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Multi-level human evolution: ecological patterns in hominin phylogeny

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Summary - *Evolution is a process that occurs at many different levels, from genes to ecosystems. Genetic variations and ecological pressures are hence two sides of the same coin; but due both to fragmentary evidence and to the influence of a gene-centered and gradualistic approach to evolutionary phenomena, the field of paleoanthropology has been slow to take the role of macro-evolutionary patterns (i.e. ecological and biogeographical at large scale) seriously. However, several very recent findings in paleoanthropology stress both climate instability and ecological disturbance as key factors affecting the highly branching hominin phylogeny, from the earliest hominins to the appearance of cognitively modern humans. Allopatric speciation due to geographic displacement, turnover-pulses of species, adaptive radiation, mosaic evolution of traits in several coeval species, bursts of behavioral innovation, serial dispersals out of Africa, are just some of the macro-evolutionary patterns emerging from the field. The multilevel approach to evolution proposed by paleontologist Niles Eldredge is adopted here as interpretative tool, and has yielded a larger picture of human evolution that integrates different levels of evolutionary change, from local adaptations in limited ecological niches to dispersal phenotypes able to colonize an unprecedented range of ecosystems. Changes in global climate and Earth's surface most greatly affected human evolution. Precisely because it is cognitively hard for us to appreciate the long-term common destiny we share with the whole biosphere, it is particularly valuable to highlight the accumulating evidence that human evolution has been deeply affected by global ecological changes that transformed our African continent of origin.*

Keywords - *Multilevel theory of evolution, "Sahara pump" hypothesis, Mosaic evolution, Turnover pulses, Bursts of innovation, "Final wave" hypothesis.*

A multi-level approach to evolution

The evolutionary "Modern Synthesis" has provided a fundamental contribution in unifying population genetics with the ecological process of natural selection. It was based on the quite aprioristic idea that every macro-evolutionary phenomenon (i.e. any evolutionary change occurring at the species level and above) should have been reducible to the micro-evolutionary level of variations of gene frequencies in biological populations, under selective pressures (Huxley, 1942). George Williams (1966) baptized "phyletic gradualism" this kind of genetically based gradualism and, according to Stephen J. Gould & Richard Lewontin (1979), this idea has been the dominant "paradigm" in evolutionary biology for the greatest part of the twentieth century.

Modern Synthesis actually was not a monolithic research programme. Some of the founding fathers – among others Theodosius Dobzhansky (1937), Ernst Mayr (1963) and George G. Simpson (1944) – recognized that some evidence (concerning paleontological, biogeographical, and biological patterns) could be interpreted as not strictly gradualistic as for the tempo and/or the mode of evolution. In order to account for the origin of species, Ernst Mayr proposed the well-known pattern of allopatric speciation, which matches genetic changes at population level with environmental and geographical macro-evolutionary triggers, factors of geographical isolation of populations and random genetic drift (Coyne & Orr, 2004). While from the gene-centered perspective the evolutionary process flows through "vertical" changes from micro- to macro-levels, in Mayr's view speciation processes are largely influenced also by "horizontal" displacements, i.e. geographical and climatic events. In other words, the genealogical continuity of change (i.e. variations of gene frequencies) interacts with ecological instabilities and disturbances.

In the 1970s the new discipline of paleobiology (Sepkoski, 2012) contested through quantitative methods the ancillary role of paleontology in evolutionary studies, putting macroevolution at the center of the stage. The paleontological record was re-read in new ways, no longer as just the side-effect of the accumulation of micro-evolutionary processes. Two Mayr's pupils, Stephen J. Gould and Niles Eldredge (Eldredge & Gould, 1972; Gould & Eldredge, 1993) developed the "punctuated equilibria" theory, according to which a significant part of the evolutionary change concentrates in rapid (geologically speaking) events of speciation in peripheral isolates, which undergo different processes (selection, drift, migration) that eventually produce the clado-genetic pattern in allopatry that we see in several phylogenies (Eldredge & Lieberman, 2014). In this view, speciation is the driver of major morphological changes.

Molecular evidence proved that a substantial percentage of evolutionary genetic change is associated with bursts of punctuational branching in phylogenies (Pagel *et al.*, 2006; Pagel & Venditti, 2014). Moreover, although recent studies based on updated mathematical models established that sympatric and parapatric speciation may frequently occur in nature too, allopatry still may be considered the "null hypothesis" of speciation (Coyne & Orr, 2004).

If so, macroevolution could be defined in terms of "patterns and processes pertaining to the birth, death, and persistence of species" (Eldredge & Lieberman, 2014, p. 185). The micro- and the macro- dimension of evolutionary processes are two conceptually separated, but empirically intertwined levels. The vertical dimension of evolution (i.e. changes deriving from the transmission of selected genetic modifications) is strongly interrelated with the horizontal dimension of climatic and geographical factors, able to produce episodic ecological changes which, in turn, affect genetic and genealogical relations among organisms, populations and species.

According to the "hierarchy theory of evolution" proposed by Niles Eldredge, environmental events may have different magnitude: the greater is the magnitude, the greater ecosystems change; the greater the loss of higher taxa, the more different will be the newly evolved taxa. Eldredge compares his model to the "water sloshing in the bucket - the size of the sloshes depending on how hard the bucket is jolted" (Eldredge, 2008, p. 14). According to the "Sloshing Bucket model", the magnitude of the ecological perturbations matches the extent of evolutionary change following three main patterns:

a) When *localized* or *sub-regional* ecosystem disturbances occur, most of the times conspecific populations which still live outside the affected area replace the groups eliminated by the physical disturbance, re-establishing similar local ecosystems. Little or no perceptible evolutionary change occurs, and stasis prevails (Eldredge, 1999, 2003).
b) When *regional* disturbances occur, they may cause too rapid changes, ecosystems collapse and many species across different lineages become extinct. At this threshold level, most of the evolutionary change seems to occur, in conjunction with the birth of new species, possibly triggering "turnover pulse" events.
c) *Global* environmental disruptions give place to mass extinctions, which affect the entire world's biotas and result in the disappearance of larger-scale taxonomic entities. At this level, modified species derive from taxa that survived the mass extinction event, eventually giving rise to radiations of larger groups.

The two “walls” of the bucket represent two different hierarchies of levels. The *genealogical hierarchy,* concerning reproduction or replication, involves genetically-based information systems: the micro-evolutionary level of genes is part of the upper level of organisms, which are nested into local breeding populations and species. The *ecological hierarchy* is about *matter-energy* transfer systems: organisms are parts of local conspecific populations seen in this case as “economic” entities acting for physical survival in their ecological niches. Local ecosystems are parts of regional ecosystems, up to encompass the whole biosphere.

Organisms are simultaneously part of the two different interacting hierarchies: as reproducing “packages” of genetic information (replicators), they are part of the genealogical hierarchy; as matter-energy transfer systems (interactors), they are part of the ecological hierarchy and their business is to survive. At the scale of local populations, reproducing groups and ecological groups often do not coincide. The process of natural selection at the level of organisms incorporates the two dimensions as well (ecological pressures and genetic variations), and it is the “bottom” of the bucket in Eldredge’s metaphor.

This hierarchical view extends the punctuated equilibria theory, and broadens the approach to evolution in a multi-level frame. Changes in ecological dynamics affect the information stored in the genealogical hierarchy, and vice versa. While evolutionary theory has traditionally been centered most on the accumulation of micro-evolutionary processes within populations, evolution takes place in wider ecological contexts, affected by even larger geophysical patterns and processes (such as astronomical events, impacts, tectonic movements, and so on) (Bennett, 1997). Lower level phenomena penetrate and transform the higher levels, but higher-level events set the stage for the agency of lower-level processes (Lieberman *et al.*, 2007). According to Peter Ward & Joe Kirschvink (2015), ecosystems (rather than species or populations) should be considered the real evolutionary entities in the long term.

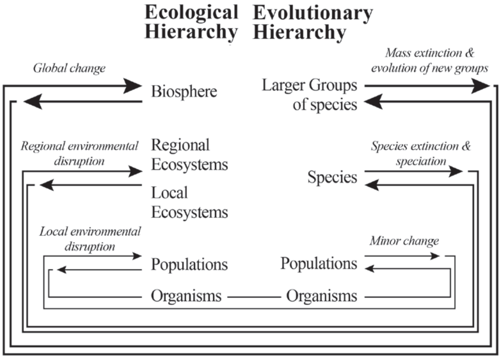

Fig. 1 - The “sloshing bucket” model (Eldredge, 2008, p.14).

Following this trend of studies (Kingston, 2007; Pievani & Serrelli, 2013), the present theoretical review aims to apply a multi-level ecological approach to some major issues emerging in recent paleoanthropological researches.

Climate instability and the first phases of hominin evolution

For a long time phyletic gradualism has been the privileged model in paleoanthropology, giving place to a linear pattern of human phylogeny, where no more than one single polytypic species of hominids could have existed at the same time and geographical range (Dobzhansky, 1962; Mayr, 1963).

Fifty years later, the consensus on how human evolution occurred has largely changed. Advanced tools of integrated analysis and the extensive use of new dating techniques are available. The paleontological and archaeological record has been largely expanded. The growth of the empirical basis of paleoanthropology, together with new convergent evidence coming from different fields (paleontology, molecular biology, paleo-biogeography, paleo-ecology), made the linear model of a single anagenetic evolution completely untenable (despite its episodic resurgence for limited periods of human evolution: see for example Lordkipanizde *et al.*, 2013, about an alleged single polymorphic species of early *Homo*). The pioneering works of Elisabeth Vrba (1980), and Niles Eldredge & Ian Tattersall (1982), followed by other contributions on the same track, have shaped a perspective on human evolution more focused on the key role played by paleo-ecological, environmental and biophysical factors.

Recent paleontological data point to the presence, between 7 and 4.5-4.4 Mya, of at least four species of earliest candidate hominins, nested in three putatively different genera: *Sahelanthropus tchadensis* (6-7 Mya), *Orrorin tugenensis* (6-5.7 Mya), *Ardipithecus kaddaba* (5.8-5.2 Mya) and *Ardipithecus ramidus* (4.5-4.4 Mya). Although there is no general consensus, most paleoanthropologists are prone to include such forms in the hominin clade (Wood & Grabowski, 2015), due to a series of derived traits common to our lineage, suggesting significant behavioral innovations such as: reduction and changes in morphology of canines, which hint a dietary shift; location and orientation in *foramen magnum*, inferences about posture and gait, and other postcranial elements (such as features of the pelvis or lower limbs) which involve a dependence on upright posture and facultative bipedal locomotion. At the same time, many traits related to feet, upper limbs, pelvis, cranial capacity, show slight or no anatomic innovations. This mix of derived and retained traits seems connected to hybrid forms of locomotion, whereas quadrupedalism could alternate to bipedalism, or even to a forest bipedalism, as proposed for *Ar. ramidus* (White *et al.*, 2009; for a comment see Cerling *et al.*, 2010). The “mosaic” anatomy of these earliest hominins suggests the idea of a series of adaptive postural “experiments”, right around the putative time when hominin lineage branched from chimpanzees lineage. The biogeographic area of these forms covers the East African Rift System, until South Africa, apart from the enigmatic *S. tchadensis*, found 2,500 km west of the Great Rift Valley (henceforth GRV).

What about the remote causes of such an early branched phylogeny? Evidence gathered from soil carbonates (Levin *et al.*, 2004; Wynn, 2004; Ségalen *et al.*, 2007; Quade & Levin, 2013), n-alkane carbon isotopes in marine sediments (Feakins *et al.*, 2013), fossilized mammal teeth (Harris *et al.*, 2008; Brachert *et al.*, 2010), matched with model simulations (Sepulchre *et al.*, 2006; Prömmel *et al.,* 2013; Sommerfeld *et al.*, 2014) established a long term aridity trend in East Africa during the Neogene, modulated by periods of high climate variability and shorter periods of relative stability. While the general aridity trend was due to a global cooling phase started at the end of Paleocene, the wet-dry variability for tropical Africa was affected by the intertwining action of the Milankovitch cycles and the progressive rifting and tectonic uplift of East Africa, which progressively stopped the warm and wet air streams from the Atlantic Ocean (Vrba, 1992; Bobe, 2006; deMenocal, 2011; Antón *et al.*, 2014). These climate and environmental changes transformed the eastern and southern African environment from a relatively flat, homogenous region covered with tropical mixed forest, to a heterogeneous region, with high mountains and a mosaic of habitats, ranging from cloud forests and closed woodlands to grasslands and deserts (Cerling *et al.*, 2010).

In this African ecological scenario, the populations of apes which remained isolated in the northern and eastern side of GRV adapted to an unprecedented mix of ecological niches and to a different and fluctuating climate (Pickford, 2006; White *et al.*, 2009). Early hominins lived in a hybrid environment, on the edge of the deep forest. Novel adaptations for the earliest alleged members of the hominin sub-family - including bipedalism, the diminution of the canine premolar honing complex, the advent of megadontia - seem directly associated with such an instable and fluctuating context, characterized by selective pressures related to the increasing extension of open habitats (Cerling *et al.*, 2011).

At the micro-evolutionary level of different hominin populations, likely episodic forms of bipedalism emerged between forests and woodlands, maybe initially evolving as a morphological and postural change with enhanced fitness in terms of thermoregulation functions or social control, afterwards co-opted for survival in more open habitats like grasslands (Wheeler, 1991;

Pickford, 2006; Cerling *et al.*, 2011). Whichever hypothesis might be advanced for the emergence of bipedalism (for a review see Niemitz, 2010), this costly reorganization of bodily architecture, associated with changes in dietary habits, should have increased the flexibility in performing a set of alternative behaviors (a major advantage in unstable environments).

We see here the matching between a mosaic of unstable environments (the ecological hierarchy, above mentioned) and a mosaic of transition forms with different adaptations (the genealogical hierarchy). Genus *Australopithecus* appeared from 4 to 4.2 Mya in similar environmental conditions, as recorded by fossil remains assigned to *A. anamensis* (Kenya). This new species appears to be adapted to a more arid habitat, if compared to *Ardipithecus*. Anatomical analyses hint that, while the latter was probably more accustomed to a woody environment rich of trees or forests punctuated by some clearings, the former lived in more open habitats, covered by grasslands alternating with forests and woodlands (White *et al.*, 2009).

Mosaic evolution at the dawn of genus *Homo*

Australopithecus is a highly diversified and long-lived genus (4.2-1.8 Mya). In addition to the established species, such as the above mentioned *A. anamensis, A. afarensis* (Kenya, Ethiopia, 3.8-2.9 Mya) and *A. africanus* (South Africa, 3-2.4 Mya), there are other species of *Australopithecus* or similar forms whose assignment remains controversial: *A. bahrelghazali* (Chad, 3.5-3 Mya); *Kenyanthropus platyops* (3.5-3.3 Mya, Kenya), *A. garhi* (2.5 Mya, Ethiopia), *A. sediba* (1.95 Mya, southern Africa), and the very recent *A. deyiremeda* (3.5-3.3 Mya, Ethiopia) (Haile-Selassie *et al.*, 2015).

Like early hominins, each of these australopithecines reveals a unique mix of anatomic features with several innovations (mainly related to dentition and posture) foreshadowing typical features of genus *Homo*, melted with retained traits (related to the length of thoracic limbs, toes and fingers, facial shape, low cranial capacity). These complexes of traits point to a diversified diet, an advanced bipedalism and mixed styles of locomotion, with residual adaptations for climbing and arboreal life (Senut, 2006). Australopithecine anatomies show adaptive flexibility, which fits quite well with a changing African niche, because of a persisting climate instability. This enhanced ecological eurytopy enabled hominins to colonize habitats that had hitherto been off limits to hominoids.

Australopithecines lived in Africa for 2 Mya, without changes in brain volumes, covering a wide area, from southern Africa to eastern and northern, with temporal overlapping and close geographic proximity (like in the case of *A. afarensis* and putative *A. deyiremeda* in the Afar region). Quite surprisingly, a stone tools industry has been discovered at Lomekwi 3 site, West Turkana, Kenya, exactly in this period, at 3.3 Mya, predating the Oldowan by 700.000 years, and conjecturally in association with *Kenyanthropus platyops* (Harmand *et al.*, 2015). Thus a scenario with a plurality of species and maybe different bursts of early technological innovation is arising.

When genus *Homo* emerged (at 2.8 Mya according to recent finds - Villmoare *et al.*, 2015), bipedalism became first prevalent and then obligate. This evolutionary transition was carried out by a few species morphologically instable or by a plurality of separated species, each one with a specific set of traits. It follows that also the transition from a smaller hominin, more adapted to an arboreal lifestyle, to an obligate bipedal, reveals the pattern of a “mosaic” evolution (Berger, 2013; Harcourt-Smith, 2015). Climate instability and habitat fragmentation were the macro-evolutionary challenges. A plurality of adaptive strategies, sharing the same flexibility, was the answer.

The consilience of different data (from biogeography, molecular biology, paleo-climatology, geophysics, paleo-ecology) highlighted this pattern. In terms of a multilevel theory of evolution, on the ecological side of the hierarchy, we see a set of diversified behavioral experiments, triggered by the outside forces that operate at the macro-evolutionary level of species and genera in eastern and southern Africa, such as fluctuations in global climate and environmental changes at the regional level. Each species found its own way and strategies of ecological flexibility or dietary specialization (as in the case of genus *Paranthropus*). On the genealogical side of the hierarchy, micro-evolutionary processes occurring at the lower level of populations produced a set of different adaptive changes (documented in the fossil record as we know it today), shaped by the unstable selective pressures of their environment.

The emergence of genus *Homo:* punctuated bursts of speciation and turnover pulses

The patterns of hominin extinction, speciation, and behavioral evolution appear to be strongly associated with climate changes in Africa in the past 5-6 Mya. The bursts of diversification from 2.9 to 2.6 Mya, and from 2.4 to 2 Mya, are especially relevant from a macroevolutionary point of view. In this timeframe, the hominin branching tree reached its larger extension, disproving any claims of linearity for human phylogeny. Beyond the steady presence of the later representatives of the genus *Australopithecus* (*A. africanus*, *A. sediba*, and *A. garhi*), *A. afarensis* became extinct at ca. 2.9 Mya, after almost 1 Mya of apparent morphological stasis, and the genus *Homo* appears to emerge shortly after. The fossil jawbone of an early *Homo* found in 2013 in Ledi-Geraru (Afar) has been recently dated back to ca. 2.8-2.75 Mya (Villmoare *et al.*, 2015), antedating for 500 Kya the oldest known *Homo* fossil found in Hadar, only 30 km far from there. Hadar is also the discovery site of more than 100 individuals of *A. afarensis* (Gibbons, 2015). Another genus, i.e. *Paranthropus*, emerged at 2.7 Mya (*P. aethiopicus*, East Africa, 2.7-2.3 Mya). We observe hence an astonishing co-habitation of different genera in eastern and southern Africa just before and at the beginning of Pleistocene (with regard to the Pliocene-Pleistocene boundary, we use the revised time scale approved by IUGS).

The early taxa belonging to the genus *Homo* include *H. habilis* (eastern and southern Africa) and *H. rudolfensis* (eastern Africa, 2.4-1.9 Mya), but not all researchers are convinced about the need to recognize two taxa within early *Homo* (Wood & Grabowski, 2015). *Paranthropus* includes also *P. robustus* (southern Africa, 2.0-1.5 Mya) and the long-lived *P. boisei* (East Africa, 2.3-1.2 Mya). These multiple different species and genera living in an extended area, from Ethiopia to southern Africa, show again a mosaic of traits related to different environmental niches, often in close geographic contact with each other. This impressive radiation of hominin forms and the concomitant climatic instability and habitat fragmentation strongly suggest a high incidence of geographic speciations and a punctuational pattern of change. This branching picture of human phylogeny is very far from the anagenetic view held by the fathers of Modern Synthesis, and much more similar to the evolutionary history observed in other coeval mammalian taxa (McKee, 2001).

On the side of the ecological hierarchy, we know that during the past 3 million years there were two major intensifications of the cyclic cold extremes during Earth's climate fluctuations. The first one was at the beginning of Pleistocene, when regular and cyclical climatic fluctuations occurred in connection with variations in Earth's orbit and tilt of the spin axis (Shackleton, 1995; Bennett, 1997; Raymo & Huybers, 2008). Some modelling experiments suggested that this drop in global temperatures was also influenced by the continental drift, which gave place to the formation of the Isthmus of Panama (Maier-Reimer *et al.*, 1990; Haug & Tiedemann, 1998) or, in an alternative hypothesis, to the closing of the Indonesian Seaway (Cane & Molnar, 2001). In consequence of any of these events, the ocean streams may have changed their pattern, the ocean surface cooled down, the direction of winds deviated. The polar ice cap began to expand, reaching lower latitudes at regular intervals (Shackleton *et al.*, 1984). All these phenomena triggered severe Ice Ages, with intense and continuous fluctuations between glacial and interglacial phases.

Related to these global changes, East African climate became even drier in consequence of the long term aridity trend, while in the short term it became more instable with the alternation of high and low climate variability and cycles of moisture and aridity (e.g. long high variability intervals lasted from 3.2 to 2.9 Mya and from 2.8 to 2.5 Mya – Potts, 2012). Because of these and other events related to tectonic movements and volcanism, periods of relatively stable environment and the aridity trend alternated with lengthy intervals of habitat unpredictability and resource uncertainty, with wide diversity of vegetation setting and heterogeneity of ecological niches (deMenocal, 1995; 2011; Bobe & Behrensmeyer, 2004; Kingston, 2007; Cerling *et al.*, 2011; Antón *et al.*, 2014).

We may suggest that, due to habitat fragmentation in African environments, many peripheral populations became isolated, providing the best conditions for the expected occurrence of extinction events, allopatric speciations and adaptive radiations in a punctuational evolutionary mode. This could be the macro-evolutionary reason why the human evolutionary tree reached its maximum extension right around this turbulent geological period. An adequate account for the current paleo-anthropological evidence "suggests a pulsed/threshold nature of hominin speciation and migration events" (Maslin *et al.*, 2015).

Paleontologist Elisabeth Vrba studied the effects of climate fluctuations on Plio-Pleistocene African fauna, namely mammals, since the 1980s. She observed that many different species (like antelopes, rodents and others) disappeared, replaced by others. The pattern of these appearances/disappearances is "abrupt" (in geological terms) and cross-genealogical. It shows two sorts of change: ecological-biogeographical and evolutionary. These "fundamental patterns of the evolution" (Lieberman *et al.*, 2007) configure the hypothesis of a "turnover pulse" in African Plio-Pleistocene mammals (Vrba, 1992, 1993, 2000, 2015). As mentioned above, in a multilevel ecological perspective these patterns are usually the consequence of intermediate magnitude events, between global and local disruptions (the point B in the aforementioned Sloshing Bucket model, section 1). A disturbance at the regional scale is required to initiate most vicariance, dispersal, extinction and speciation events. If environmental changes produce barriers and habitat fragmentation at a regional scale, then allopatry in populations of different species is likely to occur, by vicariance or dispersal, setting the conditions for speciation and extinction events (Vrba, 1992). The fragmentation of geographic ranges influences different taxonomic groups, which simultaneously react to the environmental forcing changing their population structure.

Vrba's hypothesis focuses on the implications of climatic oscillations for the evolution of new forms, functions, and species in hominins and other mammals. An alternative hypothesis, proposed by Richard Potts (1998, 2012, 2013), focuses on a putative inter-specific selection for adaptability (recently, Vrba stressed the compatibility of the two models – Vrba 2015). The evolutionary and biogeographic patterns of diversification in tropical Neogene mammals documented by Vrba (1992) have been affected by climatic oscillations between arid and moist phases, and by the subsequent environmental fragmentation, which caused repeated episodes of vicariance, followed by geo-dispersal.

Hadar and Ledi-Geraru formations in Afar, related to the discovery of the earliest representatives of genus *Homo* (in particular the jawbone fossil dated ca. 2.8-2.75 Mya) and to several specimens assigned to *A. afarensis*, have been recently identified as an area where repeated turnover pulses occurred. Paleoanthropologist Kaye Reed identified in Hadar a faunal turnover, at about 3 Mya, associated with an open wooded grassland landscape (Reed, 2008). Other turnover pulses have been spotted in the near Ledi-Geraru area, about 2.84-2.58 Mya (Di Maggio *et al.*, 2015, p. 1355). These documented faunal turnovers outline a clear confirmation of Vrba's hypothesis and a straightforward example of the intertwined action of genealogical and ecological forces.

At the same considered span of time, around 2.7 Mya, genus *Paranthropus* emerged, simultaneously with the earliest extensive Arctic glaciation

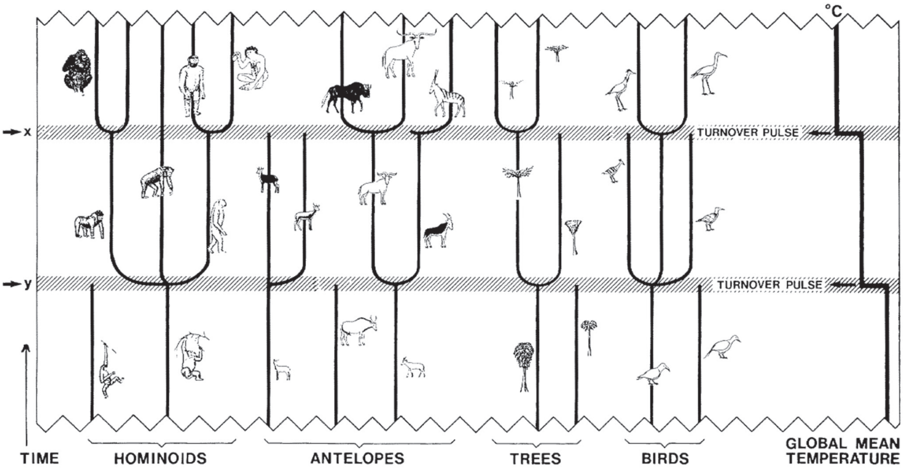

Fig. 2 - "Turnover-pulses: in this hypothetical diagram, major climatic changes at times y and x initiated turnover pulses, that is, coincident speciations and extinctions in groups as different as hominoids, antelopes, trees, and birds" (Vrba, 1992, p. 13).

which in Africa coincided with the spread of Sahara desert, dryness and significant increase in C-4 grass proportion (Bonnefille, 2010; Vrba, 2015). *Paranthropus* was equipped with a powerful masticatory apparatus, specialized for a vegetarian diet almost completely based on C4 plants, being *P. boisei* more focused on grasses and sedges, while *P. robustus* on tree fleshy fruits, as well as variable C4 resources, as stable carbon isotope analyses have proven (Sponheimer *et al.*, 2013). *Paranthropus* was adapted for consuming tough or gritty foods, which nonetheless had the effect of broadening the range of food items consumed, allowing these forms to subsist in varied environments (Wood & Strait, 2003). In the same period and within the same instable environment, *Homo* developed completely different strategies, which reveal increased behavioral flexibility, with larger brains, reduction of the posterior teeth size, dietary flexibility, production of stone artifacts (Antón *et al.*, 2014). As Vrba (2015, pp. 1859-1860) pointed out, the known hominin record mostly coincides with major climatic changes and speciation pulses in all larger African mammals as well. Climate instability, turnover pulses and a plurality of genera feature the still unclear birth of genus *Homo*.

The worldwide spread of genus *Homo*: biogeography, dispersal, macroevolutionary trends

While all the australopithecines and *Paranthropus* became extinct in different times after 2 Mya, genus *Homo* outlived and gave rise to something like a geographical adaptive radiation on a global scale. Again, macro-evolutionary factors played a crucial role in the process.

Around 2 Mya, a new way of being human emerged in the eastern and southern African regions. *H. ergaster* (ca. 1.9 Mya - 900 Kya) presents many innovative traits which involve brain size expansion, life history (shortened inter-birth intervals, delayed development), body size and shape, post-cranial anatomy, dietary flexibility. In a still fluctuating and changing environment, all these innovations seems related to adaptive versatility, growing capacity in niche construction, all features essential to colonize new environments. As a matter of fact, this form went out of Africa shortly after speciation, concomitantly with the beginning of recent glaciations, and probably in consequence of the ecological instability (Antón *et al.*, 2014).

The limited available fossil evidence suggests that *H. ergaster* was the first hominin able to go out of Africa. From the southern and eastern areas of Africa, populations of *H. ergaster* went towards northern regions, going up to the Nile corridor and reaching the Middle East, across the Jordan Valley, up to Dmanisi, Georgia (1.85 Mya). Then, a part of them turned towards the East and reached the South and East Asia (Java, Indonesia, 1.66 Mya; maybe with a genealogical connection with the later *Homo floresiensis*); another part went to Europe forming the regional branch of *Homo antecessor*.

An interesting ecological hypothesis has been proposed in order to account for hominin first dispersals. During climate fluctuations, Sahara oscillates from a dry environment to a more humid and green one, producing a sort of "pump effect": when in the green phase, with rivers and large grasslands (documented in recent times as well), it attracted large herbivorous mammals, which were chased by predators, followed in turn by *Homo* populations of scavengers, across the green Sahara and up to the Mediterranean sea and Middle East. Conversely, when in the arid phase, Sahara rejected all them towards the coasts and southwards. In short, Sahara may have pulled up and brought out the populations as consequence of these climatic and environmental fluctuations (Calvin, 2002).

Similarly, the "pulsed climate variability hypothesis" describes the African paleo-climate in which early human evolution could have occurred, invoking different macro-evolutionary mechanisms and patterns such as turnover pulses, variability selection hypothesis and allopatric speciations (Shultz & Maslin, 2013; Maslin *et al.*, 2014, 2015). This scenario relates the periodic hominin dispersal events to the presence or absence of lakes and rivers. When the lake basins were dry they became uninhabitable and hence hominin populations would have been forced to move to the north and south. The absence of lakes may have facilitated allopatric speciations in some key refugia. When the basins were filled with water, the wet conditions could have been even more conducive to dispersal because they may have allowed hominin populations to expand both northwards and southwards in search of resources, generating a pumping effect pushing them towards the Sinai Peninsula or into Southern Africa (Maslin *et al.*, 2014).

This connection between environmental instability and changes in the ecological relationships among different species, involving vicariance and dispersal processes, could possibly shed light on the secret of the mobility in the genus *Homo*, never experienced before by other hominins. The combination of the Sahara pump hypothesis with the "dispersal phenotype" showed by *H. ergaster* could be a starting point to catch the reasons why human populations went out of Africa several times after 2 Mya. Also in this case, micro-evolutionary factors (adaptations to local selective pressures) match with macro-evolutionary patterns and processes.

During the Pleistocene and its ice ages, the territories were plenty of mobile physical barriers. Geographical expansion through highly fragmented and diversified habitats produced a predictable fragmentation of populations. Vicariance and dispersal of human populations out of Africa, thus, may have triggered pulses of allopatric speciations, now in Eurasia too. This could be the reason for the remarkable morphological variation showed by the fossil record assigned to genus *Homo* and found in different parts of the Old World after 1.8 Mya: *H. ergaster* in Africa; *H. erectus* (1.8 Mya - 100 Kya) in China and Indonesia; the still debated *H. georgicus* in Georgia; *H. antecessor* (1.2 Mya - 780 Kya) in Europe. Four putative different species: almost an adaptive radiation.

After this first out of Africa, several clues point to a second Out of Africa, held by the single, polymorphic, and widespread species named *H. heidelbergensis*, around 800-600 Kya (Manzi, 2012). This new kind of humanity spread across a wide area encompassing Africa and Eurasia, and it is the candidate common ancestor of several subsequent geographically distinct trajectories, local varieties, new species such as *Homo neanderthalensis* in Europe. Finally, a third wave of expansion out of Africa were carried out by *Homo sapiens* since 130-100 Kya.

According to a multilevel and ecological approach to human evolution, the interpretation proposed by Lordkipanidze *et al.* (2013) about the existence of a unique polymorphic species of early *Homo* ca. 2 Mya (*H. erectus ergaster georgicus*) is less tenable than the hypothesis which argues for the existence of three or more distinct species (see also Antón *et al.*, 2014). The biogeography of genus *Homo*, with several "out of Africa" processes and repeated spreading across a strongly diversified macro-area, full of geographic barriers, which extend from southern Africa to Far East and West Europe, in a situation of intense ecological instability, is much more compatible with a model of multiple geographic speciations. The return to an anagenetic model of human evolution needs to assume, against any parsimony, a gene flow throughout different continents (for a criticism of the "lumper" phylogenetic speculation in Lordkipanidze *et al.*, 2013, see Wood, 2014).

Furthermore, the "mosaic nature" of *A. sediba* and the strong morphological variation showed by the specimens of *H. erectus* in Dmanisi, being both of them coeval of other three different African taxa (i.e. *H. ergaster*, *H. habilis* and *H. rudolfensis*), hint that "the early diversification of *Homo* was a period of morphological experimentation", and overall that "the intra- and inter-taxon diversity observed in early hominins cannot be understood apart from its environmental context" (Antón *et al.*, 2014, p. 5).

Despite all the technical difficulties in demarcating real paleontological species, at least *Homo antecessor* in West Europe, *Homo heidelbergensis* in Africa and *Homo floresiensis* in Indonesia (from 74-95 Kya to 18 Kya) highlight clear morphological branching divergences, as well as *Homo sapiens* (200 Kya-) and *Homo neanderthalensis* (200-40 Kya – Higham *et al.*, 2014) stand out as definite morphologically distinct forms (confirmed or not the hybridization hypothesis). It follows that, even adopting the less branching phylogenetic hypothesis, there is no support for anagenetic trends in the evolution of genus *Homo*.

According to De Salle & Tattersall (2012), even the encephalization trend along human evolutionary history has not been a stable and gradual course within a single lineage, but a trend emerging and modulated in different human species or regional varieties: "the average brain size increase among members of the hominid family during this time as due to the preferential survival of larger-brained species, rather than to inexorable brain enlargement in one central lineage" (De Salle & Tattersall, 2012, p. 281).

The emergence of cognitively modern humans: the "final wave" model

Also the speciation of *Homo sapiens* in Africa, ca. 200 Kya, has been affected by climate instability and dry phases. *H. sapiens'* early physiological and anatomical traits are the large globular skull (average 1400 cc), a tall and slim body, a further delay in development process if compared to the other recent human species. The birth of cognitively modern humans, however, seems to be more recent, as if anatomy and behavior were temporally disjointed. Only around 80-60 Kya, robust findings point to an unprecedented appearance of symbolic expressions throughout the areas of distribution of *H. sapiens*. Engravings and decorations found in South Africa, dated 75 Kya, are probably the clues of a first "burst" of innovation, emanating from a putatively symbolic intelligence in some populations. Innovative symbolic behaviors appeared in Europe quite later, in association with Cro-Magnon *Homo sapiens*, and after recent dating, also in Sulawesi island at about the same period (ca. 40 Kya) (Aubert *et al.*, 2014).

Biogeography becomes crucial also in this case. This recent evidence corroborates the idea that the bursts of behavioral and cognitive innovation in South Africa are related to a growing population of *H. sapiens* (carrying L3 mt-DNA haplogroup) that was expanding out of Africa, carrying the symbolic and linguistic capacities showed by the members of this groups later in Europe and Far East. Otherwise, it would be less parsimonious to think that the very same cave paintings evolved two times, independently, in Europe and Sulawesi, like a sort of "cultural convergence". A different biogeographic framework is emerging: rock art may have deeper origins outside both western Europe and Sulawesi, dating back to the earliest period of the final global dispersal of our species. If this is true, symbolic intelligence has been physically carried out of Africa by the last, very successful, wave of human expansion.

Molecular data matched with biogeographical analyses shed further light on this scenario. The low level of genetic diversity observed in our species mostly out of Africa (Kaessmann *et al.*, 2001; Huff *et al.*, 2010) may be connected with substantial reductions occurred in human populations, namely with one or more population "bottlenecks". A possible hypothesis stresses the role of both climate crises and repeated waves of expansion out of Africa carried out by *H. sapiens* several times (the major three being around 120-100 Kya, 85-50 Kya, and 60-50 Kya). Only the third "final wave" would have been the crucial one for the future of our species out of Africa, giving place to a series of founder effects due to the planetary diffusion of our ancestors (Deshpande *et al.*, 2009; Pievani, 2012a).

Molecular data suggest that "all mt-DNA lineages found outside Africa derive from just two haplogroups (M and N) that descend from L3 haplogroup" (Jacobs & Roberts, 2009) and L3 haplogroup increased in population size right between 86 Kya and 61 Kya. Therefore, this African haplogroup seems to correspond to the ancestral population from which all mt-DNA lineages, found outside Africa today, descend. According to this biogeographical model, the entire human population outside Africa descended from the same African founder group. As a corroboration, the decrease of the genetic variance in human populations is strongly correlated with their geographic distance from Africa (Ramachandran *et al.*, 2005; Li *et al.*, 2008).

Also recent archaeological data show that the emergence of symbolic behaviors coincides significantly with this final wave. New southern African chronological reconstructions of Still Bay and Howieson's Poort industries (from about 75 Kya to 60 Kya) confirm the occurrence of ephemeral and punctuated bursts of technological and behavioral innovation, linked to climate changes and demographic fluctuations in southern Africa (Jacobs & Roberts, 2009; Jacob *et al.*, 2008). Jacob and Roberts argue that local environmental changes in southern Africa during the Middle Stone Age triggered several demographic expansions and contractions in *Homo sapiens* populations, consequently affecting social networks and bursts of cultural innovation.

It is possible that symbolic intelligence, maybe triggered by a fully articulated language, emerged during this crucial timeframe in South Africa, promoting the key cultural innovations which in turn triggered the final wave out of Africa ca. 60-50 Kya (Atkinson, 2011; Pievani, 2012a). The symbolic behaviors may have arisen in such a complex ecological condition, with different ephemeral cultures produced by networks of hunter-gatherer groups.

The "final wave" evolutionary model is an example of close intertwining between different levels of explanation and factors: biogeographic patterns; paleo-climate parameters; demography; social networks; expansions and migrations; molecular data; archaeology and material cultural evolution. The ecological hierarchy of evolutionary levels, affecting the phases of expansion and contraction of populations, can influence behavioral changes. Demographic expansions at the lower level of single populations tend to extend the network of social contacts and to increase cultural exchanges, while contractions break the social and economic networks and produce fragmentation and isolation among hunter-gatherer communities (possibly with local innovations as well). Behavioral and cultural innovations may produce demographic expansions, in a positive feedback loop. Therefore, "a spark of human ingenuity" (Jacobs & Roberts, 2009) could have given to L3 haplogroup a competitive advantage in terms of technological and communication efficiency, social cohesion, group coordination. Such a spark became a strong catalyzer to ignite and fuel the positive feedback of behavioral innovation and demographic expansion that led our species to a worldwide spread.

Sporadic expressions of symbolic behaviors are glimpsed also in Neanderthals, and now maybe in *H. erectus* too, even since 540 Kya with the first putative abstract patterns engraved on a fresh water shell from the site of Trinil, Java (Joordens *et al.*, 2015). These episodic cognitive expressions may hint “incipient language capabilities” (Antón *et al.*, 2014), but they are not comparable with the systematic and global behavioral change we can find in the later *H. sapiens* populations. Nevertheless, as in the case of bipedalism and other major transitions in human evolution, “mosaic” expressions of symbolic intelligence could have preceded the complex and systematic behaviors we see in *H. sapiens*. Thus we can conjecture multiple pathways of cognitive evolution, among the plurality of branches which characterizes human phylogeny even recently. Different hominin populations and species may have followed a range of symbolic trajectories in which “modern cognition is represented by different mosaics of cultural innovations” (d’Errico & Banks, 2013, p. 373).

Concluding remarks

These recent models integrate archaeological, paleo-climatological, paleontological, molecular and demographic data in order to explain both the biological and the cultural evolution of cognitively modern humans. A multilevel approach to evolution provides a useful framework for bringing together and unifying the observed interplays between patterns and processes which belong to different evolutionary hierarchies (ecological and genealogical), structured along different levels. The toolbox of evolutionary theory is richer than in the past (Pievani, 2015).

Micro-evolutionary explanations which appeal to processes occurring below the species level and within biological populations - i.e. gene frequencies, adaptations by natural selection, sexual selection, and genetic drift - are fundamental, but they have to be integrated with macro-evolutionary patterns above the species level, giving due relevance to ecological and geophysical patterns and processes in human evolution (Pievani, 2012b). The physical and ecological world is not a mere backdrop of evolution: it changes, and such large-scale changes had profound effects on human evolution as well (Eldredge, 1999).

The interactions between the biotic and abiotic factors shaped the main features of human evolution. The genus *Homo* is descendant of such a complex intertwining of different levels of evolutionary change. It is the consequence of an explosion of punctuated equilibria and turnover pulses in early Pleistocene, which were in turn the side effects of environmental changes caused by the Ice Ages in Africa. The same inconstant environmental conditions might have promoted our attitude to dispersal, until the “final wave” of cognitively modern humans spreading out of Africa. We humans may be the effect of a sequence of large-scale climatic and ecological disturbances which shook the water in the African “sloshing bucket” of evolution.

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