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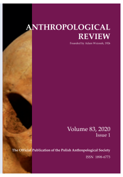

What have the revelations about Neanderthal DNA revealed about *Homo sapiens*?

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Abstract: Genetic studies have presented increasing indications about the complexity of the interactions between *Homo sapiens*, Neanderthals and Denisovans, during Pleistocene. The results indicate potential replacement or admixture of the groups of hominins that lived in the same region at different times. Recently, the time of separation among these hominins in relation to the Last Common Ancestor – LCA has been reasonably well established. Events of mixing with emphasis on the Neanderthal gene flow into *H. sapiens* outside Africa, Denisovans into *H. sapiens* ancestors in Oceania and continental Asia, Neanderthals into Denisovans, as well as the origin of some phenotypic features in specific populations such as the color of the skin, eyes, hair and predisposition to develop certain kinds of diseases have also been found. The current information supports the existence of both replacement and interbreeding events, and indicates the need to revise the two main explanatory models, the Multiregional and the Out-of-Africa hypotheses, about the origin and evolution of *H. sapiens* and its co-relatives. There is definitely no longer the possibility of justifying only one model over the other. This paper aims to provide a brief review and update on the debate around this issue, considering the advances brought about by the recent genetic as well as morphological traits analyses.

Key words: Human evolution, admixture, genetics, morphology, *Homo sapiens*

The growing discoveries about Neanderthal and Denisovan DNA have been raising striking new information concerning both groups of hominins (Kuhlwilm et al. 2016; Sankararaman et al. 2016; Vernot et al. 2016; Roger et al. 2017). According to Rogers (2017a, b) and Fernando and Joshua (2019), the descriptions of the diverse forms of interactions that existed, have increasingly allowed the understanding that the human history is much more complex than what would have been supported by just one, or another particular model currently not recognized. However, it might bring the need for revision and acceptance of assumptions of models, as the Multiregional Evolution, that was previously refuted (Manderscheid and Rogers 1996; Larh and Foley 1998; Stringer 2002; 2012; 2014; 2016; Weaver 2012).

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One of the new data that brings such discussion is related to one femur from Germany's Hohlenstein-Stadel Cave and a jawbone from Belgium's Scladina Cave, both dated to 120 ka (Peyrégne et al. 2019). They have added more information about the population history in Neanderthals during the Middle and Late Pleistocene. Overall, the results of the genetic data indicate similarity of the mtDNA (maternal information) of a Neanderthal girl, dated 90 ka, found in an Altai cave, in Siberia, to the 120 ka DNA of some Western Europe individuals.

This finding emphasizes how the process of interbreeding and, potentially, replacement, might have been recurrent among several populations of hominins, mainly those within the genus *Homo* (Paul et al., 2019). Eventually, such information may come in line to give support to the explanation of our own emergence and expansion of the model called "Out of Africa", but not only this model.

This is only one of several examples of interactions between Neanderthals and *Homo sapiens* (Kuhlwilm et al. 2016; Sankararaman et al. 2016; Vernot et al. 2016; Roger et al. 2017; Dannemann and Kelso 2017) which put into question the two main current models oriented to explain the emergency and evolution of *Homo sapiens*: the Out of Africa and the Multiregional model. A brief revision and update on the debate around this issue, considering the advances brought about by the recent genetic as well as morphological traits analyses is the goal of this paper.

The emergence and evolution of *Homo sapiens* under two different views

The explanatory models that deal with the origin of *H. sapiens*, as well as the evolution of the genus *Homo*, changed from the 1980s onward (Manzi, 2011). Briefly, there has been a gradual substitution of ideas that considered the unilinear evolution of several groups of hominins living spatially separated, but converging to a single pattern, for ideas focused on a single origin of *H. sapiens*, with their subsequent divergence (Schwartz and Tattersall, 2010). However, this change occurred slowly, both due to the theoretical clashes marked by divergent theoretical tendencies and the paleoanthropological data which appeared in increasing but slow rhythm (Caspari and Wolpoff, 2013; Trinkaus, 2013).

In the mid-twentieth century, the paradigm shared among many scholars was based on the existence of a single human species, which would have evolved gradually and sequentially throughout Pleistocene, but concomitantly in different places: the so-called "Polycentric Evolution Theory" by Franz Weidenreich (1947). It is a model by which the regional sequences were reasoned as an interconnected web evolving in a single common direction. Thus, it would be considered a unilinear concept oriented towards convergence, as previously suggested by Aleš Hrdlička (1927).

Although Weidenreich's theory (1947) was based on assumptions supported by other scientific models, the explanation of orthogenesis as the determining factor, as outlined by polycentric evolution, was rejected by the Modern Synthesis (Huxley 1942), and finally by Coon's model (Coon 1962), which admitted parallel evolution occurring strongly isolated in various regions of the world. This would have several consequences for the ideas concerning the formation of distinct biologic groups created at that time, as well as its refutation. One of those is the hypothesis for the evolution of the Presapiens, in particular deriving from the discussions related to the Fontéchevade cranial remains, linked to the Swanscombe and Steinheim specimens (Vallois 1954). In this case, and according to Howell (1952), Neanderthals and modern humans would have separated only during the Eemian Interglacial period. After this event, the Preneanderthals of Southwest Asia would have evolved into modern humans, while the Preneanderthals of Europe would have become the robust classic Neanderthals. However, this concept was not supported by subsequent research (Bräuer 2008), in special those that revealed affinities of Presapiens with Neanderthals and Preneanderthals (Hublin 1985; Hublin and Tillier 1981, 1992; Trinkaus 1981; 1983). In addition, discoveries of some hominids, such as the partial skulls of Arago and Biache St. Vaast, demonstrated only one lineage in Europe that led to the Neanderthals (Bräuer 1984a, b). No diachronic tendency of reduction in size could be observed in the Neanderthals of the Near East, and the subsequent review of dating revealed that early modern humans and Neanderthals were almost contemporaneous in this region (Trinkaus 1986; 1992; Hublin 1992).

During the 1960s and 1970s, only a few researchers insisted on the idea of local continuity between modern and ancient populations, and by the late 1970s the question of the origin of modern humans was once again widely open. Some researchers, such as Milford Wolpoff (1980a, b), continued to emphasize evolutionary continuity in Europe and elsewhere, while others, such as Howells (1976), assumed a recent common origin of modern humans.

In the early 1980s a new period of discussions about Modern Human origins emerged, focusing mainly on two alternative models, the Multiregional Evolution and the Out-of-Africa. Wolpoff et al. (1980a, b; 1984) proposed the Multiregional Evolution model, which was largely based on Weidenreich's theory of polycentric evolution (1947). According to this perspective, the present human diversity would have been the result of small and constant changes between the populations and within the species as a whole, occurring from the original geographic diffusion of the genus *Homo* (Wolpoff, 1970; Thorne and Wolpoff 1981; 1992; Wolpoff et al. 1984; 1994). This model suggests that there would have been successive stages and / or regional variants within a generalized archaic species – *Homo erectus* and later within *H. sapiens* (Wolpoff 1980b). The result was a progression of regional changes that, with the persistence of a single polymorphic humanity in each geological time period, was evolving into variants of the modern species (Thorne and Wolpoff 1981; Wolpoff 1980a). As a consequence, the *H. sapiens* taxon would include the existing humanity, but also extinct morphotypes such as Neanderthals in Europe and the Near East, as well as several archaic humans in Africa and East Asia during the Middle Pleistocene, known as "archaic *H. sapiens*" (Wolpoff 1986), later called *H. heidelbergensis* (Schwartz and Tattersall 2010). Thus, under the same specific name, *H. sapiens*, each of these morphotypes was assigned to a different subspecies, with the adoption of a trinomial nomenclature – *H. sapiens neanderthalensis* and *H. sapiens sapiens* (Trinkaus 1983, such as supported by the hypothesis of *Homo sapiens sensu lato* (Wolpoff et al. 1994).

This hypothesis was based on the observation of a certain degree of "regional continuity" present in the morphologies of archaic and modern populations within each geographical area, as suggested by Frayer and colleagues (1993). This observation, however, was gradually challenged (Lahr 1994; Larry and Foley 1998; Waddle 1994; Weaver 2012; Stringer 2012; 2014; 2016), mainly because such model would not agree with much of the genetic data that suggested a "Single Origin" for all modern humans (Klein, 1995; Larh, 1994, 1996; Lahr and Foley, 1998; Stewart and Stringer, 2012; Relethford, 2001; Underhill et al. 2001; Serre and Pääbo, 2004). This last approach recognizes the geographical branching of the *Homo* lineage during the Pleistocene and the existence of regional forms, but, differently, sustains the continuity up to the present of only one of these branches, the one originated in Africa which would be the unique source of all current diversity (Stringer and Andrews 1988; Stringer 2006; 2012). Thus, this view, driven by more ecological rather than behavioral or cultural motifs, associates the earlier *Homo* groups to the diffusion and adaptation to the diversity of environments, many of which not tropical (Manzi 2011). In this case, *H. erectus* can be seen only as a species from the Far East (Java and China), while its African counterparts are considered as a distinct species, *H. ergaster* (Wood 1991). At the same time, other groups were named as distinct species, or had the old name reconsidered, such as *H. rudolfensis* (Wood 1991), *H. heidelbergensis* (Rightmire 1996), *H. antecessor* (Bermudez de Castro et al. 1997) *H. rhodesiensis* (Hublin 2001), *H. georgicus* (Gabounia et al. 2002).

According to Manzi (2011), although the identification of all these different species clearly implies an overestimation of interspecific diversity, this gives a clearer and more intelligible meaning to the human varieties that were formerly concealed, being also referred to *H. erectus* (sensu lato) or to the entity called " archaic *H. sapiens*".

Bräuer (1982) was the first to propose the Out-of-Africa model, initially called "Afro-European sapiens" hypothesis, since Europe provides the best evidence for replacement. This model suggested an origin of modern humans only in Africa followed by their dispersion into Asia and Europe, finally replacing the archaic populations. In this case it is important to stress that "Replacement" would be assumed in the place of "Interbreeding", supported by the Multiregional model (Bräuer 1984; 1992; 2008).

The paleoanthropological data provide information able to point to at least two distinct waves of immigration into Europe occurring sequentially, one during the Early Pleistocene, and the other at the beginning of the Middle Pleistocene (Manzi, 2011). The first wave is documented only in Spain and is related to a fossil dated to 1.2 Ma found in the TE9 stratigraphic layer of the "Sierra del Elefante" (de Castro et al. 2011), and jaw fragments found in the TD6 layer of the "Gran Dolina", dated in more than 780 Ka (de Castro et al. 1997; Carbonell et al. 2008). Initially the traces found in Gran Dolina were referred to as *Homo antecessor* (de Castro et al. 1997). However, the advancement of research and discovery of TE9 led the group of researchers to suggest that there had been more than one speciation event, which then led them to rename the TE9 specimen as *Homo sp* (de Castro et al., 2011) so as not to consider a necessary link of such specimen to *H. antecessor*.

Homo antecessor and *H. heidelbergensis* would have competed against each other for the same phylogenetic position in the current evolutionary trees of the genus *Homo*, seen as provisional alternative models of human evolution (Manzi 2011). The *H. antecessor* is considered by the Spanish researchers (de Castro et al. 1997) as the species ancestral to the evolutionary divergence that would lead to the evolution of Neanderthals in Europe and the emergence of *H. sapiens* in Africa. Alternatively, *H. heidelbergensis* was claimed for this same role by other authors (Rightmire 1996). In this context, the "Sima de los Huesos" material is clearly connected to the Neanderthals and is characterized by a number of features that later on in the Pleistocene will become typical of this group (Dean et al. 1998). Thus, the *H. heidelbergensis* would acquire a regional European identity in continuity with *H. neanderthalensis*, but differently would evolve in a specific African lineage that would lead to *H. sapiens* (Manzi 2011).

The identification of such features is fundamental to construct a meaning for *H. sapiens* regardless of the model used to support its origin and evolution, because our species exists primordially due the differences recognized in relation to the *H. neanderthalensis* (Schwartz and Tattersall 2010; Caspari and Wolpoff 2013). In this case, although virtually all classical osteometric measurements show some degree of overlap between the two groups, the overall evaluation of shape by geometric morphometry demonstrates a clear separation between the craniofacial anatomy of the two species (Harvati 2007; Lieberman 2011; Harvati et al. 2004;). The Neanderthals also show remarkable differences in the post-cranium as well as development standards and obstetric features (Pearson 2000; Ponce de León and Zollikofer, 2001; Harvati 2007; Weaver and Hublin 2009) which support a separation from *H. sapiens* (Tattersall and Schwartz 2000; 2006; Schwartz and Tattersall 2002; 2005).

For Rightmire (1998, 2008), which advocates the "single species" model, there are problems in the definition of an African Middle Pleistocene species that is separated from existing European or East Asian lineages, and would have lived in the same time interval. In addition, according to him, and Smith et al. (2010), morphological diversity does not necessarily indicate multiple species in the Middle Pleistocene. However, it is also be possible to demonstrate the existence of other relatively small specificities in each of the groups. These specificities became more evident since 400 Ka, with the formation of regional morphological differences finally established in 100 Ka, with *H. neanderthalensis* in Europe and Central Asia, modern humans in Africa, *H. erectus* in Asia and *H. florensiensis*, in Australasia (Smith 2010).

In general, the chronology, topology, and phylogenetic dynamics related to the large geographic dispersion of the archaic human beings ancestors of the origin of both Neanderthals and modern humans is still unclear (Rightmire 2008; Hublin 2009; Stringer 2012). Tattersall (1986), for example, suggested from a macroevolutionary perspective based on "punctuated equilibrium", that the observed morphological variation within this group could represent multiple species. In other words, it would lead to cladogenesis. However, for Smith (2010), the observed differences do not mean, even with significant morphological distinctions, that two populations may become different species, unless a reproductive barrier is established between them.

Considering just models oriented to explain the origin of *H. sapiens*, and in accordance with Smith and Ahern (2013), the "Out-of-Africa" was an influential model during the 1980s because genetic information obtained by methods used at the time supported the morphological evidence consistent with a single demographic scenario. Some of the first and main works towards this approach were presented by Cann, Stoneking and Wilson (1987); Delson (1988), and Stringer and Andrews (1988). In these works, information from mtDNA was used to support a common ancestor originated in Africa, around 200.000 Ka. Although these findings were reinforced by other studies (Vigilant et al. 1991; Stoneking et al. 1992; Nei and Roychoudhury 1993), the data accumulated after a series of genetic investigations along the last decades do not indicate the occurrence of only replacement or interbreeding, but both, often at the same time.

Discussion

In the last decade, the improvement of techniques for extracting genetic material has provided information about the separation as well as interactions of several groups of the genus *Homo* who coexisted during the Middle and Late Pleistocene (Green et al. 2010; Prüfer et at., 2014; Meyer et al., 2014; Kuhlwilm et al., 2016; Harris and Nielsen, 2016; Vernot, B. et al. 2016; Fernando, A. and Joshua, G. 2019). In one of these studies, the analysis of isolated sequences of mitochondrial (mt) DNA from a hominin femur recovered from excavations occurred between 1994 and 1999, in Atapuerca, Spain, revealed a similarity to mtDNA from another specimen from the Denisova Cave, located in Altai, in Southeast Siberia, which is approximately 4,000 km from Spain (Meyer et al. 2014).

The Denisovans, as they are called, are an extinct archaic group of hominins, previously unknown, related to both Neanderthals and modern humans (Prüfer et al. 2014). Through the bone remains recovered from the Denisova Cave a genomic sequence was determined (Meyer et al. 2014). The complete sample consists of two upper molars identified as Denisovans – D4 and D8, one deciduous tooth – D2 and a finger phalanx –D3, three bones of Neanderthal – D9, D5, D15, one fragment of bone belonged to hominin hybrid (Neanderthal – Denisovan) – D11, and other three human fragments of bones, not able to be fixed in any specific group (*Homo* sp.) – D14, D6 and D16 (Douka et al. 2019).

The Denisovans teeth were estimated to be chronologically located between 194,4 ka and 51,6 ka, the Neanderthal bones were estimated between 147,3 ka and 90,9 ka, and the bone with mixed genome – D11, was found to be between 118,1 to 79,3 ka.

Genetic information indicates that there was a separation between Neanderthal and Denisovan populations from the future modern humans, between 550 and 765 Ka. However, analysis of the Denisovan genome suggests that Neanderthals and Denisovans diverged between 381 and 473 Ka, while Neanderthals diverged from modern humans for at least 430 Ka (Prüfer et al. 2014).

The evidence for mtDNA indicates Denisovans different from both *H. neanderthalensis* and *H. sapiens*, but that shared a common ancestor around 1.0 Ma (Kuhlwilm et al. 2016). The origin of these three clades corresponds to the morphological discontinuity that occurs in the fossil record before the appearance of *H. heidelbergensis*. Thirteen mtDNA sequences as well as three other consensual sequences referring to the fossil of Sima de los Huesos could also provide estimation for age and time of divergence of the Denisovans. The dates for the Sima de los Huesos fossils range from 150 to 640 Ka, with one-point estimates of about 400 Ka, while the time of divergence between these hominins and that of Denisova ranges from 400 to 1.060 Ka, with estimates in about 700 Ka (Meyer et al. 2014; Prüfer et al. 2014).

Despite the separation of the two groups, there was also the opposite effect, that is, a mixture between archaic and modern human populations, which mainly resulted in specific Neanderthal DNA loci inclusions into *H. sapiens* (Sankararaman et al. 2014; Vernot and Akey 2014; Racimo et al. 2015; Fu et al. 2016; Harris and Nielsen 2016; Gittelman et al. 2016; Simonti et al. 2016; Dannemann and Kelso 2017; Dannemann et al. 2017). One of the first studies in this direction pointed out that Neanderthals shared more genetic variants with present-day humans in Eurasia than with present-day humans in sub-Saharan Africa, indicating that the separation occurred before the divergence of Eurasian groups from each other (Green et al. 2010). Further information is also progressively being revealed, such as the Neanderthal gene flow into modern humans outside Africa, Denisovan gene flow into Modern Human ancestors in Oceania and continental Asia (Meyer et al. 2012; Sankararaman et al. 2016, Vernot et al., 2016), Neanderthal gene flow into Denisovans (Rogers et al. 2017), and possibly the gene flow of an unknown archaic group that diverged from other strains more than one million years ago into Denisovans (Sankararaman et al. 2014; Mondal et al. 2019).

In one of the analyzes, for example, the Altai genomes for a Neanderthal and a Denisovan specimen were compared with the sequences of chromosome 21 of a Neanderthal from Spain and another from Croatia (Kuhlwilm et al. 2016). The results indicated that an early divergent population of modern humans in Africa also contributed genetically to the Neanderthal ancestors, about 100 Ka. However, the Neanderthal group in question was located in the mountains of Altai. In contrast, this genetic contribution was not detected, either in Denisovan or in the two European Neanderthals. Thus, it was concluded that the ancestors of the Neanderthals of the Altai Mountains and modern humans met and crossed, possibly in the Near East, many thousands of years earlier than reported in other surveys (Sankararaman et al. 2012).

The case of "Lapedo Boy", found in the Lagar Velho Shelter, Portugal (Zilhão and Trinkaus, 2002; Almeida et al. 2007; Zilhão et al. 2007) as well as the Oase 1 and 2 found in Peştera cu Oase, Romania (Crevecoeur et al. 2009), contrast the ideas used to support an absolute division between *H. sapiens* and *H. neanderthalensis* (Schwartz and Tattersall 2010).

At first, based only on comparative morphology and anatomical evolution studies the two cases were admitted as examples of hybridity between the two groups (Rougler et al. 2007; Zilhão et al. 2007). However, subsequent analyzes based on genetic material extracted from the Oase skeleton finally confirmed hybridization, with 6 to 9% of Neanderthal genomic material, and more importantly, this information corroborated the hypothesis based on the morphological analysis (Rougier et al. 2007; Zilhão et al. 2007; Fu et al. 2015). Nevertheless, for some researchers such cases indicate the rarity with which the interactions with offspring between the two groups must have occurred, since only about 4% of Neanderthal DNA has been identified in modern Europeans DNA (Meyer et al., 2014; Prüfer et al., 2014; Kuhlwilm et al., 2016).

In general, there are examples in which the importance of the "Out of Africa" hypothesis is assigned in order to understand the emergence and evolution of *H. sapiens*, as what is the case introduced in this paper, which broach and event of replacement (Wei-Haas 2019). Nevertheless, most of the research in human paleogenetic developed since the beginning of the 21st century reiterate the importance of interbreeding and hybridization (Green et al. 2010; Meyer et al. 2014; Prüfer et at. 2014; Sankararaman et al. 2014; Vernot and Akey 2014; Racimo et al. 2015; Fu et al. 2016; Gittelman et al. 2016; Harris and Nielsen 2016; Kuhlwilm et al. 2016; Simonti et al. 2016; Vernot et al. 2016; Dannemann and Kelso 2017; Dannemann et al. 2017; Fernando and Joshua 2019). These findings bring back the importance of the Multiregional Model as another potential explanation for the origin of *H. sapiens*.

The bases of the Multiregional Model were widely criticized (Manderscheid and Rogers 1996; Larh and Foley 1998; Weaver 2012; Stringer 2012; 2014), mainly due to discontinuity in the fossil record outside Africa, and also as related to the incompatibilities in the gene flow needed to explain the evolution of Modern Man proposed by such a model. In this case, there was resistance to the ideas used for indicating the existence of morphological traits as evidence of archaic and modern continuity in China and Australia (Groves, 1989; Habgood, 1989; 1992; Larh and Foley, 1994; Lahr, 1994, 1996; Lieberman, 1995; Stock and Lahr, 2007; Li et al., 2017). The other criticism, based on the fossil record indicated that the *Homo* genus in the Pleistocene would have different and not convergent evolutionary trajectories in the various regions of the planet (Stringer 2002). That is, would be consistent with a regional differentiation rather than a single modernization trajectory.

Now, the new data coming from genetic material point out that in fact there were many moments of interbreeding between different hominin groups, existing since the Middle Pleistocene. It allows reconsidering the Multiregional Model, even though works dealing with the morphological character show substantial differences between Neanderthals and ourselves (Harvati 2003; 2015; Harvati et al., 2004; Schwartz and Tattersall 2002; 2005; Tattersall and Schwartz 2000; 2006; Tattersall 2007). Such differences may not have been a great obstacle for the genetic exchange between the several co-contemporaneous groups and, consequently, hybridization, even considering the low incidence of this occurrence (Prüfer et at. 2014; Meyer et al. 2014; Kuhlwilm et al. 2016).

In the case of the Neanderthals and *H. sapiens*, once they met, there may have been cases of violence, xenophobia, as well as ontogenetic, morphological and behavioral differences that might have affected the recognition of sexual partners and the behavioral systems related to mating and, consequently, to the reproduction, as reported in chimpanzees and bonobos (Overmann and Coolidge 2013). However, the genetic data show that this was not always the case.

According to Groves (2007), reproductive isolation may or may not be the result of speciation. And, species that hybridize are not necessarily close relatives of one another. This would be in agreement with several cases of hybridization between distinct species, such as caudate amphibians – *Triturus cristatus* and *Triturus marmoratus* – characteristic of flat and open meadow regions of Europe (Arntzen and Wallis 1991). In this case hybridization occurs, probably unidirectionally, since all the hybrids possess mtDNA of *T. cristatus*. However, there is evidence that some genes would have entered the "pure" species on both sides, with exchanges occurring at the time of hybridization (Arntzen and Wallis 1991). In primates there are also several cases of hybridization (Arnold and Meyer 2006), reported among New World Monkeys, as identified in *Saimiri* species (Carneiro et al. 2016; Mourthe et al. 2019) as well as in Old World Monkeys, as *Pan troglodytes* and *Pan paniscus* (Vervaecke and Elsacker 1992; de Manuel et al. 2016).

Whatever the forms of interaction that have impacted in the origin and diversity of current human populations, one must be cautious in the search for specific approaches that support circumstantially better explanations concerning those interactions to the exclusion of others. The human history gradually uncovered by genetic evidence has shown how complex must have been these interactions, and how the extreme models of explanations are unable to correctly describe the magnitude of the evolution of *H. sapiens* and its co-relatives. As assumed by Sjödin et al. (2012) it is now recognized that a phylogenetic origin of modern humans cannot be more supported by and African only origin. In addition, the events of interbreeding between Neanderthals and modern populations refutes models in which all living humans would recall their ancestry to a restricted and small African population that had completely replaced other archaic human species on their way out of the continent (d'Errico and Stringer 2011). There is increasing genetic evidence of cases of interbreeding between *H. sapiens*, Neanderthals and Denisovans, what is directly consistent with the Multiregional Model.

Perhaps it is time to elaborate a different explanation that encompasses the several events regarding the evolution of hominin groups since the Middle Pleistocene to the present. However, this does not mean that is necessary to create yet another Model. Maybe it is time to reconcile the ones already existing, to find a common explanation that support this so vast horizon of possibilities that is Humanity.

Authors' contributions

SG has developed the discussion presented and the main structure for the paper; HPS collaborated in terms of revision, correction and adaptation of sentences and ideas in order to clarify its comprehension.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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References

Almeida F, Alves N, Ponce De León M, Pierson B, Duarte C, Bártolo P, et al. 2007. The Lapedo Child Reborn: Contributions of CT Scanning and Rapid Prototyping for an Upper Paleolithic Infant Burial and Face Reconstruction. The Case of Lagar Velho Interpretation Centre, Leiria, Portugal. In: D Arnold, F Iccolucci and A Chalmers, editors. The 8th International Symposium in Virtual Reality, Archaeology and Cultural Heritage Vast. Short and Project Papers from VAST. 69–73.

Arnold M, Meyer A. 2006. Hybridization in primates: one evolutionary mechanism. Zool 109(4):261–76.

Arntzen J, Wallis G. 1991. Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. Evolution 45:805–26.

Bons P, Bauer C, Bocherens H, De Riese T, Drucker D, Francken M, et al. 2019. Out of Africa by spontaneous migration waves. PLoS ONE 14(4):1–25.

Bräuer G. 1982. Current problems and research on the origin of *Homo sapiens* in Africa. Humanbiol Budapest 9:69–78.

Bräuer G. 1984a. A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In: FH Smith, F Spencer, editors. The Origins of Modern Humans. A World Survey of the Fossil Evidence. Liss, New York. 327–410.

Bräuer G. 1984b. The “Afro-European *sapiens*-hypothesis” and hominid evolution in East Asia during the Late Middle and Upper Pleistocene. Cour Forsch Inst Senckenberg 69:145–65.

Bräuer G. 1992. Africa’s place in the evolution of *Homo sapiens*. In: G Brauer, FH Smith, editors. Continuity or Replacement: Controversies in Homo sapiens Evolution. Rotterdam, Balkema. 83–98.

Bräuer G. 2008. The origin of modern anatomy: by speciation or intraspecific evolution? Evol. Anthropol 17:22–37.

Cann R, Mark S, Allan W. 1987. Mitochondrial DNA and human evolution. Nature 325(6099):31–6.

Carbonell E, De Castro J, Parés J, Pérez-González A, Cuenca-Bescós G, Ollé A, et al. 2008. The first hominin of Europe. Nature 452(7186):465–69.

Carneiro J, Rodrigues-Filho L, Schneider H, Sampaio I. 2016. Molecular data highlight hybridization in squirrel monkeys (Saimiri, Cebidae). Genet Mol Biol 39(4):539–546.

Caspari R, Wolpoff M. 2013. The process of Modern Human Origins: the evolutionary and demographic changes giving rise to modern humans. FH. Smith, J Ahern, editors. The Origins of Modern – Biology Reconsidered – Chapter 11. New Jersey, John Wiley & Sons. 355–91.

Coon C. 1962. The Origin of Races. New York, Knopf.

Cortés-Ortiz L, Jr. T, Canales-Espinosa D, García-Orduña F, Rodríguez-Luna E, Bermingham E. 2007. Hybridization in large-bodied New World primates. Genetics 176: 2421–25.

Crevecoeur I, Rougier H, Grine F, Froment A. 2009. Modern Human cranial diversity in the Late Pleistocene of Africa and Eurasia: evidence from Nazlet Khater, Peştera cu Oase, and Hofmeyr. Am J Phys Anthropol 140:347–58.

D’errico F, Stringer C. 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures. Philos Trans Royal Soc B 366(1567):1060–69.

Dannemann M, Kelso J. 2017. The contribution of neanderthals to phenotypic variation in modern humans. Am J Hum Genet 101(4):578–89.

Dannemann M, Prüfer K, Kelso J. 2017. Functional implications of Neandertal introgression in modern humans. Genome Biol 18:61.

De Castro Jm, Arsuaga J, Carbonell E, Rosas A, Martínez I, Mosquera M. 1997. A hominid from the lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. Science 276 (5317):1392–95.

De Castro Jm, Martinón-Torres M, Gómez-Robles A, Prado-Simón L, Martín-Francés L, Lapresa M, and others. 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): a comparative morphological study. J Hum Evol 61:1–11.

De Manuel M, Kuhlwilm M, Frandsen P, Sousa V, Desai T, Prado-Martinez J, et al. 2016. Chimpanzee genomic diversity reveals ancient admixture with bonobos. Science 354(6311):477–81.

Dean D, Hublin JJ, Holloway R, Ziegler R. 1998. On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. J Hum Evol 34(5):485–508.

Delson E. 1988. One source not many. Nature 332:206.

Fernando A, Joshua G. 2019. Multiple episodes of interbreeding between Neanderthal and Modern humans. Nat ecol Evol 3:39–44.

Frayer D, Wolpoff M, Pope G. 1993. Theories of modern human origins: the paleontological test. Am Anthropol 95:14–50.

Fu Q, Posth C, Hajdinjak M, Petr M, Mallick S, Fernandes D, et al. 2016. The genetic history of Ice Age Europe. Nature 534(7606):200–05.

Gabounia L, De Lumley M, Vekua A, Lordkipanidze D, De Lumley H. 2002. Découverte d'un nouvel hominidé à Dmanisi (Transcaucasie, Geórgie). Comptes Rendus Palevol 1(4):243–53.

Gittelman R, Schraiber J, Vernot B, Mikacenic C, Wurfel M, Akey J. 2016. Archaic hominin admixture facilitated adaptation to out-of-Africa environments. Curr Biol 26:3375–82.

Green R, Krause J, Briggs A, Maricic T, Stenzel U, Kircher M, et al. 2010. A draft sequence of the Neandertal genome. Science 328:710–22.

Groves C. 1989. A regional approach to the problem of the origin of modern humans in Australasia. In: P Mellars, C Stringer, editors. The Human Revolution. Edinburgh, Edinburgh University Press. 274–85.

Groves C. 2007. Species concepts and speciation: facts and fantasies. In: W Henke, I Tattersall, editors. Handbook of Paleoanthropology. Springer. 1861–79.

Habgood P. 1989. The origin of anatomically-modern-humans in Australia. In: P Mellars, C Stringer, editors. The human revolution: behavioural and biological perspectives on the origins of modern humans. Princeton, Princeton University Press. 245–74.

Habgood P. 1992. The origin of anatomically modern humans in East Asia. In: G Bräuer, FH Smith, editors. Continuity or replacement: controversies in Homo sapiens evolution. Rotterdam, Balkema. 273–88.

Harris K, Nielsen R. 2016. The genetic cost of Neanderthal introgression. Genetics 203:881–91.

Harvati K. 2003. The Neanderthal taxonomic position models of intra- and inter-specific craniofacial variation. J Hum Evol 44:107–32.

Harvati K. 2015. Neanderthals and their contemporaries. In: W Henke, I Tattersall, editors. Handbook of Paleoanthropology, 2nd Edition. Springer. 2243–79.

Harvati K, Frost S, McNulty K. 2004. Neanderthal taxonomy reconsidered: implications of 3D primate models of intra and interspecific differences. Proc Natl Acad Sci U.S.A 101(5):1147–52.

Howell F. 1952. Pleistocene glacial ecology and the evolution of "classic Neanderthal" man. Southwest J Anthropol 8:377–410.

Howells W. 1975. Neanderthal man: facts and figures. In: RH Tuttle, editor. Paleoanthropology: Morphology and Paleoecology. The Hague: Mouton. 389–407.

Howells W. 1976. Explaining modern man: evolutionists versus migrationists. J Hum Evol 5:577–96.

Hublin J. 1985. Human fossils from the North African Middle Pleistocene and the origin of *Homo sapiens*. In: E Delson, editor. Ancestors: The Hard Evidence. New York, Liss. 282–88.

Hublin J. 1992. Recent human evolution in northwestern Africa. Philos Trans Royal Soc B 337(1280):185–92.

Hublin J. 2001. Northwestern Africa and Middle Pleistocene hominids and their bearing on the emergence of *Homo sapiens*. In: L Barham, K Robson-Brown, editors. Human Roots: Africa and Asia in the Middle Pleistocene. Bristol, CHERUB, Western Academic and Specialist Press. 99–121.

Hublin J. 2009. The Origin of Neandertals. Proc Natl Acad Sci U.S.A 106(38):16022–27.

Hublin J, Tillier A. 1981. The Mousterian juvenile mandible from Irhoud (Morocco): a phylogenetic interpretation. In: C Stringer, editor. Aspects of Human Evolution. London. Taylor and Francis. 167–85.

Hublin J, Tillier A. 1992. L'*Homo sapiens* en Europe occidentale: gradualisme et rupture. JJ Hublin, AM Tillier, editors. Aux Origines *d'Homo sapiens*. Paris, Presses Universitaires de France. 291–327.

Huxley J. 2010. [1942] Evolution: The Modern Synthesis. M Pigliucci, GB Müller. Cambridge, MIT Press.

Douka K, Slon V, Jacobs Z, Ramsey C, Shunkov M, Derevianko A, et al. 2019. Age estimates for hominin fossils and the onset of the Upper Paleolithic at Denisova Cave. Nature 565(7741): 640–3.

Klein R. 1995. Anatomy, behaviour and modern human origins. J World Prehist 9:167–98.

Kuhlwilm M, Gronau I, Hubisz M, De Filippo C, Prado-Martinez J, Kircher M, et al. 2016. Ancient gene flow from early modern humans into Eastern Neanderthals. Nature 530(7591): 429–33.

Lahr M. 1994. The Multiregional Model of modern human origins: a reassessment of its morphological basis. J Hum Evol 26:23–56.

Lahr M. 1996. The Evolution of Modern Human Diversity. Cambridge, Cambridge University Press.

Lahr M, Foley R. 1994. Multiple dispersals and modern human origins. Evol Anthropol 3:48–60.

Lahr M, Foley R. 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. Yearb Phys Anthropol 41:137–76.

Lieberman D. 1995. Testing hypotheses about recent human evolution from skulls. Curr Anthropol 36: 159–97.

Lieberman D. 2011. The evolution of the human head. Belknap Press of Harvard University Press.

Li ZY, Wu XJ, Zhou LP, Liu W, Gao X, Nian XM, and others. 2017. Late Pleistocene archaic human crania from Xuchang, China. Science 355:969–72.

Manderscheid E, Rogers A. 1996. Genetic admixture in the Later Pleistocene. Am J Phys Anthropol 100:1–5.

Manzi G. 2011. Before the emergence of *Homo sapiens*: overview on the Early-to-Middle Pleistocene fossil record (with a proposal about *Homo heidelbergensis* at the subspecific level). Int J Evol Biol, Review Article:1–12.

Meyer M, Kircher M, Gansauge M, Li H, Racimo F, Mallick S, et al. 2012. A high-coverage genome sequence from an archaic Denisovan individual. Science 338:222–6.

Meyer M, Fu Q, Aximu-Petri A, Glocke I, Nickel B, Arsuaga JL, et al. 2014. A mitochondrial genome sequence of a hominin from Sima de los Huesos. Nature 505(7483):403–18.

Mondal M, Bertranpetit J, Lao O. 2019. Approximate Bayesian computation with deep learning supports a third archaic introgression in Asia and Oceania. Nature Communications 10:246.

Mourthe I, Trindade R, Aguiar L, Trigo T, Bicca-Marques J, Bonatto S. 2019. Hybridization between neotropical primates with contrasting sexual dichromatism. Int J Primatol 40(1):99–113.

Nei M, Roychoudhury A. 1993. Evolutionary relationships of human populations on a global scale. Mol Biol Evol 10: 927–43.

Pearson O, Grine F, Barham L, Stringer C. 2000. Human postcranial remains from the Middle and Later Stone Age of Mumbwa Caves. L Barham, editor. The Middle Stone Age of Zambia, South Central Africa. Bristol, Western Academic & Specialist Press. 149–64.

Peyrégne S, Slon V, Mafessoni F, de Filippo C, Hajdinjak M, Nageli S and others. 2019. Nuclear DNA from two early Neandertals reveals 80,000 years of genetic continuity in Europe. Sci. Adv. 5: eaaw5873.

Ponce De León M, Zollikofer C.P. 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. Nature 412(6846):534–8.

Prüfer K, Racimo F, Patterson N, Jay F, Sankararaman S, Sawyer S, et al. 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505(7481):43–54.

Racimo F, Sankararaman S, Nielsen R, Huerta-Sánchez E. 2015. Evidence for archaic adaptive introgression in humans. Nat Rev Genet 16:359–71.

Relethford J. 2001. Genetics and the search for modern human origins. New York, Wiley-Liss.

Rightmire GP. 1996. The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? J. Hum Evol 31(1):21–39.

Rightmire GP. 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. Evol Anthropol 6(6):218–27.

Rightmire GP. 2008. *Homo* in the middle pleistocene: hypodigms, variation, and species recognition. Evol Anthropol 17(1):8–21.

Rogers A, Bohlender R, Huff C. 2017a. Early history of Neanderthals and Denisovans. Proc Natl Acad Sci U.S.A 114(37):9859–63.

Rogers A, Bohlender RJ, Huff C. 2017b. Reply to Mafessoni and Prüfer: Inferences with and without singleton site patterns. Proc Natl Acad Sci U.S.A 114(48):E10258–60.

Rougier H, Milota S, Rodrigo R, Gherase M, Sarcina L, Moldovan O. And others. 2007. Peştera cu Oase 2 and the cranial morphology of early modern Europeans. Proc Natl Acad Sci U.S.A 104(04):1165–70.

Sankararaman S, Patterson N, Li H, Päabo S, Reich D. 2012. The data of interbreeding between Neanderthals and Modern Humans. PLoS Genetics 8(10):1–9.

Sankararaman S, Mallick S, Dannemann M, Prüfer K, Kelso J, Pääbo S et al. 2014: The genomic landscape of Neanderthal ancestry in present-day humans. Nature 507(7492):354–7.

Sankararaman S, Mallick S, Patterson N, Reich D. 2016. The Combined Landscape of Denisovan and Neanderthal Ancestry in Present-Day Humans. Curr Biol 26:1241–7.

Schwartz J, Tattersall I. 2002 Bodo and the concept of *Homo heidelbergensis*. H Seidler, K Begashaw, editors. 25 years of Bodo, Proceedings of the 4th Phillip V Tobias Lecture on Human Evolution. Addis Ababa: National Museum 107–27.

Schwartz J, Tattersall I. 2005. The Human Fossil Record, Craniodental Morphology of Early Hominids (Genera Australopithecus, Paranthropus, Orrorin) and Overview (Volume 4). New York, Wiley Liss.

Schwartz J, Tattersall I. 2010 Fossil evidence for the origin of *Homo sapiens*. Yearb Phys Anthropol 53:94–121.

Serre D, Pääbo S. 2004. Evidence for gradients of human genetic diversity within and among continents. Genome Res 14:1679–85.

Simonti C, Vernot B, Bastarache L, Bottinger E, Carrell D, Chisholm R, and others. 2016. The phenotypic legacy of admixture between modern humans and Neandertals. Science 351:737–741.

Sjödin P, Sjöstrand A, Jakobsson M, Blum M. 2012. Resequencing data provide no evidence for a human bottleneck in Africa during the penultimate glacial period. Mol Biol Evol 29(7):1851–60.

Smith F. 2010. Species, populations, and assimilation in later human evolution. In: CS Larsen editor. A Companion to Biological Anthropology. Oxford: Wiley-Blackwell. 357–78.

Smith F, Ahern J. 2013. Introduction: thoughts on Modern Humans origins: from 1984 to 2012. In: FH Smith, C Ahern, editors. The Origins of Modern Humans, Biology Reconsidered. New Jersey, John Wiley & Sons. XI–XXV.

Smith T, Tafforeau P, Reid D, Grün R, Eggisn S, Boutakiout M. et al. 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci U.S.A 104(15):6128–33.

Stewart J, Stringer C. 2012. Human evolution out of Africa: the role of refugia and climate change. Science 335:1317–21.

Stock J, Lahr M, Kulatilake S. 2007. Cranial diversity in South Asia relative to modern human dispersals and global patterns of human variation. In: MD Petraglia, B Allchin, editors. The Evolution and History of Human Populations in South Asia. Springer 245–68.

Stoneking M, Sherry ST, Redd AJ, Vigilant L. 1992. New approaches to dating suggest a recent age for the human mtDNA ancestor. Philos Trans Royal Soc B 337:167–76.

Stringer C, Andrews P. 1988. Genetic and fossil evidence for the origin of modern humans. Science 239:1263–8.

Stringer C. 2002. Modern human origins: progress and prospects. Philos Trans Royal Soc B 357(1420):563–79.

Stringer C. 2006. The origins of modern humans 1984–2004. In: H Soodyall, editor. The prehistory of Africa. Johannesburg, Jonathan Ball 10–20.

Stringer C. 2012. The status of *Homo heidelbergensis* (Schoetensack 1908). Evol Anthropol 21:101–7.

Stringer C. 2014. Why we are not all multiregionalists now. Trends Ecol Evolut 29:248–51.

Stringer C. 2016. The origin and evolution of *Homo sapiens*. Philos Trans Royal Soc B 371(1698):1–12.

Tattersall I. 1986. Species recognition in human paleontology. J. Hum Evol 15:165–75.

Tattersall I. 2007. Neanderthals, *Homo sapiens*, and the question of species in paleoanthropology. Journal of Anthropological Species 85:139–46.

Tattersall I, Schwartz J. 2000. Extict Humans. Boulder, Westview Press CO.

Tattersall I, Schwartz J. 2006. The distinctiveness and systematic context of *Homo neanderthalensis*. In: K Harvati, T Harrison, editors. Neanderthals Revisited. New York, Springer. 9–22.

Thorne A, Wolpoff M. 1981. Regional continuity in Australasian Pleistocene hominid evolution. Am J Phys Anthropol 55:337–49.

Thorne A, Wolpoff M. 1992. The multiregional evolution of humans. Sci Am 266:76–83.

Trinkaus E. 1981. Neanderthal limb proportions and cold adaptation. C Stringer, editor. Aspects of Human Evolution. London, Taylor & Francis 187–224.

Trinkaus E. 1983. The Shanidar Neandertals. New York, Academic.

Trinkaus E. 1986. The Neandertals and modern human origins. Annu Rev Anthropol 15:193–218.

Trinkaus E. 1992. Morphological contrasts between the Near Eastern Qafzeh-Skhūl and late archaic human samples: grounds for a behavioral difference? In: T Akazawa, K Aoki, T Kimura, editors. The Evolution and Dispersal of Modern Humans in Asia. Tokyo, Hokusen-Sha Publishers 277–94.

Underhill P, Passarino G, Lin A, Shen P, Foley R, Lahr M. 2001. The phylogeography of Y chromosome binary haplotypes and the origins of modern human populations. Ann Hum Genet 65:43–62.

Vallois H. 1954. Neanderthals and presapiens. J Royal Anthropol Inst 84:11–30.

Vernot B, Akey J. 2014. Resurrecting surviving Neandertal lineages from modern human genomes. Science 343:1017–21.

Vernot B, Tucci S, Kelso J, Schraiber J, Wolf A, Gittelman R, et al. 2016. Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. Science 352:235–9.

Vervaecke H, Elsacker V. 1992. Hybrids between common chimpanzees (Pan troglodytes) and pygmy chimpanzees

(Pan paniscus) in captivity. Mammalia 56(4):667–9.

Vigilant L, Stoneking M, Harpending H, Hawkes K, Wilson A. 1991. African populations and the evolution of human mitochondrial DNA. Science 253:1503–8.

Weaver T. 2012: Did a discrete event 200.000–100.000 years ago produce modern humans? J Hum Evol 63:121–6.

Weaver T, Hublin JJ. 2009. Neandertal birth canal shape and the evolution of human childbirth. Proc Natl Acad Sci U.S.A 106 (20): 8151–8156.

Wei-Haas M. 2019. Ancient DNA reveals new twists in Neanderthal migration: genetc surprises pulled from 120.000-year-old bones showcase the nuanced history of this close human relative. Nature-Science & Innovation. Retrieved from: https://www.nationalgeographic.com/science/2019/06/neanderthals-spread-across-europe-asia-gets-new-twist-from-ancient-dna/

Weidenreich F. 1947. Fact and speculations concerning the origin of Homo sapiens. Am Anthropol 49:39–48.

Wolpoff M. 1980a. Paleoanthropology. New York, Knopf.

Wolpoff M. 1980b. Cranial remains of Middle Pleistocene European Hominids. J Hum Evol 9(5):339–58.

Wolpoff M. 1986. Describing anatomically modern Homo sapiens: a distinction without a definable difference. V.V. Novotný, A. Mizerová (Eds.): Fossil Man: New Facts, New Ideas, Papers in Honor of Jan Jelínek's Life Anniversary. Anthropos (Brno) 23:41–53.

Wolpoff M, Thorne A, Smith F, Frayer D, Pope G. 1994. Multiregional evolution: a worldwide source for modern human populations. M Nitecki, D Nitecki, editors. Origins of anatomically modern humans. New York, Plenum. 175–99.

Wolpoff M, Hawks J, Frayer D, Hunley K. 2001. Modern human ancestry at the peripheries: a test of the replacement theory. Science 291:293–7.

Wood B. 1991. Koobi Fora Research Project, Volume 4: Hominid Cranial Remains. Oxford, Clarendon Press.

Zilhão J, Trinkaus E. 2002. A brief history. In: J Zilhão, E Trinkaus, editors. Portrait of the artist as a child: the gravettian human skeleton from the Abrigo do Lagar Velho and its archaeological context. Ministério da Cultura: Instituto Português de Arqueologia. 13–27.

Zilhão J, Constantin S, Danciu A, Rodrigo R, Trinkaus E, Gherase M, et al. 2007. The Peştera cu Oase people, Europe's earliest modern humans. In. P Mellars, K Boyle, O Bar-Yosef, C Stringer, editors. Rethinking the Human Revolution. Cambridge McDonald Institute for Archaeological Research. 249–62.