-hoarding practices emerged, such as incest. The domestication of various creatures by man entails that domesticates become dependent on humans for survival and reproduction. Plant domesticates have nutritional and water needs that human must satisfy if they are to become valuable crops. Animal domesticates have their own particular needs and lives embedded in their own cycles of life and death; of needs for sustenance; of suitable environment for reproduction and birthing. Human must attend to all these needs. That means that what previously was a fluid form of life for humans, and that made possible the epic migration from Africa to Patagonia, now became constrained by the needs of the domesticates. Water is paramount for irrigating plants and watering animals. So it is not surprising that the first states that evolved during the Neolithic demographic transition made possible by agricultural surplus are sited on river basins. Humans began to favor certain plant and animal varieties over other because of ease of husbandry, yield and durability of derived products in storage or lacking that, transformability into a long-lasting product as was done through salting, drying or

fermentation. As secondary products began to be collected the bond between domesticator and domesticated became nigh inextricable: the domesticator becomes domesticated. A further conscious effort at domestication was slavery, an institution that developed during the emergence of complex states. Further along, beginning during the Enlightenment, the valuation of slaves merged with the valuation of the newly developed global commerce. The failure at humans domesticating humans led to the partial demise of the trade though countless people still live in some form of modern bondage. The Neolithic agricultural revolution started the process; the First and Second Industrial Revolutions followed in the late 20th century by the Information Revolution completed and sealed it. Now humans, fully dependent on the purveyance through synthetic means of artificially obtained resources ultimately derived from the degradation of ecosystems are as domesticated and enfeebled as sheep. Thus humanity and its domesticates became inextricably entangled. True, only humans construct a narrative of this entanglement, but it is no less true that domesticates have constructed their narrative in our genes, and thus in our evolution. It is a magnificent irony, yet prophetic, that the guiding metaphor of mankind's largest religion is one where humans are depicted as helpless sheep under the protective guidance of an invisible deity whose son became reified as a shepherd. And the metaphor arose precisely at the geographic point where domestication emerged as a cardinal transformative element in human history. But in the end the guiding force is none other than natural selection, and it will exact its price in exchange for fitness.

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