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Physiological Gracility of Anatomically Modern Humans: Human Self-Domestication or Gene Tic)-Epigene (Tic)-Culture Co-Evolution?

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ABSTRACT: The topic of genetic and epigenetic transformations determined by repeated contacts and prolonged periods of coexistence between different human types and species during the late Paleolithic, highlighted by the data obtained from the reconstruction of the genome-wide of ancient DNA and from the analysis of samples dating back to the Middle and to the Upper Paleolithic, is addressed in section 1. The so-called *Human self-domestication hypothesis* (HSD), which points to the possibility that the reduced emotional reactivity and increased self-control resulting from HSD have created a unique form of human tolerance that allows for the expression of more flexible social skills observed in anatomically modern humans, is discussed in section 2. In section 3 an alternative explanation of how and when the anatomically modern human lineage arose is presented. Since humans began to think and feel the world in terms of *subject* and *object*, distinguishing themselves from Nature (*relation of contiguity*) and ceasing to identify with it (*relation of continuity*), the human communities also developed the ability to create and produce *culture*. Culture production plays a (epigenetic) decisive role in order to *i)* favor complex processes of coevolution between individuals of the same or different (domesticated) species, which in many cases involves symbiosis or mutualism, in order to favor increased in-group prosociality over emotional reactivity, ii) trigger epigenetic mechanisms in the rapid phenotypic changes (that can be assimilated as genetic variants), also observed as outcome of domestication along with neuroanatomical, neurophysiological and neurocognitive changes specific to anatomically modern humans, iii) favor the activation of the capacity for complex iterative learning, necessary for cultural transmission, with or without oral language.

Conclusions suggest that the recent evolution of *anatomically modern humans*, especially after the split with Neanderthals, can be understood as the outcome of gene(tic)-epigene(tic)-culture coevolution, rather than by self-domestication against emotional reactivity.

KEYWORDS: human-specific mutations; ancient genomics; human self-domestication hypothesis; psychological birth; gene(tic)-epigene(tic)-culture co-evolution

1. HOW AND WHEN THE ANATOMICALLY MODERN HUMAN LINEAGE AROSE?

Large brains, stone-tool technology, derived life-history traits and complex social behaviours have at one time or another all been seen as 'defining' of the genus Homo[1]. It is not uncommon to see the transition to the genus Homo imaginatively reconstructed from a comparison of the relatively derived morphology and behaviour of Pleistocene *H. erectus*, sometimes recognized as a different taxon, i.e. *H. ergaster*, to the much more generalized morphology and behaviour of early Australopithecus - even though no such radical transition ever actually occurred [1]. According to recent studies [2] [3] our ancestors (*Homo erectus*) experienced a severe population bottleneck between ~ 930 and 813 thousand years ago (henceforth **tya**) most likely due to climatic changes (*Mid-Pleistocene Transition* [4]), that brought the ancestral human population close to extinction and completely reshaped present-day human genetic diversity. A reshaping that marks the transition (still debated) from *H. erectus* to *H. heidelberghensis* to early *anatomically modern humans*, namely early *H. sapiens*, and to other human spices (or types?) close to anatomically modern humans, i.e. *H. neanderthalensis*[2] (the name derives from the Neander Valley in Germany, where the fossils were first found) and Denisovans (named after the Denisova Cave in Russia where the first fossils were found), and to new adaptive strategies which with late *H. sapiens* will be progressively integrated by increasingly complex and high-performance supra-adaptive strategies, including the

[1] **Humans lineage**: Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi; Mammalia; Eutheria; Euarchontoglires; Primates (*order*); Haplorrhini; Catarrhini; Hominidae (*family*); Homo (*genus*), Homo sapiens (*species*), which yes belongs to the same *taxonomic family* as the great apes, but without any other meaning than this.

[2] Contemporary depictions of Neanderthals tend to have light skin as a result of genetics research in the early to mid-2000s. Yet, using gene markers, recent study [5] examined both Neanderthals and living people DNA predicting lighter or darker skin pigmentation with about 60 percent accuracy for the living folks, little over the random chance of a coin flip. To understand the paleoanthropological roots of anatomically modern humans we need much more than this.

growing communicative and social function performed by oral language (speech).

Yet, estimating how and when the anatomically modern human lineage arose remains controversial [6]. Dating the oldest population split within modern humans using genetic data has suggested times as recent as 200 to 100 tya [7]. However, for tens of thousands of years, anatomically modern humans and other humans, such as the Neanderthals, the iconic Eurasian species of the Pleistocene, and the Denisovans from East Asia, not only came into contact multiple times and in different geographical areas, but they mixed and exchanged genetic material too.

According to [7] only a low fraction, 1.5 to 7%, of the contemporary human genome is uniquely "human", with the remainder comprising lineages shared with archaic hominins. This small human-specific fraction of the genome is enriched for genes related to neural development and function. The same researchers also found evidence for multiple waves of human-specific mutations that occurred through time, suggesting that the modern human phenotype may have developed in stages.

However, until the late 20th century, Neanderthals were regarded as genetically, morphologically, and behaviorally distinct from living humans. They occupied most of Europe and parts of Western Asia from ~300 to 30 tya. Recent discoveries about this well-preserved fossil Eurasian population have revealed an overlap between living and early humans [8][9][10]. The genomic data suggest that Neandertals mixed with modern human ancestors for the first time before 160 tya [11][12], and overlapped geographically with anatomically modern humans for a period of over 120 thousand years following the latter migration out of Africa [13] [Fig. 1].

During this period, Neanderthals and H. sapiens interbred [14][15][16], as evidenced by Neanderthal portions of the genome carried by non-African individuals today [17][11].

Nonetheless, archeological evidence paints a more complex and older story, as recent studies reported human remains with many modern features but archaic cranial morphology dated to ~ 300 tya [18], suggesting that not all human-specific traits arose at the same time and accumulation of derived morphological features in humans occurred in multiple stages (see [13]).

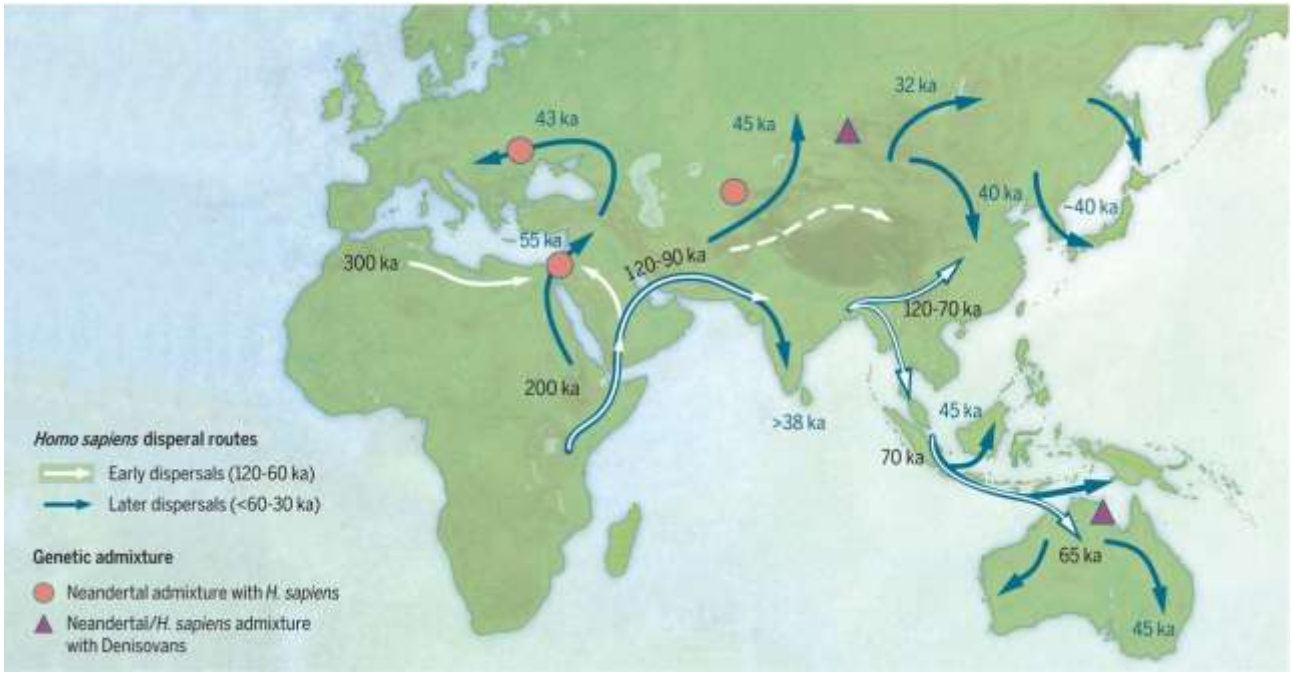

Fig. 1: Map of sites with ages and postulated early and later pathways associated with modern humans dispersing across Asia during the Late Pleistocene. Regions of assumed genetic admixture are also shown. ka, thousand years ago.
Image source: https://www.science.org/doi/10.1126/science.aai9067

To mate successfully there should be a degree of biological recognition of sameness, but until the rise of ancient genomics, the potential for a hominin hybrid had yet to be realized. Several instances of known introgression[3] later [19][13], we are now faced with having to choose between the wealth of alternative species concepts [20][21], the difficulty of which is compounded by the reality of having a range of morphological evidence for which we do not have any ancient DNA, and a collection of genetic data for which we have little or no morphological information. Species (especially extinct ones[4]) are often tricky to identify in practice,

[3] Introgression is a genetic crossover that takes place between the species of the same population via a backcross to one or both of the parent species.
[4] *Living species can provide information on the product of evolution, while fossils are necessary to provide information on the process. In the former case (extant species) we can rely on more comprehensive biological analyses, but results concern the final result of the process, not the process itself. In the latter case (extinct species) we can investigate directly the process, but samples are generally not representative neither at biological nor at statistical level.* [22]

and speciation, the process (or more probably, assortment of processes) by which new species come about, is poorly understood [23]. Fossils are necessary to provide information on the process, but samples are often not representative neither at biological nor at statistical level [24]. However, the inadequacy of the biological species concept has been well recognized for palaeontology. Perhaps the primary reason for this is that there has been no universal consensus on the traits that make us human. At present, the growing acquisition of genomic, phenotypic and behavioral data which shorten the distances between the two so far defined as different species [25], seem consistent with the possibility that *H. Neanderthalensis* and *H. sapiens*, and likely Denisovans [26][13] (see also [27]), are not different species but types of the same species, and that H. sapiens did not overpower *H. Neanderthalensis* and Denisovans to the point of extinction, as some scholars have suggested, but that one type of the three, namely *H. sapiens*, may have simply absorbed the others.

2. THE HUMAN SELF-DOMESTICATION HYPOTHESIS

(…) *symbiogenesis is more broadly applicable than just for*
the endosymbiotic origin of eukaryotes and photosynthetic eukaryotes,
and may be a useful concept to acknowledge the important role
of symbiosis for evolutionary innovation.
Duur K. Aanen

The challenge of studying human cognitive evolution is identifying unique features of our mental skills while explaining the processes by which they arose, yet our neurobiology and genome are remarkably similar to other primates. Adding to this challenge are discoveries suggesting that at least 10 different species evolved within the genus Homo. Modern theories of human cognitive evolution must now contend with growing evidence that early *Homo sapiens* is just one among many human species that evolved. With all of the evidence for interbreeding[5], it is most likely that the hominin phylogeny represents expansive networks instead of the traditional phylogenetic trees and bushes [28].

The *self-domestication hypothesis* (HSD) [29] aims at explaining, at least partially, what allowed our species to outlast as many as five other large-brained human species that shared the planet with us, some perhaps until as recently as 27 tya [30][31]. As a by-product of this HSD, humans are predicted to show traits of the *domestication syndrome* (DS) observed in other domestic animals. At least in recent specimens, domestication impacts on the body, cognition, and behavior of animals, with relevant changes becoming ultimately fixed and transmitted to the offspring. Somatic epigenetic differences, whether shaped by the environment or intentionally or unintentionally selected (pro-domestication pressure), can in turn affect phenotypic traits (*domestication phenotype* [29]). But when pro-domestication pressure persist, epigenetic changes can be assimilated as genetic variants [32][33]. Shifts in development, especially early in pre-natal development, can alter emotional reactivity and are thought to create a cascade of unselected consequences throughout the phenotype [34][35][36].

In vertebrate species, DS phenotypic changes include smaller skulls/brains, reduced teeth and snouts, neotenic features (the preservation, in adults of a given species, of physiological and morphological characteristics typical of the fetal period), altered hairiness and pigmentation, reduced sexual dimorphism, along with physiological and behavioural changes such as earlier sexual maturation, reduced reactive aggression, increased sociability, playfulness, social tolerance as well as enhanced sensibility to social and emotional cues.

Human newborns are considered *altricial* compared with other primates because they are relatively underdeveloped at birth. However, in a broader comparative context, other mammals are more altricial than humans. Humans begin life relatively helpless, with limited motor control, poor visual acuity, and the inability to effectively thermoregulate or feed themselves. We cannot sit up until 6 months, or take our first steps for a year. In contrast to animals such as horses or gazelles, which can run from their first day of life, humans are motorically incompetent. This makes infants entirely reliant on the care and protection of adults. Children are weaned and no longer dependent on their mother for food by about 3 years of age, but unlike other mammalian species, including other primates, they continue to depend on adults for care and provisioning for several years after weaning [37]. However, despite infants' immaturity in many physical domains, in the social sphere they early show a number of unlearned and ready-to-use skills. Among these *i)* the innate ability of social imitation (12-day-old babies are able to imitate the facial expression of adults, in particular the protrusion of the tongue), *ii)* early recognition of conspecifics and those who take care of them (a way in which the organization of the child's attention helps social development), and *iii)* being attuned, already in the fetal period, to sounds/language experienced as assonant, matching their needs and making them feel comfortable, preferring to listen to them at birth rather than equally complex sounds experienced as dissonant, out-of-tune, unfamiliar.

Yet these early relational modules are also shown to some extent by other vertebrates, so what makes their behavioural and social outcome so different?

[5] Hybridization is referred to a process through which there is interbreeding between species of two genetically distinct populations or species.

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In the case of humans (at least in anatomically modern humans from about 50 tya, when hominin fossils reveal a distinctive trend towards physiological gracility, compared to pre-domestication status of robust ancestral members of the genus Homo) DS phenotypic changes include loss of prognathism, a significant reduction in skeletal robusticity, especially in the cranium, smaller body size, more delicate skin, smaller mastoid features, flattened and broadened face, significantly reduced or absent tori, relatively large eyes, smallish nose, small teeth, more forward tilt of head, more backward tilt of the pelvis, limbs that are proportionally short relative to the torso, narrower joints, smoother ligament attachments, less hair but retention of fetal hair, along with physiological and behavioural changes (at least in anatomically modern humans from about ?? tya) such as a prolonged development period, faster heartbeat, lower amount of energy expended at rest, increased longevity, higher pitch of voice, loss of estrus in the female and the introduction of menopause, togheter with numerous deleterious genetic predispositions and defects, brain pathologies (brain illness etiologies suggest that they involve mostly the same areas of the brain that are the phylogenetically latest) and brain atrophy [31].
As proposed by [38] less reactive temperament in early Homo sapiens (from about 250 tya?) may have gradually replaced emotional reactivity, a process that likely intensified as our species populated its niche, with an attraction to in-group prosociality (i.e., positive but potentially selfishly motivated acts as opposed to antisocial interactions [39]) as genetic and epigenetic mechanisms [40] acted on developmental pathways. The reduced emotional reactivity that results from HSD together with increased self-control created a unique form of human tolerance allowing the expression of more flexible social skills observed in anatomically modern humans. Expanded developmental windows like those seen in domesticated animals allow this unique form of human tolerance and social cognition to develop and left anatomically modern Homo sapiens as the last human standing.
However, when applied broadly, the current correlation between domestication and *domos* and *domicile*, along with the implication that the human species is typically the domesticator, takes on an anthropocentric (exclusive) meaning. Yet hundreds of other animal species, ranging from mammals to insects, have domesticated other animal, plant, or fungi species. Coupled with the tradition of differentiating human cultures on the basis of the extent to which they were "domesticated," much literature on the subject promoted views of social hierarchies in civility, which were later used as a pseudo-scientific rationale for racist and eugenic political movements. This stain on the intellectual history of human domestication theories illustrates the complex social meanings of the concept, and its consequent ambiguity when used in explaining human evolutionary processes [41]. We take the view that domesticated species are best categorized in terms of the phenotypic traits that they broadly share, rather than in terms of human mastery, design, or orchestration. There are inherent weaknesses in the human-mastery or conditions-based views of domestication that an account based on phenotypic traits does not face. The commonly shared traits of domesticates provide the strongest and most objective means by which these animals can be considered a single category. Furthermore, there is now evidence that many of the phenotypic traits of domesticates emerge independently of any human predispositions, intentional or otherwise. A broad consensus is now emerging that "commensal" and "mutualistic" processes, together with emotional control that is observed in highly social mammals [38], can lead to domestication, whereby both the domesticator and domesticated species seek out and benefit from cohabitation [42]. This is why domestication should indicate a complex process of coevolution that is established between individuals of the same or different species, which in many cases involves symbiosis or mutualism, with or without human mastery, design, or orchestration.
In mammals, all the traits of the DS are initiated by events taking place during embryonic and fetal development. Two possible hypothesis that links genes and development have been formulated, the "*thyroid hormone hypothesis*" (THH) and "*the neural crest hypothesis*" or NCH [43]. The first focuses on thyroid hormones and the possibility of timing shifts in development (so called "heterochronic" changes) due to altered concentrations of these hormones in early development. The second suggests that the domestication syndrome is a result of changes in the migration pattern of melanocytes during neural crest formation, which simultaneously affects neurohormone levels, pigmentation, and morphology early in development [43], although not in a universal pattern across domestic mammals [29]. Recently, the role exerted by trans-regulatory molecules, notably transcription factors (TFs), in DS has also been proposed [40]. Moreover, DNA methylation, i.e. the addition of a methyl group to cytosine in CpG dinucleotides, has the potential to affect gene expression. Although DNA methylation patterns are generally maintained after cell division, they can sometimes be modified by the action of external stimuli [44][45]. Environmentally-altered DNA methylation patterns can be transmitted through the germ line and be stable in somatic tissues over generations [46].

3. FROM A *RELATION OF CONTINUITY* TO A *RELATION OF CONTIGUITY*

Most archaic and early species of the genus Homo,
after all, are still associated with long periods of stasis,
namely, a remarkable lack of changes when considered in a proper
geographical and chronological range. In sum, the taphonomic bias
may influence our perception of an extinct culture,
but it is nonetheless highly improbable that H. erectus or H. heidelbergensis
were using pen drives or riding bicycles.

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Emiliano Bruner

Humans are the only animals phylogenetically endowed with the possibility to overcome the boundaries of **behavioural stereotypy**, to which all others animals are strictly tight, in a non-occasional, stable, functional and lasting way. A possibility that can only be realized when humans start perceiving themselves as **something else from their environment** (from a *relation of continuity* to a *relation of contiguity*), a splitting condition out of which the human being become a **subject** reflected by the mirror of oneself mind (*psychological birth*) [47][48][49]. *Conscious awareness*[6] and therefore *consciousness* will be a measure of the ongoing psychic disposition given by the *process of individualization* to which our splitting condition has been subjected since then. Consciousness reveals that being can be other to itself, i.e. the existence of consciousness implies that being is in some respect other to itself. Consciousness is always directed towards an object (which can include the conscious minded), and in order for the separation of subject and object to exist in the first place, there must be some form of division in being. There could not be a distancing of being from being, as implicit in consciousness, if being itself did not have a property or mode that allowed for such distancing. With the established psychic nucleation of the relatively autonomous and independent neuropsychological complex called *epigenetic function of the real* or *state of consciousness*, the world ceases to be just lived to be also interpreted (anthropopoiesis). Psychologically, the ability to interpret the world means having to get out of a relationship of continuity with the inner-insight (embodied) and with the outer-outsight (embedded) [51][52] to project oneself out in a *somewhere else*, in a time and space measurement made by the interpretation of the world and of oneself. In making an *I-Me* distinct from an *Other than I/Me* the world is split into a subject *I-Me* observing, and an object *Other-than-I* observed, in a thesis and antithesis.

The *subject-object dichotomy* is the primal source of the antinomies, or pairs of opposites that refer to a polar relation (psychological tension) between a thesis (what I can sense) and an antithesis (what I cannot sense). Since humans began to think and feel the world in terms of subject and object, distinguishing themselves from Nature and ceasing to identify with it, the human communities also developed the ability to *make culture*.

The anthropopoiesis animated by the process of distancing induced by consciousness generates *culture*. Anthropopoiesis, and therefore cultural production, plays a (epigenetic) decisive role in order to *i)* favor complex processes of coevolution between individuals of the same or different (domesticated) species, which in many cases involves symbiosis or mutualism, in order to favor increased in-group prosociality over emotional reactivity, ii) trigger epigenetic mechanisms in the rapid phenotypic changes (that can be assimilated as genetic variants), also observed as outcome of domestication [53][54][55], along with neuroanatomical, neurophysiological and neurocognitive changes specific to anatomically modern humans, iii) favor the activation of the capacity for complex iterative learning, necessary for cultural transmission, with or without oral language [56].

That is, consciousness and culture go together. Indeed, the essential requirement for making *culture* is given by *recognize oneself as individuality distinct from the environment*, a *psychological birth* that has come to maturity only during the Middle Paleolithic [47], after a long *psycho-relational* and *psycho-biological process of individualization-nucleation* (began well over a million years ago with Homo erectus?) dedicated to satisfying the needs linked to the survival and care of offspring.

By virtue of its phylogenetic value, its intrinsic link with the survival of the species, the caring for offspring comes to play a key role in nascent cultural production. The distancing process induced by consciousness triggers a dialogic relationship between psychological birth and pregnancy. Building a dialogic relationship is equivalent to building a system in which the interacting subjects can recognize and reconstruct the way in which they both recognize and reconstruct their own world, their own affections, their own emotions, their own sense of reality. The human *inner life* must establish a dialogic relationship with the *outer world*, but for this to be possible, a shared communicative code is necessary. There is no other solution than to anthropomorphize the *outer world* by providing it with emotions, symbols, meanings generated by the *inner life*. This is why over time, millennium after millennium, the *outer world* continues to be re-born in a dialogic relation, in the image and likeness of the *inner life*'s world. The anthropopoiesis generated in the womb of this relationship becomes the epigenetic condition indispensable for the survival of the species, its only lifeline from extinction, which sooner or later will have to (imperative) give voice to the *inner life*'s world and the *outer world* also through the articulation of **oral language**.

It is likely that not all species of the genus Homo have managed to coexist beyond a certain limit (temporal, cultural, psychological?) with this tragic turning point, i.e. from a relation of continuity to a relation of contiguity, and with being split into an "object" (zoomorphic) that remains "nature" and a "subject" (anthropomorphic) forced to imagine an *identity* that allows it to be in the world not only as *nature* but also as *culture*. A tragic turning point, because the identity variable inherent in "making culture" is implacable. In fact, the identity assumed by *homo-making-culture* can prove suitable for its survival even for tens of thousands of years, but sooner or later it will have to deal with natural or cultural events, such as contact with other homo-making-culture with other identities and other ways of making culture, which will lead it to a point of crisis, to an existential crossroads where: either it is subjected to a process of re-elaboration that allows homo-making-culture to be *re-born*, to *re-cognize* itself reflected in the mirror

[6] Namely: "*(...) an enduring entity (i.e. the feeling that we are the same person across time) to which certain mental events and actions are ascribed (i.e. the feeling that we are the authors of our thoughts and actions) and which is distinct from the environment*" [50]

of its own mind, or homo-making-culture and its identity are destined to disappear. Perhaps *Homo sapiens* is the only species that, unlike *H. Neanderthalensis* and the *Denisovans* (who disappeared between 45 to 25 tya [57]), managed to heal the trauma (unnatural or too human) of *psychological birth* and to be re-born to itself, also or above all by resorting to the medicine of *musically depicting narrative* [58][59], which in the womb of culture-making has become **verbal communication**. In hindsight, we can say that equipping the mirror of the mind of homo-making-culture with "**logos**" has proven to be a successful adaptive strategy.

CONCLUSIONS

The recent evolution of anatomically modern humans, especially after the split with Neanderthals, can be interpreted as the outcome of a long-wave cascade of phenotypic, behavioral and social consequences triggered by the *psychological birth* of our distant ancestors and by the sedimentation of *consciousness*, along with a growing cultural production driven by language, musicking and other cultural strategies, rather than by self-domestication against emotional reactivity [60]. Anatomically modern humans' phenotypic, social and behavioral traits, also found in domesticated animals, should be considered as the result of a long-lasting and ongoing process of *gene(tic)-epigene(tic)-culture co-evolution*.

STATEMENT

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