

Mosaic evolution in hominin phylogeny: meanings, implications, and explanations

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Summary - In paleoanthropological literature, the use of the term “mosaic” (mosaic evolution, mosaic trait, mosaic species, and so on) is becoming more and more frequent. In order to promote a clarification of the use of the concept in literature, we propose here a classification in three different meanings of the notion of mosaic in human evolution: 1) morphological (inter-specific and intra-specific) instability in a certain phase of a branched phylogeny; 2) multiple trajectories and versions of the same adaptive trait in a branched phylogeny; 3) the trait itself as a complex mosaic of sub-traits with different phylogenetic stories (as is the case in language). We argue that the relevance of such mosaic patterns needs a macro-evolutionary interpretation, which takes into consideration the interaction between general selective pressures (promoting different versions of the same adaptation) and a cladogenetic approach in which speciation played a crucial role, due to ecological instability, habitat fragmentation, and geographical dispersals in human evolution.

Keywords - Mosaic evolution, Macro-evolutionary approach, Bipedalism, Encephalization, Symbolic behavior, Stone-tools, Human language evolution.

The term “mosaic” in human evolution

The leading perspective on human evolution has been largely modified, due to a number of different factors: the paleontological and archaeological record has been widely expanded; new dating methods and tools of integrated analysis are available; the possibility to integrate a great amount of new convergent evidence coming from different fields – such as paleontology, molecular biology, paleo-biogeography, paleoecology, social studies – is increasing more and more. All these changes and the dramatic expansion of the empirical basis have made it clear that the linear model of a single anagenetic evolution is today hardly tenable (despite its recent resurgence for restricted periods of human evolution: see Lordkipanidze *et al.*, 2013 and Rightmire *et al.*, 2017, about an alleged single polymorphic species of early *Homo*). Today, the scientific community is generally unanimous in replacing the

old linear anagenetic model of human phylogeny with the cladogenetic Darwinian model of a knotty and irregularly branched tree. However, the more new data and findings are available, the more the general picture of hominin phylogeny seems puzzling and problematic, which raises new research questions.

Despite the fact many efforts have been made to put in order and explain the tangled puzzle of kinships and evolutionary trajectories, the picture of the hominin tree remains full of question marks and blind spots, especially following discoveries in recent years. *Ardipithecus ramidus* has weakened the dominant framework of the 20th century that used living African apes, especially chimpanzees, as proxies for the immediate ancestors of the human clade. Referring to a “missing-link” between humans and such alleged apelike ancestors, after “Ardi”, no longer makes sense (White *et al.*, 2015). A stone tool industry has been found at the Lomekwi 3 site, West Turkana (Kenya), at 3.3 Mya, predating the Oldowan by

700,000 years, and conjecturally not in association with a *Homo* species (Harmand *et al.*, 2015). A jawbone fossil from Hadar and Ledi-Geraru formations in Afar was recently dated to ca. 2.8–2.75 Mya, pushing back the origin of the genus *Homo* by 400,000 years (Villmoare *et al.*, 2015). The amazing number of remains from the Rising Star caves, South Africa, have been associated to the new species *Homo naledi*, which dates to 315–236 Kya (Dirks *et al.*, 2017). This bizarre human species had a very small brain (560 cc in males) and an australopithecine-like body in a combination with modern human-like derived traits, such as hands suited to handling tools and precision grip. Surprisingly, it lived in the African continent at the same time of the Neanderthals, which were evolving in Europe, and maybe of the early *Homo sapiens*, which were emerging in the African continent. Fossil remains from Jebel Irhoud, Morocco, have been dated to ca 315 Kya and associated to hominin forms which were endowed with teeth, jaws and faces indistinguishable from anatomically modern humans, but also with elongated and non-globular skulls (Hublin *et al.*, 2017).

According to several authors, hominin phylogeny seems to proceed through so-called “mosaic-like patterns”, with several coeval species evolving along different trajectories, and showing combinations of derived and retained traits. Despite the fact the use of the term “mosaic” in the human evolution field is widespread today among specialized scholars, the meaning of this word seems yet to be univocally defined. The growing importance of the term “mosaic” in reference to the characterization of hominins key features and the current lack of precision in the use of this term in literature might be an indication that we need novel conceptual tools to better focus on the new paleo-anthropological picture.

The goal of the present review is, on the one hand, to examine the main uses of the notion of “mosaic” in the literature related to the human research field. Furthermore, the essay aims to investigate the possible patterns and processes which undergo such mosaic-like changes in biological and cultural human evolution.

Mosaic type 1: hominin morphological instability

Mosaic evolution is a pervasive pattern that has characterized, in general, the evolutionary patterns of several groups of organisms throughout Earth’s history (Hopkins & Lidgard, 2012). De Beer (1954, p. 163) firstly coined the term of mosaic evolution with reference to the urvogel *Archaeopteryx*, indicating the presence of a mixture of ancestral and derived traits. Today, it has been largely proven that some adaptations can evolve with different timing and stages within a single lineage so that a given organism shows a mosaic of ancestral and evolving descendant characters in respect to its own ancestors. Mosaic evolution results from multiple influences molding morphological traits and implies the hierarchical organization of organismal traits into semiautonomous subsets, or modules, which reflect differential genetic and developmental origins. The degree of independence of the modules can be quantified using statistical tests providing in this way a strong evidence of the presence of mosaic evolution in a taxon or in a lineage (beyond the seminal work by Olson & Miller 1958, see in particular Adams, 2015; Clarke & Middleton, 2008; Felice & Goswami, 2018; Goswami & Polly 2010; Klingenberg, 2008, 2009; Klingenberg & Lobón, 2013; Londe *et al.*, 2015).

Mosaic-like patterns play a major role in human evolution field. In *The Science of Human Evolution*, John Langdon (2016, pp. 129–131) argues that “When paleontologists compare a single ancestral species with a known descendant, there is an expectation that a fossil intermediate in time will be similarly intermediate in all anatomical features. However, these different species of hominin do not tell a simple linear story. Each body part has its own history and has evolved at a different pace and sometimes a different direction in each species to produce unique combinations of anatomy”. This is what paleoanthropologists generally call “mosaic evolution”: a differentiated evolution and a “potential independence of traits” (Gould, 1977b, p. 58), combined in different ways from species to species. The term

“mosaic” refers here to the description of what we call “hominin morphological instability”, which means specific morphological assemblages or modules evolving independently from each other, in a non-harmonious way and at different rates when compared with other related species. As S.J.Gould wrote, “The concept of ‘mosaic evolution’ [...] refuted the notion of harmonious development by affirming that individual organs could have independent phyletic histories, despite the evident correlation of parts within any organism” (Gould, 1977a, p. 234).

The six articles of the 2013 special issue that *Science* dedicated to the anatomy of *Au. sediba* (ca.1,98 Mya) are good examples of what the term “mosaic” concretely means. These studies, along with other research published in the previous three years, provide a comprehensive examination of the anatomy of the new species which was found in 2008 in Malapa, South Africa. *Au. sediba* appears phylogenetically distinct from *Au. afarensis*, but close to *Au. africanus* for what regards the highly heritable nonmetric dental traits and it also shares derived traits with the genus *Homo* (Irish *et al.*, 2013). Some mandibular materials and other features of the cranium and skeleton share similarities with those of other australopithecines, but differ from *Au. africanus* both in size and shape, as well as in their ontogenetic growth trajectory (De Ruiter *et al.*, 2013). The upper limbs are largely “primitive” in their morphology, well suited for arboreal climbing and possibly suspension, and therefore similar to other australopithecines (Churchill *et al.*, 2013). However, *Au. sediba*’s hand presents a suite of derived *Homo*-like features, such as a long thumb and short fingers associated with precision gripping (Kivell *et al.*, 2013). Even the thorax morphology reveals a mosaic combination of retained and derived traits (Schmid *et al.*, 2013) and many features of the vertebral column are largely derived, with the highly flexible spine showing a configuration which is quite similar to the Nariokotome *H. erectus* skeleton (Williams *et al.*, 2013). Finally, the morphologies of the heel, midfoot, knee, hip, and back are unique and peculiar (De Silva *et al.*, 2013).

The team leader of the Malapa enterprise, Lee Berger, refers to “The mosaic nature of *Australopithecus sediba*” (Berger, 2013) in his introduction to the 2013 *Science*’s special issue. In the final part of the text, Berger writes that “This examination of a large number of associated, often complete and undistorted elements gives us a glimpse of a hominin species that appears to be mosaic in its anatomy and that presents a suite of functional complexes that are different from both those predicted for other australopithecines and those of early *Homo*”; concluding that “Such clear insight into the anatomy of an early hominin species will clearly have implications for interpreting the evolutionary processes that affected the mode and tempo of hominin evolution and the interpretation of the anatomy of less well preserved species”.

Another paradigmatic example which can illustrate this sense of “mosaic evolution” is the anatomy of *Homo naledi*. Recently dated to 236-335 Kya (Dirks *et al.*, 2017), the species was discovered in the Rising Star cave complex, South Africa, which is today the largest assemblage of a single hominin species yet found in the African continent. *H. naledi* shows a similar body mass and stature to small-bodied human populations, but it also has a small endocranial volume, ranging from 465 cm³ to 560 cm³ (Schroeder *et al.*, 2017), which is analogous to australopithecine species. The dentition is small and simple in occlusal morphology but still primitive (Berger *et al.*, 2015). Cranial morphology is unique, nevertheless sharing traits (i.e., aspects of cranial form, facial morphology, and mandibular anatomy) with species across the genus *Homo*, such as *H. habilis*, *H. rudolfensis*, *H. erectus* and Middle Pleistocene *Homo* (Laird *et al.*, 2017). *H. naledi*’s hand possesses a combination of primitive and derived features never seen in any other hominin, with strongly curved proximate and intermediate phalanges, but also with a wrist, thumb and palm that suggests enhanced object manipulation ability (Berger *et al.*, 2015; Kivell *et al.*, 2016). The same mosaic assemblage can be found in the morphology and inferred function of the foot, which is predominantly modern

human-like, well adapted for striding bipedalism, but still different from modern humans in having more curved proximal pedal phalanges (Harcourt-Smith *et al.*, 2016, p. 1). All these unique or derived features are still combined in a marked mosaic fashion with more “primitive” australopith-like trunk, upper-limb and shoulder, pelvis and proximal femur (Fuerriegel *et al.*, 2017; Marchi *et al.*, 2017; Williams *et al.*, 2017). As Lee Berger *et al.* (2015, p. 23) insightfully observe, “In light of this evidence from complete skeletal samples, we must abandon the expectation that any small fragment of the anatomy can provide singular insight about the evolutionary relationships of fossil hominins”. Thus, the phylogenetic interpretation becomes harder and harder.

Recent new evidence shows that even our species may have evolved through a mosaic-like pattern, as shown by the anatomy of the early modern human-like forms found in Jebel Irhoud, Morocco, which date to ca. 315-334 Kya (Hublin *et al.*, 2017; Stringer & Galway-Witham, 2017). These remains are associated to a possible early “pre-modern” phase in *H. sapiens* evolution and point to a surprising mosaic assemblage of features, including facial, dental and mandibular morphology that aligns with recent anatomically modern humans and more primitive endocranial and neurocranial morphology. In particular, the facial shape of Jebel Irhoud fossils shows similarities to the structure of *H. sapiens*’ face, but the shape of the braincase is retained in its form, with an elongated shape that is less globular than anatomically modern *H. sapiens*. Jebel Irhoud’s fossils could document another case of mosaic-like evolutionary transition. This new discovery does not necessarily contradict the fact that the first true *H. sapiens* actually emerged in Ethiopia at ca. 200 Kya, as a strong consilience of molecular and paleontological data attests, but it could indeed mean that the emergence of modern humans’ anatomical traits was preceded by a long and still little-known transitional phase (between 350 Kya and 260 Kya), during which different human populations (proto-*sapiens* or late forms of *H. heidelbergensis*) were evolving differentiated

mosaics of *H. sapiens*’ anatomical traits in different parts of the African continent (and not only in Ethiopia), as also recently suggested by Schlebusch *et al.* (2017).

Further examples of mosaic morphological patterns could be the anatomy of *H. floresiensis*, showing its “unique mosaic morphology” (Aiello, 2015, p. 2289), and the recent discovery of two crania from Lingjing, Xuchang (China), dated to 105-125 Kya, which exhibit a peculiar morphological mosaic of traits, namely differences and similarities compared to their probable ancestor, i.e. *H. heidelbergensis*, and their western contemporaries, namely Neanderthals and modern humans (Li *et al.*, 2017). Although a number of scholars have associated these skull caps to the still quite elusive Denisovans, this hypothesis is still awaiting genetic confirmation.

In all the above-mentioned cases, the term “mosaic” is used as a descriptive notion related to morphological instability. The mosaic describes specific anatomic module-like assemblages in which different traits have evolved at different rates and through some degrees of independence when compared with other related species. In other words, it refers to anatomical forms which show evolutionary changes in some derived or unique features, combined with other retained parts where there are no marks of apparent evolutionary innovation. These macro-evolutionary mosaic transitions in hominin phylogeny are usually connected to phases of ecological instability (Parravicini & Pievani, 2016a).

The same term may describe in literature also a situation of instability within a single species – seemingly in the case of *H. heidelbergensis*, with its regional variants in Africa, Europe and Asia, each one showing peculiar mosaic patterns in their morphologies (see, e.g., Arsuaga *et al.*, 2014) - or even within a single population. The latter case is well represented by the hominin remains from Dmanisi, Georgia. The five ancient skulls associated to *H. georgicus* are highly different from each other, but still belonging to the same single, variable population (Lordkipanidze *et al.*, 2013). For this reason, *H. georgicus* could be defined as a “surprising

mosaic” (Lordkipanidze *et al.*, 2007, p. 305) even at population level.

The anatomical assemblages in hominin species or populations, which show a combination of different traits, suggest the occurrence of different rates of disjointed changes. This is what we mean when we define here “mosaic type 1”. As Langdon (2016, p. 131) pointed out, “the most important lesson” that such a pervasive pattern of mosaic evolution “has to tell us is that human evolution is not linear, but the hominin lineage has produced a confusing array of side branches. There is not a single main trunk except in retrospect”.

Mosaic type 2: multiple phylogenetic trajectories for the same trait

The mosaic evolution of bipedal locomotion

Mosaic type 1 is the most used meaning of the term “mosaic” in human evolution literature (see how the term is employed in teaching manuals, e.g. in Lewis *et al.*, 2013). Nevertheless, the term “mosaic” appears also with a slightly different meaning. Sometimes, it describes the different ways in which a single trait evolves in multiple coeval species living in different environmental contexts. The meaning of “mosaic” in this second sense used in literature, which we will call “mosaic type 2”, appears to express a more explicative and predictive meaning than “mosaic type 1”.

The evolution of bipedalism provides a good example of mosaic type 2 pattern. We may again consider the mosaic anatomy of *Au. sediba*. The foot, in particular, shows an anatomical mosaic of traits (*sensu* mosaic-1) which is not present in either *Au. afarensis* or *Au. africanus* and the heel, midfoot, knee, hip, and back are also unique when compared to the same traits of other hominin species. This peculiar combination of anatomical parts of the feet and the lower limbs configures a unique adaptive solution for locomotion. In fact, this anatomical ensemble is consistent for a biped walking with a hyper pronating gait. In other words, a mosaic combination of different features (such as lower limbs and feet) gives

rise to a complex behavioral trait (locomotion) which is unique when compared to the same functional trait shown by other (hominin) species. As De Silva *et al.* (2013, p. 1) argue, “these bipedal mechanics are different from those often reconstructed for other australopiths and suggest that there may have been several forms of bipedalism during the Plio-Pleistocene”. So, many forms of bipedalism. *H. naledi* shows another “unique locomotor repertoire” (Harcourt-Smith *et al.*, 2016), namely a combination of primitive (shared with australopithecines), derived (shared with *Homo* species), and unique traits, “functionally indicative of a bipedal hominin adapted for long distance walking and possibly running” (Marchi *et al.*, 2017, p. 174).

These cases indicate different ways of being bipeds. If we further expand the focus by encompassing the whole hominin phylogenetic tree during a given period of time (e.g., around 1,5–2 Mya), we can see that multiple forms of bipedalism were adopted by different coeval hominin species, often living in different environmental contexts (open clearings, forest coverings, etc.). While *H. ergaster* and *H. erectus* showed advanced (or obligate) forms of bipedal locomotion, other coeval species, such as australopithecines or *Paranthropus* species, exhibited more flexible and mixed styles of locomotion, such as facultative bipedalism with residual adaptations for arboreal life and climbing (see Figure 1). It is clear, as Lee Berger *et al.* (2010, p. 204) stated, that “the evolutionary transition from a small-bodied and perhaps more arboreal-adapted hominin (such as *Au. africanus*) to a larger bodied, possibly full-striding terrestrial biped (such as *H. erectus*) occurred in a mosaic fashion”. However, the meaning of the term “mosaic” here appears to be something different than “mosaic type 1”, because in this case the term implies different variants of the same type of trait (e.g., bipedalism) across a number of coeval species living in different environments. In S.J.Gould’s words, “the concept of mosaic evolution dictates that organs will evolve in different ways to meet varying selective pressures” (Gould, 1977b, p. 66).

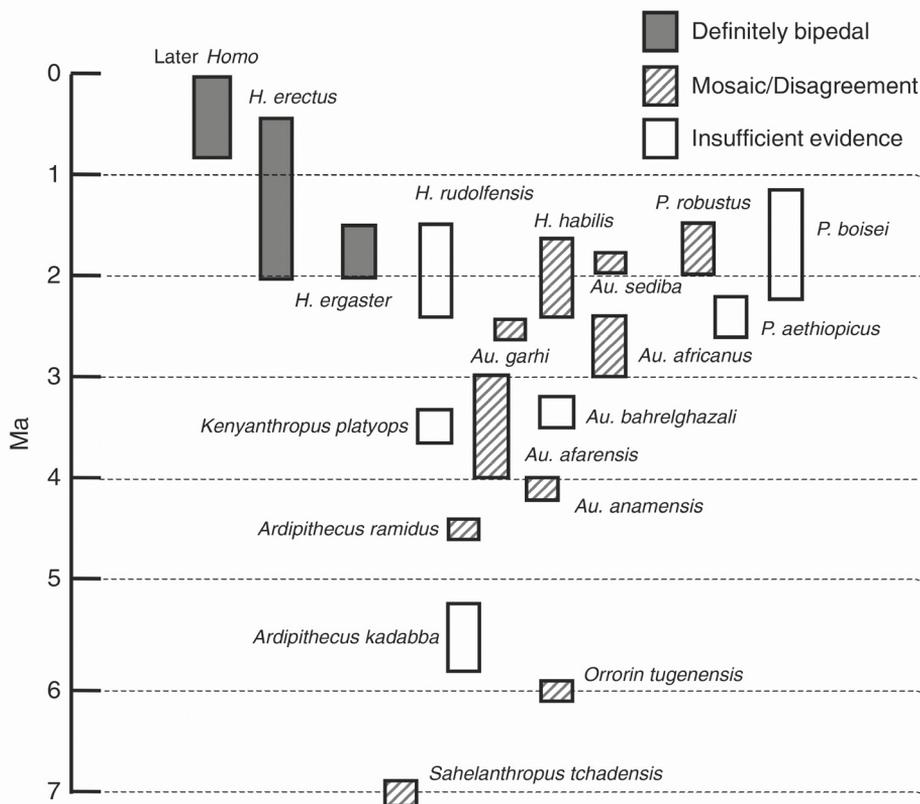


Fig. 1- From Harcourt-Smith W.E.H., 2015. Origin of bipedal locomotion. In W. Henke & I. Tattersall (eds): Handbook of paleoanthropology, 2nd edition, p. 1940. Springer, Verlag-Berlin-Heidelberg (adapted from Wood, 2002). Temporal ranges of known hominin taxa. Solid shading refers to taxa that were unequivocally obligate bipeds; cross-hatching relates to taxa where they are mosaic, or there is disagreement over the degree to which they are bipedal; no shading indicates taxa where there is insufficient evidence.

The encephalization trend and the evolution of the first stone tool industries

The evolution of hominin bipedalism clearly contradicts the long-held view of a linear and anagenetic transition from a quadrupedal apelike hominin ancestor to a fully bipedal human. In a similar fashion, even the so-called encephalization trend in the genus *Homo* could no longer be depicted as a linear trend from a small-brained hominin to the large-brained Neanderthals and anatomically modern humans.

H. naledi had an approximately 500 cm³ brain. However, it didn't live 2 Mya, as previously

supposed, but it surprisingly dates to ca. 236-335 Kya. In other words, *H. naledi* was contemporary to other human species that possessed a three times larger brain, such as the earliest anatomically modern humans and Neanderthals (Dirks *et al.*, 2017). *Homo floresiensis* skeletal remains were found during the 2001-2004 excavations at Liang Bua (Flores, Indonesia) and have been recently re-dated to between about 100 and 60 Kya (Sutikna *et al.*, 2016). This bizarre human form was about one metre tall and was endowed with an endocranial volume of 417 cm³ (Falk *et al.*, 2005).

H. naledi and *H. floresiensis* are two examples (probably an evolutionary relict or a hybrid species the former, a geographic speciation by insular dwarfism the latter) which disprove the alleged encephalization trend, as they are two very small-brained species of the genus *Homo* which lived at the same recent times of early *H. sapiens* and *H. neanderthalensis*. Furthermore, even the correspondence of a large brain with complex technological abilities seems to be ill-founded. While *H. naledi* has yet to be associated neither with lithic tool production nor with intentional use of fire, *H. floresiensis* has been connected with the production of a complex lithic industry, involving both pebble-based cores and small-flake based cores and spanning at least several hundred millennia (Moore & Brumm, 2009; Moore *et al.*, 2009). The new findings consisting of a mandible and teeth at Mata Menge (Flores), which have been attributed to direct ancestors of *H. floresiensis* and dated back to 700 Kya (van den Bergh *et al.*, 2016), have strengthened the idea of long-persistent technological abilities in association with this isolated hominin species.

In a more general picture, both the evolution of brain size and the evolution of technological skills seem to proceed through differentiated paces and mosaic type 2 patterns. The tool-making and tool-use abilities appear not to be an exclusive behavioral trait of the genus *Homo*, whose first emergence has been recently dated back to 2.8 Mya (Villmoare, 2015). Beyond the putative stone-tool-assisted consumption of animal tissues which was found at Dikika (Ethiopia) and dates to 3.39 Mya (Dominguez-Rodrigo *et al.*, 2010; McPherron *et al.*, 2010), significant findings have been recently unearthed at the Lomekwi-3 site, Kenya. They consist of a 3.3 Mya complete lithic industry, which includes 83 cores, 35 flakes, some passive elements or potential anvils, cobbles and further artefacts (Harmand *et al.*, 2015).

The well-known Oldowan lithic tools emerged 700,000 years after the Lomekwian – i.e., 2.6 Mya – in East Africa and consisted of stone industries containing simple cores and flaked pieces, along with some battered artifacts

such as hammerstones. The earliest known Oldowan stone tools appeared in localities in the Gona region of the Afar depression, north-east Ethiopia (Semaw *et al.*, 2003). By 2.4–2.3 Mya, this technology appears at sites in other regions of Ethiopia and Kenya and by 2.1–1.9 Mya it had spread throughout the Rift Valley of East Africa and basins in North and Central Africa, and afterwards all over the Ancient World (in particular, Europe, the Middle East, South Asia). We cannot tell exactly who made these Oldowan tools, because several species of hominins (belonging to at least three different genera, i.e., *Australopithecus*, *Paranthropus*, and *Homo*) are known to have originated from East Africa between 2.5 and 1 million years ago.

The appearance of the Acheulean industry dates back to approximately 1.7 Mya in East Africa (Beyene *et al.*, 2013; Diez-Martin *et al.*, 2015; Lepre *et al.*, 2011) and it spread to Europe and Asia perhaps as early as about 1 Mya (Pappu *et al.*, 2011; Scott & Gibert, 2009). Although the origin of the Acheulean is thought to have closely coincided with major changes in human brain evolution, the actual evidence from the fossil record does not support this assumption. The transition from Oldowan tools to Acheulean technology is attributed to *H. ergaster*. The passage to mode 2 technology (or Acheulean) at about 1.6 Mya appears to have not been characterized by any proven morphological change. Furthermore, the stable and unchanged presence of mode 1 lithic industry, which is thought to have lasted for more than 1 million years, is generally associated with large-brained species, such as the Asiatic *H. erectus*, with an endocranial volume of 1150 ml in the most recent specimens. The absence of mode 2 tools in Zhoukoudian and almost in the totality of the other eastern Asian sites is rather peculiar, including Java sites, where the latest presence of *H. erectus* is attested almost until the end of the Middle Pleistocene (i.e., 130 Kya). Even though “the absence of evidence is not evidence of absence”, one might intriguingly think that the eastern Asian technological traditions could have followed an autonomous trajectory, maybe due to isolation from the other human

populations which were distributed in Africa, in Europe or in other parts of Asia, as a consequence of the dispersal patterns that occurred during the first out of Africa (see below).

Therefore, mode 1 industries coexisted for several hundred thousand years with the mode 2 industries. The latter lasted from approximately 1.7 Mya to 250 Kya and the earlier Acheulean is associated with the above-mentioned *H. ergaster / erectus*, while the later Acheulean (by ca. 500 Kya), which shows more complexity, more craftsmanship in its realization, and higher symmetry and aesthetic sense than the earlier ones, is associated with the larger-brained *H. heidelbergensis*. Such handaxe/cleaver industries are contemporaneous and sometimes regionally co-occurring with the simpler Oldowan-like technologies. Acheulean and contemporaneous mode 1 industries are found throughout Africa and Eurasia, but classic handaxe and cleaver assemblages are especially characteristic of Africa, the Near East, the Indian subcontinent, and Western Europe. Elsewhere, the simpler mode 1 technologies are found, especially in Eastern Europe and most of eastern Asia (Toth & Schick, 2015).

The Middle Paleolithic industries of Europe, the Near East, North Africa, sub-Saharan Africa are usually characterized by prepared core technologies (e.g., Levallois cores, flakes, and points), side scrapers, denticulates, and retouched points and are found between approximately 250 and 30 Kya. During such a time span, hominins extended their ranges to most of the different environmental zones of Africa and Eurasia. Mode 3 industry is found in tropical, subtropical, temperate, and even periglacial climatic regimes. It is associated, in Africa, with larger-brained pre-*sapiens* hominins (sometimes assigned to *Homo helmei*) and early anatomically modern humans. Recent findings document that Acheulean technology of Olorgesailie Basin in Kenya was entirely replaced by Middle Stone Age technology already by ca. 320 Kya, i.e. tens of thousands of years earlier than previously thought (Deino *et al.*, 2018). In the Near East, mode 3 tools are associated with Neanderthals and anatomically modern humans, while in Europe they

are exclusively associated with Neanderthals. At Attirampakkam, India, luminescence dating has recently shown that processes signifying the end of the Acheulian culture and the emergence of a Middle Paleolithic culture occurred about 385 Kya, i.e. much earlier than conventionally presumed for South Asia (Akhilesh *et al.*, 2018).

Late Paleolithic stone industries (ca. 40-10 Kya), consisting of more complex technologies such as blades transformed into a variety of tool forms – including end scrapers, burins, and backed knives –, and elongated flakes that are produced by soft hammer or indirect percussion, are almost always associated with anatomically modern humans. However, some early Upper Paleolithic sites in Europe are also contemporaneous with the last Neanderthal populations that lived there (Harvati, 2015).

While in Europe, there is doubtless a difference between Middle and Upper Paleolithic assemblages, many forms typically associated with the Upper Paleolithic appear in earlier periods. Many regions in Europe (Conard & Fischer, 2000) and Africa (McBrearty & Brooks, 2000) show different patterns of cultural development. Also in the Near East, the later Middle Paleolithic is characterized by Levalloisian assemblages that were made by both Neanderthals and anatomically modern humans (Shea, 2003), which also show how tenuous the link is between anatomical and cultural evolution.

This overview evidences that the emergence and the evolution of the lithic assemblages also show heterogeneous evolutionary trajectories and mosaic type 2 patterns of development and transmission and do not provide clues for predicting when modern patterns of human behavior emerged. Rather, scattered development of both new and older technologies can be observed through heterogeneous regional patterns, often associated with different coeval hominin species.

Mosaic evolution of symbolic behaviours?

The emergence and consolidation of modern behavior accelerated its evolutionary pace in the middle of the Late Pleistocene. Culturally modern behavior is attested in many parts of Africa,

Europe, Asia, and Australia between 30 and 45 Kya through several bursts of local innovations. An increasing amount of archeological and fossil proof supports the hypothesis of mosaic polycentric bursts of symbolic intelligence, not only restricted to *Homo sapiens* as has been traditionally thought. An asynchronous appearance and disappearance of key cultural innovations is attested not only in the African Middle Stone Age, but also in the Eurasian Middle Paleolithic (300–40 Kya) before becoming fully consolidated in the cognitive modern humans (Conard, 2015; D’Errico & Banks, 2013; D’Errico & Stringer, 2011).

The Asian and Java *H. erectus* are commonly associated with the stable use of the simple Oldowan technology. However, at least one putative burst of symbolic behavior has been recently attributed to *H. erectus* in Trinil, Java, with the first possible abstract patterns engraved on a freshwater shell. This is the earliest known trace of symbolic intelligence, which amazingly dates back to 540–430 Kya (Joordens *et al.*, 2015).

A number of sporadic expressions of symbolic behaviors has been associated to Neanderthals. Burials, use of pigments, complex lithic and hafting technologies, and personal ornamentation (and not only at the end of the Neanderthal evolutionary trajectory) are among the elements that definitely challenge the idea that behavioral modernity is unique to our species (Hovers & Belfer-Cohen, 2006; Langley *et al.*, 2008; Nowell, 2010; Zilhão, 2007).

A wealth of Middle Paleolithic human skeletons appear to have been buried deliberately, both associated to anatomically modern humans and also to Neanderthals, like those in the Shanidar Cave (Iraq, 35–65 Kya) (Solecki, 1971; Trinkaus, 1983), in La Chapelle-aux-Saints (35–70 Kya) (Rendu *et al.*, 2013) or in La Ferrassie, Dordogne (France) (Zilhão, 2012). Such sporadic signals preceded the unambiguous Upper Paleolithic evidence of burials, many of which preserved opulent grave goods, such as for example, Sungir’, Dolní Věstonice, and the Grimaldi Caves.

Pigments were used in a lot of Middle Stone Age and Middle Paleolithic settings of the Late Pleistocene (Watts, 2002). Southern Africa has

provided particularly abundant evidence for the use of ground ochre during the Middle Stone Age and studies at Blombos have also documented toolkits for making and storing pigments (d’Errico & Stringer, 2011). Furthermore, a quantity of very recent evidence that surprisingly date to before 300 Kya from the Middle Stone Age sites from the Olorgesailie basin (southern Kenya) has shown that hominins at these sites exploited iron-rich rocks to obtain red pigment (Brooks *et al.*, 2018). In the Levant and Europe, strong data for the use of ochre are attested at Middle Paleolithic sites, including Qafzeh (Hovers *et al.*, 2003). Several European sites suggest that Neanderthals regularly used pigments in Middle Paleolithic contexts, including Maastricht-Belvédère (Roebroeks *et al.*, 2012), Pech de l’Azé (d’Errico & Soressi, 2002), Cueva de los Aviones, and Cueva Antón (Zilhão *et al.*, 2010).

Several Middle Stone Age incised objects testify the presence of symbolic behavior. Important examples include engraved abstract patterns on pieces of ochre dating to approximately 75 Kya (Henshilwood *et al.*, 2002) and a cross-hatched pattern drawn with an ochre crayon on a ground silcrete flake recovered from approximately 73 Kya, both from Still Bay deposits at Blombos cave (Henshilwood *et al.*, 2018). Furthermore, incised pieces of ochre were found, e.g., in Peers Cave, Klein Kliphuis (Mackay & Welz, 2008), and Klasies River Cave 1 (d’Errico *et al.*, 2012), not to mention fragments of decorated ostrich eggshells from Howiesons Poort (Texier *et al.*, 2010). The density of many of these finds in southern Africa has been interpreted as an indication of the definitive emergence of cultural modernity with fully developed modern cognitive abilities, including language (d’Errico *et al.*, 2003; Henshilwood *et al.*, 2002; Texier *et al.*, 2010).

Early evidence for the use of marine shells as ornaments come from Qafzeh Cave (100 Kya) (Bar-Yosef & Vandermeersch, 1993) and from Skhül Cave in Israel (Vanhaeran *et al.*, 2006), and from Grotte des Pigeons in Morocco (Bouzougara *et al.*, 2007). Perforated marine shell ornaments are attested in Still Bay deposits at Blombos Cave (75 Kya) (Henshilwood *et al.*,

2011) and Middle Stone Age contexts at Sibudu (d'Errico *et al.*, 2008). Starting from 40 Kya, personal ornaments have been attested in several parts of the Old World from multiple regions of Africa, Eurasia, and Australia.

Normally, the perforated shells have been interpreted as having been made and used by anatomically modern humans. However, the late Middle Paleolithic sites of Cueva de los Aviones and Cueva Antón in Spain are significant exceptions (Zilhão *et al.*, 2010). Recent dating of the flowstone capping in the Cueva de los Aviones deposit shows, in particular, that the symbolic finds made therein are 115 to 120 Kya, thus predating the earliest known comparable evidence associated with modern humans by 20,000-40,000 years (Hoffmann *et al.*, 2018). Furthermore, Neanderthals apparently produced a wide range of perforated and incised ornaments and symbolic artefacts in Châtelperronian contexts, such as Grotte du Renne at Arcy-sur-Cure (Baffier, 1999). Here, a pioneering study has confirmed that the link between Neanderthals and the artifacts is real (Welker *et al.*, 2016). Further evidence of artefacts with clear symbolic relevance have been found in other Châtelperronian sites in Europe, dating from 41 to 45 Kya, such as the Quinçay rock shelter in France, the Ilsenhöhle rock shelter in Germany, the Trou Magrite (Pontà-Lesse) site in Belgium, Fumane rockshelter in Italy and others (Zilhão, 2012).

The Mousterian levels of Grotta di Fumane (44 Kya) have revealed evidence of intentional removal of large feathers by Neanderthals for non-utilitarian use (Peresani *et al.*, 2011), and a radius bone fragment of a raven (*Corvus corax*) from Zaskalnaya VI rock shelter, Crimea (38-41 Kya) bearing seven notches, perhaps a needle, suggests advanced technological abilities in Neanderthals (Majkić *et al.*, 2017).

Annular constructions of broken stalagmites have been found in the Bruniquel Cave in southwest France. Dating to 176.5 Kya, this enigmatic structure is among the oldest known well-dated constructions made by humans living in that area, i.e., early Neanderthals, and could represent some kind of symbolic or ritual behavior, as it shows a

regular geometry of stalagmite circles that appear to have been deliberately moved and placed in their current locations (Jaubert *et al.*, 2016).

Figurative art is universally accepted as an indication of behavioral modernity and a hallmark of symbolic behavior. For this reason, Europe has always been thought as the privileged place where symbolic intelligence emerged for the first time. Several sites have provided evidence of figurative representation between 30 and 40 Kya. The earliest figurative art includes the mammoth ivory figurines and other ivory figurines and isolated representations in bone and stone from the Swabian caves (Germany) (Conard, 2003, 2009), together with the earliest examples of musical instruments (Conard *et al.*, 2009). The earliest spectacular paintings from Grotte Chauvet in the Ardèche region of southern France date to between 37-33.5 Kya (Quiles *et al.*, 2016). Other important sites include Stratzing (Austria), Abri Cellier, La Ferrassie, Abri Blanchard, and Abri Castanet (France), Peștera Coliboaia (Romania), which date to between 30-34 Kya.

But the perspective was likely biased. All these traces of symbolic behavior of the early Upper Paleolithic were presumably made by modern humans. However, Neanderthals still occupied parts of Europe at that time, roughly 40 Kya. In fact, an abstract pattern from Gorham's Cave in Gibraltar, which was found to be older than 39 Kya, was probably engraved by Neanderthal populations living there (Rodríguez-Vidal *et al.*, 2014). Furthermore, hand stencils and disks onto the wall in the El Castillo cave (Spain) date back to at least 40,800 years, meaning that such paintings could have been done by the last Neanderthals that had inhabited the Iberian peninsula for more than 200,000 years and up to 42 Kya (Pike *et al.*, 2012). The hypothesis of sporadic Neanderthal art has been recently confirmed by Hoffmann *et al.* in *Science*, who discovered paintings and engravings in three Spanish caves occupied by Neanderthal groups 65 Kya, when no modern humans (as far as we know) had yet arrived in Europe (Hoffmann *et al.*, 2018). Due to all this and further evidence, imaginative

and symbolic intelligence appear to have evolved independently among Neanderthals, and not as the result of contact with modern humans. It seems that they did not systematically practice it, but were however capable of it. The alternative hypothesis is to substantially predate the arrival of anatomically and cognitively modern humans in Europe.

In any case, the European figurative depictions appear not to be the oldest known worldwide, as has been presumed to date. Rock art traditions on the Indonesian island of Sulawesi have been recently found at least compatible in age with the oldest European ones and include twelve human hand stencils and two figurative animal depictions from seven cave sites. The earliest dated image from Maros karsts in Sulawesi shows a minimum age of 39.9 Kya, being now the oldest known hand stencil associated to *Homo sapiens* in the world (25,000 years after the Neanderthal rock paintings in Spain). In addition, a painting of a babirusa ('pig-deer') made at least 35.4 Kya ago is among the earliest dated figurative depictions in *Homo sapiens* worldwide (Aubert *et al.*, 2014). Further evidence for symbolic activity at Leang Bulu Bettue has been recently dated to 30-22 Kya (Brumm *et al.*, 2017). More recently, uranium-series analysis of calcium carbonate deposits that overlie a large reddish-orange figurative painting of an animal at Lubang Jeriji Saléh, Indonesian Borneo, yielded a minimum date of 40 Kya. This is currently the oldest date for figurative artwork in the world. In the same site, two reddish-orange-coloured hand stencils yielded a minimum uranium-series date of 37.2 Kya and a third hand stencil has a maximum date of 51.8 Kya (Aubert *et al.*, 2018).

The emergence of behavioral modernity does not appear to reflect a quantum leap from archaic to modern patterns of behavior. It may not have been a revolution, but rather a mosaic transition. Especially, it seems to shape a mosaic type 2 picture in which advanced technologies and symbolic behaviours follow regionally and temporally different trajectories, at least in two human species. In short, these patterns configure a patchy and mosaic evolution of complex

cultural behaviours and symbolic communication across the Old World (Conard, 2015).

In conclusion, mosaic type 2 describes appropriately the way in which crucial traits in human evolution appear to have evolved. Looking from the broadest perspective, the above-described major transitional phases of hominin evolution (related to locomotion, foraging and diet, encephalization, technological and symbolic behaviours) reveal a series of mosaic type 2 patterns which occur at a different and higher level than the mosaic type 1 patterns. According to Robert A. Foley, 2016, each of the identified transition patterns should be considered as a different element composing the much broader mosaic picture which configures the human evolution taken as a whole.

Mosaic type 3: when the trait itself is a mosaic

The most recent literature regarding the evolution of human language has also described the emergence of this faculty through the notion of mosaic. However, the use of the term seems to reveal a slightly different, and possibly third, meaning.

Since Charles Darwin's time, the origin of human language has been investigated by several scholars, who have always considered this faculty as a single monolithic trait. Hauser *et al.* (2002) proposed to distinguish a "faculty of language in a broad sense" (FLB) and a "faculty of language in a narrow sense" (FLN). According to this proposal, FLB includes the sensory-motor system (i.e., speech), the conceptual-intentional system (i.e., semantic) and the faculty of language narrow sense itself. FLN consists of the abstract linguistic computational system alone (i.e., syntax), and involves the computational mechanisms for recursion and the ability to produce a potentially infinite range of expressions from a finite set of elements. The authors claim that it is likely that only the human brain possesses FLN, which has to be considered as a derived trait of *H. sapiens*, evolved for certain evolutionary reasons and then coopted for different functions (a case of exaptation). On

the other hand, the other FLB components are thought to have evolved gradually, and to be shared with other non-human vertebrate species.

The interesting issue in this proposal, beyond whether it works or not when compared with the empirical data, is that language is no longer treated as a single trait, but as a *mosaic of different elements* with distinct functions that intertwine in a complex way. This idea is still awaiting to be seriously tested, but it has already led to a series of fruitful hypotheses (see Fitch, 2012; Hurford, 2003; Okanoya, 2007, Pievani, 2014, 2016; Suman & Pievani, 2015).

According to this literature, the traits composing the faculty of language could have evolved by following different trajectories. Some of them could have evolved through functional direct adaptations, some others through exaptive processes, while others as by-products of structural or developmental constraints. In this “tree thinking” approach to language, we see different evolutionary histories and different combinations of subsystems involved in language. Some of them may be very old and come before the genus *Homo*, and then functionally coopted in new ecological niches (for example, the lowering of the larynx – Fitch, 2012). Others could be more recent and even typical of our species, as is supposedly the case for the syntactic aspects of language. Some traits have homologues or analogues in other extant species and could be studied comparatively, while some others are likely to be unique to our species.

The language faculty is therefore composed of multiple interacting subsystems, which involve phonetic, semantic, symbolic and pragmatic capacities. All these different elements combine together and form a single complex trait. We propose here to connect this idea with the recent evidence concerning the bushy hominin evolutionary tree. The hypothesis of language as a mosaic of traits works very well when matched with the extant paleoanthropological data. As we described above in the paragraph “Mosaic evolution of symbolic behaviors?” about symbolic behavior, an increasing amount of archeological and fossil findings supports the conjecture

that innovations indicative of modern cognition are not actually restricted to *Homo sapiens*. Asynchronous appearance and disappearance of key cultural innovations have been witnessed not only in the African Middle Stone Age, but also in the Eurasian Middle Paleolithic (300–40 Kya) before becoming fully consolidated. Several of these mosaic expressions of symbolic behaviors are also today associated to Neanderthals, and in one case even to *H. erectus*. Therefore, sporadic expressions of linguistic behaviors – for consolidated reasons linked with symbolic and imaginative intelligence – could have predated the more complex and systematic behaviors of the anatomically and cognitively modern humans. In other words, a plurality of hominin populations and species could have followed multiple and non-linear trajectories of cultural and cognitive evolution across the different branches of the recent human phylogeny (D’Errico & Banks, 2013).

This third concept of mosaic concerns a given behaviour or structure, previously supposed to be a single trait, which is then found to be the result of the convergence of multiple traits characterized by different evolutionary trajectories in hominin branched phylogeny. The mosaic type 1 concept applies to any individual or species showing a mixture of derived and retained traits. Similarly, the mosaic type 3 notion may apply to any complex trait that is found to be a combination of derived and retained sub-components evolving through different rates. Some sub-components could be *derived traits*, which evolved in a punctuational fashion, while some others may be *retained traits*, which evolved gradually and was shared with different species, so stepping beyond the old-fashioned debate between the gradualist and the punctuational view of human language evolution (Parravicini & Pievani, 2016b). Furthermore, mosaic type 3 involves a phylogenetic notion related to the evolution of a single trait, thus sharing the same logic as mosaic type 2. In this respect, for example, further traits beyond language could be linked with mosaic type 3 pattern, such as the above-mentioned case of bipedalism (see *The mosaic evolution of bipedal locomotion*) where it has been hypothesized to be

Tab. 1 - The table summarizes three different types of mosaic notions, with their most widespread meaning, which emerged from the analyses conducted in the literature. The table also provides a list of some paradigmatic case-studies that exemplify each of the mosaic type.

TYPE OF MOSAIC	MEANING IN LITERATURE	PARADIGMATIC CASE STUDIES
Mosaic type 1	Strong variability of the morphological assemblages evolving in hominin species independently from each other, at different rates when compared with other related species. The same pattern can be observed within a single species or a single population.	<ul style="list-style-type: none"> • <i>Au. sediba</i>, <i>H. naledi</i>, <i>H. floresiensis</i>, with their very peculiar morphological assemblages. • The early phase of <i>Homo sapiens</i> evolution. • The regional variants of <i>H. heidelbergensis</i> and the population of <i>H. georgicus</i> in Dmanisi.
Mosaic type 2	Traits following regionally and temporally different trajectories and evolving in multiple coeval species that live in different environmental contexts. Usually, this pattern ends with the macro-evolutionary consolidation of the trait itself.	<ul style="list-style-type: none"> • Multiple forms of bipedalism. • Encephalization proceeding through differentiated pace within multiple coeval species. • The evolution of lithic assemblages and symbolic behaviours.
Mosaic type 3	Behaviour or structure, previously supposed to be a single trait, which is then found to be the result of the convergence of multiple traits characterized by different evolutionary trajectories in hominin branched phylogeny.	<ul style="list-style-type: none"> • Human language, no longer treated as a single trait, but as a mosaic of different elements and combinations of subsystems with distinct functions that intertwine in a complex way.

the result of a mosaic-combination of sub-traits (like lower limbs and feet) that follow different evolutionary trajectories across the hominin phylogenetic tree (see Table 1 for a brief conceptual summary about the three mosaic types).

The three mosaic types described so far aim at clarifying some conceptual differences in the use of the term “mosaic” that are largely unseen in literature. The identification of different mosaic types intends to provide a conceptual distinction for an unclear use of the term, but it says nothing about the biological processes at the base of the terminological differentiation. Such a mosaic approach calls therefore for new hypotheses concerning the underlying mechanisms. A plurality of patterns seems to be required to account for such a mosaic evolution of traits, because they are not “modeled” by a single selective agent for a single function, but could be the result of different processes, such as exaptations, multi-level factors, niche construction processes, phenotypic plasticity dynamics, in the light of an extended neo-Darwinian research program (Pievani, 2014; 2016; Suman & Pievani, 2015).

Explaining mosaic evolution through a macro-evolutionary approach

If the clarification of the three possible meanings of “mosaic evolution” is useful, we still lack an explanation for the somehow odd evidence associated with such mosaic traits belonging to different species. The processes of natural selection and genetic drift occurring at the micro-levels of organisms and populations seem insufficient to fully explain the macro-evolutionary patterns which have broadly affected the hominin evolution (i.e., episodes of adaptive radiations, mosaic evolution of traits in several coeval species, serial dispersals out of Africa and so on). The macro-evolutionary patterns emerging from the field currently point to the need for an ecological extension of the evolutionary theory, namely when applied to human evolution, which is able to account for the complex interactions among ecological and genealogical factors and between the micro-evolutionary levels of the organisms and populations, and the macro-level of species and higher taxa in a broader geo-physical

scenario (Parravicini & Pievani, 2016a; Eldredge *et al.*, 2016).

According to the paleontological data, mosaic evolution implies both a diversification of putative species or sub-species, each one bearer of a different combination of sub-traits, and the achievement of a final version (among the possible others) which is more successful than others (as for bipedalism, expanded brain, modern behaviours, etc.). The overall effect is a major evolutionary transition, but realized through multiple morphological and behavioural trajectories. Therefore, the most parsimonious explanation for this phenomenon seems to be the interaction between general selective pressures in human evolution (promoting different versions of the same adaptation; in other words, several adaptive peaks) and a highly branched phylogeny – due to ecological instability, habitat fragmentation, and geographical dispersals – in which speciation played a crucial role.

We can test this hypothesis with the paleontological data. At the beginning of our phylogeny, four species of early hominins belong to three different putative genera between 7 and 4.4 Mya: *Sahelanthropus tchadensis* (6-7 Mya), *Orrorin tugenensis* (6-5.7 Mya), *Ardipithecus kadabba* (5.8-5.2 Mya) and *Ardipithecus ramidus* (4.4 Mya). These forms show a combination of retained and derived features (mosaic type 1), suggesting different hybrid forms of locomotion, which could alternate quadrupedalism and bipedalism, or even “forest bipedalism” as is supposedly the case for *Ar. ramidus* (Lovejoy *et al.*, 2009; White *et al.*, 2009; for a comment see Cerling *et al.*, 2010). The mosaic type 1 anatomies of these putative earliest hominin forms suggest the occurrence of multiple postural “adaptive experiments” at about the time of divergence between hominin lineage and chimpanzee lineage.

The biogeographic area where these hominins lived covered the East African Rift System and South Africa, apart from *S. tchadensis* which has been surprisingly found 2,500 km west of the Rift Valley, maybe because of an early geographical dispersion. The entire region was affected by a long term aridity trend during the Neogene,

modulated by periods of strong climate variability alternating with relative stability. The progressive rifting and tectonic uplift of East Africa blocked the warm and wet air streams from the Atlantic Ocean, and these climate and environmental changes transformed eastern and southern Africa from a flat and homogenous region full of tropical mixed forest, to a heterogeneous region, with high mountains and a mix of habitats ranging from cloud forest and woodlands to grasslands and deserts (Bobe, 2006; Cerling *et al.*, 2011; deMenocal, 2011). Thus, the importance of climatic and environmental factors already appears in this first phase of hominin evolution.

Mosaic type 1 and type 2 patterns prevail in a strongly changing and fluctuating ecological scenario. The populations of apes isolated in the eastern and southern African regions were forced to adapt to an unprecedented mix of fragmented ecological niches characterized by an ever-changing climate (Pickford, 2006; White *et al.*, 2009). The effects of such an unstable and fluctuating context of life could be closely associated with bursts of novel adaptations – which possibly include different forms of bipedalism and further innovations like the diminution of the canine premolar honing complex, the advent of megadontia, and so on – for the earliest putative hominin species. Therefore, selective pressures connected to an increasing extension of open habitats could have favored the emergence of episodic and heterogeneous forms of bipedalism. Whichever hypothesis might be advanced for the emergence of bipedalism (see Niemitz, 2010, for a review), a patchy distribution of different unstable environments closely interrelates with a mosaic type 2 transition of forms capable of different locomotor adaptations, to be intended as multiple strategies of facultative bipedalism.

Fossil remains associated with *Au. anamensis* (Kenya) establish the first appearance of the genus *Australopithecus* at 4-4.2 Mya, which was highly diversified (with about 7-8 different species) and very long-lived (spanning from ca. 4.2 Mya to 1.8 Mya). Compared to the genus *Ardipithecus*, which was more adapted to a woody environment rich in forests and punctuated by clearings,

australopithecines were adapted to more arid and open habitats, covered by grasslands alternating with forests and woodlands (White *et al.*, 2009). Again, each of these australopithecines reveals a unique assemblage of anatomic features with several innovations (mainly related to dentition and posture) which align with typical features of the genus *Homo*, combined with retained traits (related to facial shape, low cranial capacity, the length of thoracic limbs, toes and fingers). Such heterogeneous combinations of traits compose unique original mosaic type 1 morphologies. In particular, limb anatomy points to advanced bipedalism and mixed styles of locomotion, with residual adaptations for arboreal life and climbing, which was well suited to a changing niche and unstable climate (Senut, 2006).

In this range of adaptive strategies, some were characterized by a greater ecological flexibility (in locomotion or diet) while others, as in the case of *Paranthropus*, by an increase in specialization of dietary habits.

After the emergence of the genus *Homo*, at around 2.8 Mya (Villmoare *et al.*, 2015), bipedal locomotion became first prevalent and then obligate. Once again, the evolutionary transition in locomotion came about in parallel in a plurality of separated morphologically unstable species (mosaic type 2), each one showing a mix of specific sets of traits (mosaic type 1). Mosaic type 2 patterns could be considered as a macro-evolutionary “laboratory” of mosaic-like experimentation which is carried out by a number of different related forms in multiple ways, usually ending with the macro-evolutionary consolidation of the trait itself (seemingly by a sorting process among species or populations with differential fitness). In the case of bipedalism, the mosaic type 2 pattern ends with the consolidation of a stable form of obligate bipedal behavior. This trend, however, is not so definitive as to exclude further residual mosaic experiments (see for example the still elusive exception of *H. naledi*'s locomotion, *The mosaic evolution of bipedal locomotion*). Therefore, the turbulent climatic and environmental scenario that characterized most of the transition phases of human evolution may help us to better understand

also the macro-evolutionary reasons behind the explosion of diversification and branching of hominin species and consequent mosaic patterns of evolution that occurred, e.g., between 3 and 2 Mya, with multiple phenomena of extinction and evolution of unprecedented hominin species and maybe even genera.

Afterwards, the plethora of species which diversified after the two first out of Africa processes (resulting from *Homo ergaster* at 2 Mya and from *Homo heidelbergensis* at 800-600 Kya) show marked mosaic type 1 combinations of traits, probably due to the different geographical trajectories followed by the human populations. The high fragmentation of habitats due to the harsh climatic conditions of the Old World, combined with the planetary dispersion of the genus *Homo*, could explain this adaptive radiation. The conformation of these areas, strongly diversified, full of geographic barriers, in a situation of intense climatic and ecological instability, is highly compatible with a mosaic type 1 and mosaic type 2 patterns related to multiple geographic speciation processes, as shown by the fossil record. Even the patterns of dispersal and migration of the human species across the Eurasian continent could be closely related to macro-evolutionary factors, linked to climate fluctuations and habitat instability, as argued by Mark Maslin and colleagues in their “pulsed climate variability hypothesis” (cf. Maslin, 2017).

The encephalization trend in the genus *Homo* seems no longer to follow the old-fashioned model of a stable, gradual, and linear evolution. On the contrary, it appears to follow a mosaic type 2 evolution, as we saw above (see *The encephalization trend and the evolution of the first stone tool industries*). Recent evidence shows that the *Homo* species with large brains, such as *H. sapiens* and Neanderthals, evolved at the very same time of other *Homo* species endowed with relatively small brains, like *H. naledi* and *H. floresiensis*.

We can base our understanding of the mosaic evolution of human brain on the idea that most of the evolutionary changes are concentrated in rapid (geologically speaking) events of speciation in peripheral isolates, which undergo different

processes (selection, drift, migration) triggering the cladogenetic pattern in allopatry that our phylogeny (like many others) shows (Eldredge & Lieberman, 2014). In this view, speciation could be the driver of major morphological and behavioural changes, which occur mainly during the early stage in which a new species emerges, followed by a period of apparent stasis.

Keeping this perspective in mind, the fog surrounding the cases of *H. naledi* and *H. floresiensis* seems to thin. Some archaic traits shown by *H. floresiensis*, including the skull size, suggest that its ancestors were small-bodied and closely related to the early-*Homo* species, such as *H. habilis* and *H. rudolfensis* (Argue *et al.*, 2017), apart from the adaptations due to the insular dwarfism. Similarly, *H. naledi*, which dates to around 236-335 Kya, shows a mosaic combination of traits, some of which are also typical of the early-*Homo* species or even of the latest australopithecines living between 2 and 2,5 Mya (such as the small brain, the basin, the curved fingers and so on – see **Mosaic type 1: hominin morphological instability**). While some African *H. heidelbergensis* were evolving into *H. sapiens*, groups of *H. naledi* with brains three times smaller and still adapted to an arboreal life wandered in southern Africa. At the same time, *H. floresiensis* was living in Indonesia, with its small brain and, nonetheless, its technologies. This is highly surprising from a gradualistic and anagenetic perspective, but not so much if we assume a pluralistic approach to evolution, which takes into consideration the possibility of punctuational and mosaic patterns in genus *Homo* evolution. In such a perspective, it is possible that *Homo naledi* and *Homo floresiensis* are something like evolutionary “wrecks” that survived locally for a long period of time, showing a very persisting and resilient morphological stasis in their respective mosaic of traits.

According to this view, the so called encephalization trend, similar to other mosaic type 2 patterns, could be a paradigmatic example of a species sorting mechanism (cf. Vrba & Gould, 1986), where a multiplicity of coeval species, following different evolutionary trajectories

(included geographically local stasis), undergo a process of differential success of some hominin species or populations compared to other hominin species or populations. The success of one version of the complex trait as the final stage of the mosaic type 2 evolution across a number of different species appears to be the outcome of a process of sorting, at the end of which only one species actually survived, i.e. *H. sapiens*, after a demographic competition with other coeval human species (mainly *Homo neanderthalensis* and Denisovans).

This hypothesis goes in the same direction of recent research authored by Bernard Wood and colleagues, according to which hominin brain size to different extents at different times could be influenced by both micro- and macroevolutionary changes, with a major role played by large-scale climate and environmental changes, habitat fragmentation and vicariance, interspecific interactions and so on. In particular, they also argue, “if species with larger ECVs (endocranial volumes) are found to have higher diversification rates (origination minus extinction rates), this may suggest that species sorting also caused clade-level ECV to increase. [...] If species sorting is borne out, it would suggest that all three mechanisms known to influence phenotypic evolution within a clade (i.e. anagenesis, directional speciation and species sorting) were acting in concert at multiple taxonomic scales to produce the directional ECV trend observed at the hominin clade level” (Du *et al.*, 2018, p. 6).

According to the Smithsonian Institution’s *Human Origins Program Team*, directed by Rick Potts, well-proven stages of climate change, ecological instability and habitat variability, which occurred repeatedly at (geologically) short intervals, favored inter-specific processes of adaptability selection, i.e. a selection of gene pools that favored greater versatility in adaptation and greater ecological flexibility. These processes may have triggered behavioral innovations in hominin species, such as the spread of technological abilities, as a strategy to successfully buffer the deleterious effects deriving from unstable ecological conditions (Potts & Faith, 2015).

The patchy spread of lithic industries throughout Africa and Eurasia, which occurred in a period of major climatic change, with several cold/warm and dry/humid oscillations, appears to confirm Potts' "variability selection hypothesis". The above-mentioned case of Olorgesailie basin in Kenya (see above, *The encephalization trend and the evolution of the first stone tool industries and Mosaic evolution of symbolic behaviours?*), where evidence of advanced technology, complex social behavior and symbolic intelligence were found before 300 Kya, is paradigmatic. According to Potts *et al.* 2018, an increased pace of environmental changes, well documented in the Olorgesailie sequence, with prolonged wet-dry climate oscillation, more pronounced erosion-deposition cycles, tectonic activity, with consequent impressive faunal turnover, were crucial in order to account for that development of Middle Stone Age technological, social, and cognitive innovations in human behavior. "Foraging unpredictability, with increased potential for resource scarcity, describes the conditions in which human hunter-gatherers broaden the spatial scale of the landscape they encounter through a combination of wider mobility, information and resource sharing, and the maintenance of resource exchange networks. [...] We thus hypothesize that the emergence of the MSA and its wholesale replacement of the Acheulean in the Kenya rift by ~320 kya ago represents an evolutionary response to resource landscapes that were less predictable in time (as a result of amplified climate variability throughout eastern Africa) and were also more heterogeneous in space (as a result of local tectonic activity)" (Potts *et al.*, 2018, p. 89).

The ecological scenario, which is highly fragmented and unstable due to climate oscillation, fits very well, in general, with the proved presence of a plurality of hominin species, and for the same reason, it is an ideal context to better understand the series of attested different bursts of early technological innovation. From the first lithic cultures, such as the Lomekwian tools dated 3.3 Mya (Harmand *et al.*, 2015) to the more recent artifacts typical of the first cognitively modern humans, the so-called "cumulative culture" of genus *Homo* appears to have

proceeded through a scattered and mosaic-like fashion, with punctuated bursts of innovation and long periods of apparent cultural stasis.

African chronological reconstructions of Still Bay and Howieson's Poort industries (from about 75 Kya to 60 Kya) represent, to date, the earliest traces of behavioral modernity: they show the occurrence of ephemeral and punctuated bursts of technological and behavioral innovations, linked to climate changes and demographic fluctuations in southern Africa. Local environmental changes in southern Africa during the Middle Stone Age triggered a number of demographic expansions and contractions in *Homo sapiens* populations, and they consequently affected social networks and bursts of cultural innovations (Jacobs & Roberts, 2009; Jacob *et al.*, 2008).

Also the data related to the evolution of symbolic behavior and language (*Mosaic evolution of symbolic behaviours?* and **Mosaic type 3: when the trait itself is a mosaic**) do not show a strictly linear model, but rather patterns of mosaic type 2 and type 3 evolution, with scattered bursts of cultural innovations, preceding the consolidation of the so-called behavioral modernity in cognitively modern humans. Different hominin populations and species (from *H. erectus* and Neanderthals to *H. sapiens*) seem to have followed different trajectories of cultural evolution among the branches of human phylogeny (D'Errico & Banks, 2013; Parravicini & Pievani, 2016a).

As D'Errico & Stringer (2011, p. 1061) argued, the cognitive prerequisites of modern human behavior may have been already "largely in place among the ancestors of Neanderthals and modern humans", and "social and demographic factors, arguably triggered by climate change", may account for "the asynchronous emergence, disappearance and re-emergence of modern cultural traits among both African 'modern' and Eurasian 'archaic' populations".

High climatic and environment instability might be an important factor which contributed to triggering the final wave of the cognitively modern humans, and maybe the series of further migratory waves outside Africa which preceded it, as attested by recent high-resolution

genetic studies on a wide scale (Pagani *et al.*, 2016; for the “final wave” model, Pievani, 2012). Therefore, the so-called “Paleolithic Revolution” could be due not only to cultural diffusion but also to demic diffusion, that is, a diffusion that was brought about by the arrival of new groups of hunters-gatherers which left Africa. It was, in fact, a complex transition that was preceded by many failed attempts and was probably not exclusive to *H. sapiens*. The other human species, before extinction also due to the contact with groups of *Homo sapiens*, were exploring the potentialities of symbolic intelligence in their own way, through mosaic type 2 and mosaic type 3 patterns of diversifications occurring at species and population levels.

Conclusion

Summing up, the three patterns of mosaic evolution here presented suggest that human evolution has been much more similar to a multiple exploration of adaptive possibilities than to a linear process of achievements, with several species showing faster pace in the evolution of some heterogeneous traits and slower pace in others, each carrying a mosaic combination of traits, each of them being closely connected to the local environmental contingencies. The result of such complex and diversified mosaic evolution is that the key transitions that shaped humanity as we know it (bipedalism, social complexity, lithic technologies, use of fire, articulated language, symbolic intelligence) do not seem to have been developed in unison by one dominant species at a time, but may have been developed by several species at a time, in scattered and punctuated ways and rates. Macro-evolutionary processes - like climate changes, environmental instability, ecological unpredictability - seem to be crucial in order to better understand such mosaic patterns that characterized hominin evolution. Mosaic evolution could also shed light on the emergence of *H. sapiens*, a species among many, which appeared around 200 Kya in Africa, and which carried an unprecedented mosaic of

anatomical and cognitive traits that, 100,000 years later, made it particularly flexible, mobile, creative, invasive and talkative. Now we are the only representative of the genus *Homo*, a late and contingent exception, which likely emerged from a mosaic process of species sorting within a highly fluctuating ecological scenario.

Author contributions

Andrea Parravicini wrote the sections: “The term “mosaic” in human evolution”, “The mosaic evolution of bipedal locomotion”, “Mosaic evolution of symbolic behaviours?”, “Explaining mosaic evolution through a macro-evolutionary approach”.

Telmo Pievani wrote the sections: “Mosaic type 1: hominin morphological instability”, “The encephalization trend and the evolution of the first stone tool industries”, “Mosaic type 3: when the trait itself is a mosaic”, “Conclusion”. Both authors revised and approved the final manuscript.

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Editor, Giovanni Destro Bisol



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