What does *Homo antecessor* tell us about the origin of the "emergent humanity" that gave rise to *Homo sapiens*?

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There was a time and place in which a new and emerging humanity diverged from the fundamental mainstream of the evolution of hominins, represented by *Homo erectus* s.l. This divergence would have given rise to several species included in a new adaptive landscape, which would include a trend towards a new pattern of growth and development and an increase of the brain volume. The new emergent humanity would eventually lead to the appearance of *Homo sapiens* in Africa perhaps 300,000 years ago (Hublin *et al.* 2017). But, was Africa the cradle of humanity to which we belong?

Apparently, it is. This would imply that species belonging to this new genealogy would have originated in Africa and would have left this continent towards Eurasia. For many, the last common ancestor (LCA) of H. sapiens and H. neanderthalensis is represented by the species H. heidelbergensis, a possible African and Eurasian species which could include specimens like Bodo, Kawbe, Petralona, Mauer, Arago, Bilzingsleben, Yunxian, Dali, or Jinniushan. But we could also consider the African species H. helmei, which other authors have included in the genealogy of H. sapiens (Mirazon-Lahr & Foley, 2001). As we will explain below, the elusive Denisovans as well as the species H. antecessor (Bermúdez de Castro et al., 1997) should be also considered part of this new humanity.

At the end of the XX century, *H. antecessor* was proposed as the best candidate to represent the LCA of modern humans and Neanderthals (Bermúdez de Castro *et al.*, 1997). This species was named after the study of the remains

provided by the excavation of level TD6.2 of the Gran Dolina cave site (Sierra de Atapuerca, Spain) (Carbonell *et al.*, 1995). The age of these fossils has been estimated between 0.80 and 0.85 million years ago (Ma) based on studies of paleomagnetism, biochronology, and geochronology (ESR, thermoluminiscence [TL], and thermally transferred optically stimulated luminiscence [TT-OSL]) (Martinón-Torres *et al.*, 2019 and references therein). The fact that the paleogenetic studies were pointing to a more recent split for these lineages (e.g. Endicott *et al.*, 2010 and references therein) was an important handicap for the acceptance by the scientific community of *H. antecessor* as candidate to represent the LCA.

H. antecessor exhibits a modern-like midface that can be observed in both immature and adult individuals (Arsuaga et al., 1999). The most complete specimen is ATD6-69 (Hominid 3), which preserves most of the left side of the midface (Bermúdez de Castro et al., 1997). Although this specimen belonged to an immature specimen, the theoretical models based on the growth of the anatomically modern humans and Neanderthals conclude that the final phenotype of the Hominid 3 would be modern-like (Freidline et al., 2013). These authors suggest that the appearance of the modern face derive from a generalized pattern, and that that some of the facial features that characterize H. sapiens may have developed multiple times in human evolution by means of a process of convergence. According to these authors, the modern humanlike facial morphology present on the ATD6-69

specimen is primitive whereas the midface of the Middle Pleistocene hominins (*H. heidelbergensis*) and Neanderthals would be derived. The midface of the anatomically modern humans would have derived independently from that of the Africa Middle Pleistocene hominins like Bodo or Kabwe.

In contrast to these conclusions, Lacruz et al. (2019) point out that the face is a very complex system from both the morphological and physiological point of view. These authors emphasize that there are important constraints in the development of the face and the surrounding cranial structures, and that the facial growth is closely integrated with the development of the braincase and other cranial regions, making of homoplasy an unlikely phenomena. Apart from H. antecessor and the later Middle Pleistocene hominins from Africa (Jebel Irhoud), other Asian specimens, like those of Zhoukoudian, Dali, Nanjing, and Jinniushan show a modern-like midface (Lacruz et al., 2019). According to these last authors, a modern-like midface would be considered as a symplesiomorphy shared by H. antecessor, H. sapiens, and some Asian Middle Pleistocene hominins, instead of a convergence as suggested by Freidline et al. (2013).

In addition, the morphological study of the TD6.2 fossils shows that H. antecessor shares some cranial, mandibular, dental, and postcranial features with H. neanderthalensis and several European Middle Pleistocene specimens (see a review in Bermúdez de Castro et al., 2017). Since these features were previously considered diagnostic of Neanderthals, either H. antecessor belongs to the Neanderthal lineage (i.e., a sister species) or represents a taxon closely related to the origin of this genealogy. One of the scenarios posed by Stringer (2016) contemplates the possibility that H. antecessor was a lateral and extinct branch of the path that leads to the LCA. According to this author, in this scenario (Figure 2 of Stringer, 2016) the LCA had not yet been identified (Ancestor X). This scenario is similar to that depicted in Figure 1 of this report. Since H. antecessor is not far from the LCA and the clade including H. sapiens, it represents one of the best fossil opportunities to approach the origin of our species.

It is important to emphasize that *H. ante*cessor can be well-differentiated from Asian *H.* erectus by a set of cranial and dental features (e.g., Xing, et al., 2018) and could be part of the evolutionary change towards the new emergent humanity at the late Early Pleistocene. The expression of both Neanderthal and modern features in *H. antecessor* shared with African and Eurasian specimens invites us to make a reflection on the place where this speciation event took place.

Some authors have proposed that all expansions of hominins into Eurasia have occurred after an "out of Africa" episode (e.g., Abbate & Sagri, 2011). This scenario is tacitly admitted without debate, except for exceptions (e.g., Bermúdez de Castro *et al.*, 2013), although a greater role of Eurasia in the evolution of the genus *Homo* has also been claimed (Dennell & Roebroeks, 2005; Martinón-Torres *et al.*, 2007). This hypothesis leads us to explore possible scenarios, where the evidence provided by the TD6.2 hypodigm must have an obliged prominence.

In a first scenario, Africa could be the place of origin of H. antecessor, and later the origin of the LCA. The African branch of the LCA would have originated the species H. sapiens approximately 300,000 years ago (Hublin et al., 2017). Variations of this scenario contemplate the possibility of an intermediate species (H. helmei) between H. heidelbergensis (a candidate to be the LCA) and H. sapiens (Stringer, 1996) or the possibility that H. helmei was the true LCA (Mirazón-Lahr & Foley, 2001). If this scenario is correct, we should find in Africa the trace of the features that are present in H. antecessor and that will become characteristic of some Middle Pleistocene hominins like those from Sima and H. neanderthalensis.

As an alternative and a more parsimonious scenario, we have hypothesized that Southwest Asia (including especially the Levantine Corridor) could be the place where important events occurred for the future of the new emergent humanity (Bermúdez de Castro *et al.*, 2013). The Near East could be the establishment area for a hominin population, as it has been suggested that the environmental conditions in this region remained stable and favorable for continuous hominin residence during the Pleistocene (Almogi-Labin, 2011). Southwest Asia could be the origin of the hominins that gave rise to H. antecessor, but also the origin of the LCA. It is interesting to point out that Southwest Asia has been identified as a biodiversity hotspot and a potential source of phylogenetic diversity (see Carrión et al., 2011 and references therein). This hypothesis would imply population movements towards Europe, Asia and Africa of hominins in continuous evolution in those regions of Southwest Asia (Bermúdez de Castro et al., 2013, 2018). These population movements would explain: i) the diversity observed in Europe during the Middle Pleistocene (e.g., Bermúdez de Castro et al., 2018 and references therein); ii) the probable origin of Neanderthals in this region (Bermúdez de Castro et al., 2018); iii) the presence of a symplesiomorphic midface in Europe (including that of H. antecessor), Asia, and Africa (Lacruz et al., 2019); and iv) the origin of the LCA following between 0.55 ad 0.76 Ma, (see Meyer et al., 2016).

It is well known that during Early-Middle Pleistocene transition (c. 1.2-0.5 Ma) the lowamplitude 41-ka obliquity-forced climate cycles of the earlier Pleistocene were replaced progressively in the later Pleistocene by high-amplitude 100-ka cycles (e.g., Almogi-Labin, 2011). Although progressive aridification occurred in Africa during this period an onwards, the Pleistocene climate of Africa experimented repeated oscillations in temperature and rainfall, shifting between humid-warm phases (pluvials) and arid-cool phases (interpluvials) (see Owen et al., 2018 and references therein). With these changes, which affected the flora and fauna, there is no reason to deny the possibility that the door of the Levantine Corridor would open at specific moments of the late Early and Middle Pleistocene and allow the passage to Africa from Eurasia (and vice versa) of human groups at different moments.



Fig. 1 - In this hypothetical phylogeny, H. antecessor would be the first hominin belonging to a lineage derived from a basal species, which we could identify with H. erectus s.l. This lineage would also be the origin of other hominins, such as the African and Eurasian genealogies which most scholars lumped in H. heidelbergensis. According to the results of Gómez-Robles et al. (2013), following one of the scenarios proposed by Stringer (2016), as well as the reflections made by Lacruz et al. (2019) H. heidelbergensis would not necessarily be the common ancestor of H. sapiens and H. neanderthalensis and other related hominins. That unknown ancestor would be very close to both H. antecessor and H. heidelbergensis. A: H. antecessor; D: Denisovans; H: group of H. heidelbergensis; LCA: last common ancestor; N: H. neanderthalensis; S: H. sapiens; SH: Sima de los Huesos.

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Author Contributions

José María Bermúdez de Castro and María Martinón-Torres have contributed equally do the design of the hypothesis presented in this report.

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