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Light has been thrown (on Human Origins)

A Brief History of Paleoanthropology, with Notes on the "Punctuated" Origin of *Homo sapiens*

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1. *Darwin's predictions*

In *The Origin of Species by means of Natural Selection*, Darwin spent only a line to comment – or, rather, to predict the development of our knowledge in the decades to come – about the evolution of our species: «light will be thrown on the origin of man and his history» (Darwin [1859]: 488). However, the day after that troubled publication, when all the 1.250 copies went out of print, an intense debate started; and this debate was not on orchids, chaffinches or turtles. As a matter of fact, most of the arguments were aroused by the relationships of monkeys and apes with *Homo sapiens*, and – more than a risky prediction – that single line toward the end of the book became the focus of a general debate on his theory. Thus, in a sense, Charles Darwin was prudent because he was aware that this issue – the nature and origin of ourselves as a species – would have been the real or, at least, the main target of all the controversies that were expected to emerge after a theoretical framework (natural selection) was given to a phenomenon that had already been largely debated among naturalists: the phenomenon known as "biological evolution".

The main controversial topic was faced soon by Thomas Henry Huxley, particularly when he published a volume in three parts with the eloquent title *Evidence as to Man's Place in Nature* (Huxley [1863]). This was also the book that inspired the conference by Filippo De Filippi in Turin, which represented the official entrance of the Darwinism in Italy (De Filippi [1864]). After a decade, Darwin himself devoted an entire theoretical treaty in two volumes on both human evolution and sexual selection: *The Descent of Man* (Darwin [1871]).

Some other predictions were put forward in this book by Darwin. One, for instance, was when he stated that Africa should have been our more probable homeland, in view of the greater affinities of our species with gorillas and chimpanzees – which actually live in Africa at present – than with the Asian orangutangs (Darwin [1871]: 199). It is remarkable that at Darwin's time the only discoveries of fossil humans where from Europe and, at the same time, other scientists were suggesting to look toward the Far East, influenced by our affinities with the ape of the Indonesian islands of Borneo and Sumatra. Always in the *Descent of Man*, Darwin argued that the fossil record – thus, the science of paleontology – could never have the opportunity to shed light on the process of evolution. The hard evidence represented by the fossil record is too dispersed in space and time, he reasoned, to represent a concrete support for our evaluation of the natural history of extinct and living creatures, as well as for our understanding of the evolutionary mechanism implied (Darwin [1871]: 201).

Fortunately, he was wrong on this very last point. After almost 150 years, the discoveries and achievements of paleoanthropology – just a newborn science at the Darwin's time – demonstrate that he was rather pessimistic about such heuristic approach, as we will briefly recall in this paper.

2. *Neanderthals and Cro-Magnons*

A first "fossil light" on human evolution was actually there a few years before the publication of *The Origin of Species*. An incomplete skeleton had been occasionally discovered in 1856 by workers in a cave (Feldhofer Grotto) of the Neander Valley, or Neanderthal, not far from Dusseldorf in Germany. We will not go into details here, but we should recall that the morphology of that skeleton appeared sufficiently different from the modern range of variation to allow the identification of an extinct human species, referred to as *Homo neanderthalensis* (King [1864]).

Other specimens pertaining to the same human type had been found in the previous decades at a site in Belgium and from a quarry in Gibraltar and many more Neanderthals will come later from other European localities in Belgium, Croatia, France, and Germany. Thus, at the beginning of the 20th century, all these discoveries had largely demonstrated that the skeleton from Neanderthal was not an isolate enigmatic finding, but the genuine representative of an extinct human species.

Nevertheless, according to some scientists (e.g. Huxley [1863], [1864]), this fossil evidence failed to represent the expected evolutionary link between apes and ourselves – the so-called «missing link» they were looking for – particularly in view of the large cranial volumes and big brains showed by the representatives of such an extinct humanity. Conversely, this feature suggested that the Neanderthals were a collateral and partially diverging side-branch, rather than an ancestor of *Homo sapiens*. It is astonishing to see how this view may be close to how we interpret the Neanderthals today (e.g. Stringer, Gable [1993]; Trinkaus, Shipman [1993]; Harvati, Harrison [2006]) in view of an extraordinary greater variety of data, including samples of their DNA (e.g. Green *et al.* [2010]).

Not even the so-called Cro-Magnons were appropriate to be considered as intermediate between non-human primates and recent humans. Such anatomically modern creatures are known after the fossil skeletons that were found in the eponymous rock shelter in Southern France (Broca [1868]). These specimens displayed a morphology in many respects identical to extant human populations and were considered in close relationship with the authors of the magnificent manifestations of prehistoric rock art discovered in 1879 at Altamira, in northern Spain. Thus, these modern-looking specimens appeared (and actually are) fossil representatives of our own species, *Homo sapiens*.

Always in Europe, between 1908 and 1912 the discoveries at Piltdown, in England (Dawson, Woodward [1913]), arose in consequence of a deplorable episode of forgery that we only have the possibility to mention here. Nevertheless, it is important to recall that it represented a useful test – unintentional of course – to evaluate the potential of the emerging science of paleoanthropology, which was capable to reject a false evidence, as it successfully happened in the following decades well before the definitive exposure of the fraud (Weiner, Oakley, Le Gros Clark [1953]).

3. *The missing link*

Thomas Huxley had written: «...the structural differences which separate Man from the Gorilla and the Chimpanzee are not so great as those which separate the Gorilla from the lower apes» (Huxley [1863]: 123). What was missing was just a ring in the chain, capable of definitively connecting the greater apes with humans. This could have fasten *Homo sapiens* to other living creatures: in a word, to nature. The German morphologist and embryologist Ernst Haeckel also hypothesised the existence in the past of such a missing link (Haeckel [1874]) and introduced a theoretical name in latin: *Pithecanthropus alalus* (that is, from Greek, “ape-man incapable to speak”).

Influenced by these ideas, as well as convinced that our closest relative is the Indonesian orangutang, the Dutch anatomist Eugène Dubois went to the Islands of

Sumatra and Java, in Indonesia, toward the end of the century and really found... the missing link. In 1891 a molar tooth came from the excavations in the bank of the Solo River at Trinil, in central Java, followed by a calotte, which appeared extremely flat (platycephalic), with heavy brow-ridges and a receding forehead, clearly more archaic than a Neanderthal and with an encephalic volume midway the extant apes and present humankind. In 1892, his workers found also a modern-looking femur and eventually, in 1894, he gave to these discoveries the name of *Pithecanthropus erectus* ("ape-man", because of the calotte; "upright walker", because of the morphology of the femur) (Dubois [1894]; see also Campbell [1965]: 15-16). Half a century later, it has been proposed to include these fossils, together with other similar specimens found during the first half of the XX century in Java and China, within the genus *Homo*, representing a single species referred to (because of priority rules) as *Homo erectus* (Mayr [1950]).

Now, we might consider that, although some light began to be thrown, one of the Darwin's predictions was still waiting for being verified. As a matter of fact, with the Neanderthals, the Cro-Magnons and even with the *Pithecanthropus* we were still looking for in Eurasia.

In other words: what about Africa...?

4. *Eventually in Africa*

In 1924, a young anatomist teaching at the University of Witwatersrand in Johannesburg, Raymond Dart, disclosed the gates of Africa to the study of human evolution. The almost occasional discovery of an infantile cranium coming from the limestone quarries of Taung gave rise to the identification of a kind of extinct "ape-man" that he named *Australopithecus africanus* (Dart [1925]), advocating the formidable intuition that the species represented by such a diminutive specimen was a small-brained, but bipedal ancestor of *Homo sapiens*.

The Taung discovery is among the «most significant finds in the history of paleoanthropology (...) because of its status as the first recognised member of a totally new, previously unknown, major group of fossil hominids» (Meikle, Taylor Parker [1994]: 52). However, Dart's claim did not persuaded the academic community and he was severely criticised. Many were favourable to admit that the Taung child was the representative of a new species of fossil primate, but they did not accept that it might be ancestral to ourselves.

Subsequently, however, thanks to the efforts of the Scottish palaeontologist Robert Broom, from the contiguous caves of Sterkfontein, Kromdraai, Swartkrans (all near

Johannesburg), and from those of the Makapansgat Valley (in the Northern Province of South Africa), a number of fossil came to light between the '30s and the '40s (Broom [1936], [1938], [1949]). It was therefore possible to discover adult individuals of *Australopithecus africanus*, giving definitive support to the Dart's hypothesis. Moreover, a different type of our putative ancestors came to light in some of those caves: it appeared unquestionably more heavy than *Australopithecus africanus*: "robust" in many dental traits and skeletal features of the masticatory apparatus. This new type of South-African ape-man received various binomial appellatives – including that of *Paranthropus robustus* (Broom [1938]) that is still in use today – suggesting the existence of different contemporaneous lineages of australopithecines or, alternatively, a single evolutionary trajectory from a generalised type (*Australopithecus*) towards a more derived one with increasing masticatory, thus dietary, specialization (*Paranthropus*). It was not possible at that time to have a clear picture of these South-African findings in terms of chronology, because of the complex process of deposition within the karstic cave systems where these and other fossils were found.

More light – also in terms of absolute chronology – had to come from another extraordinary area for human paleontology: East Africa. This region started to become of interest for researchers and open to international expeditions only after the end of the '50s. It was in 1959, in fact, that a fossil specimen came eventually to bless the efforts of Louis and Mary Leakey, who were looking for human ancestors and Palaeolithic stone tools since 1931 in one of the most celebrated among the East-African localities. This is the site known as Olduvai Gorge, a very special area along the Great Rift Valley, in Tanzania. A robust type of "australopithecine", similar but even more specialized than the *Paranthropus robustus* found in South Africa, was discovered there in stratigraphic association with stone tools of the earliest Paleolithic. It was named *Zinjanthropus boisei* (Leakey [1959]), now commonly included within the genus *Paranthropus* as a distinct species referred to as *Paranthropus boisei*.

Was such a robust australopithecine the first tool-maker? Was this massively-toothed and bipedal ape the author of the lithic artefacts that the Leakey found in the same stratigraphic levels at Olduvai? The most reliable answer is not positive and this became clear in the following years: particularly when Louis Leakey, Phillip Tobias, and John Napier (1964) described a small sample of other fragmentary fossil pieces found at Olduvai, and gave them the name of *Homo habilis*.

The relatively larger volume of the braincase suggested by these new fossils from Olduvai and some dental features were consistent with the interpretation of these pieces of bones and teeth as representatives of some kind of primordial humankind: creatures still close to the australopithecines, but to be included within our own genus *Homo*. The debate about the taxonomic and phylogenetic status of *Homo habilis* is still controversial, but those and other fossils – found subsequently at Olduvai and elsewhere, particularly in localities around the Lake Turkana, in Kenya (e.g. Wood [1991]) – are indeed there. These fossils demonstrate that around 2 million years before present (probably half a million of years earlier) a new kind of human ancestors, ecologically interpreted as "scavengers", were capable to produce elementary stone tools. They were also at an earlier stage of what we may consider the fundamental process of our evolution: a process usually referred to as "encephalization", represented by the progressive increase in endocranial volume, but not only (e.g. Bruner, Manzi, Arsuaga [2003]).

At the beginning of the '70s, our knowledge about the early African human ancetors was broaden again, in terms of geography, chronology, and taxonomy. Certainly, the pinnacle of this stage in the history of the research was the discovery by Don Johanson of a very popular fossil specimen: the skeleton nicknamed and known as "Lucy" (formally AL 128-1), which was found at Hadar, Ethiopia, in 1974 (Johanson, Taieb [1976]). During the same decade and subsequently, other important discoveries were made in Ethiopia and in Tanzania, including the footprint fossil track that came to light at Laetoli, not far from Olduvai. A new species was described merging these discoveries, thanks to the collaboration between Don Johanson, Tim D. White, and Yves Coppens (1978): the name given to the new species is *Australopithecus afarensis*, probably the best known "pre-human" taxon that we know at present (e.g. Kimbel, Rak, Johanson [2004]). It extended our knowledge about the australopithecines to the range between 4 and 3 million years before present. It also made clearer that these ancestral representatives of our evolutionary tree were bipedal creatures; in this sense, they were like us, despite they were also more similar to apes as far as endocranial volume and body proportions are concerned. Like the other australopithecines, they already had a peculiar combination of dental traits, including the enlargement of molars and premolars and the reduction of canines and incisors. As a whole, they furnished the best evidence about features and adaptations midway between apes and humans, much better than those that could have been expected by the evolutionary biologists of the XIX century, Charles Darwin included.

5. *Phylogenetic trees*

Thus, toward the end of the ‘70s, a fundamental improvement concerning the human evolutionary tree and the phylogeny of the hominids was introduced in combination with the description of *Australopithecus afarensis*, viewed as the most ancient and the most archaic fossil representative of our evolution ever discovered. This scenario put the new species at the origin of our ancestry, leading to a divergence between the australopithecines, on one hand, and the genus *Homo*, on the other hand. It is noteworthy that the geometry of such an evolutionary tree is very similar to what we believe now (Fig. 1), showing a major divergence around 2.5 million years before present.

The most notable difference is that the number of extinct species considered at that time (about 6) is almost nothing with respect to the number of taxa (more than 20; see Fig. 1) we recognise at present. We may also notice (for instance, looking at the most popular hominid genealogy published in Johanson, Edey [1981]) that a sequential and linear pattern of evolution was the rule in the scenarios of the late '70s. Evolutionary trees of that time, in fact, still foresee continuous and progressive anagenetic lineages, following the so-called “phyletic gradualism” influenced by the Modern Synthesis of the ‘40s (e.g. Huxley [1942]). However, during the same decade, a model usually called “punctuated equilibria” was suggested from a paleontological perspective (Eldredge, Gould [1972]), where it was claimed a crucial contribution of cladogenetic events (or “speciations”, as opposed to “phyletic evolution”) in evolutionary processes. When applied to human evolution, this “heretic” model tends to imply a bushy hominid tree (Gould [1977a]), richer in both several species and punctuated speciations than those expected according to any gradualistic model, which is strictly consistent in turn with the micro-evolutionary paradigm of the Synthesis.

According to a convinced lumper such as Tim D. White, Gould’s prediction could have pushed nowadays paleoanthropologists to «herald each new fossil as evidence of ancient hominid biodiversity» (White [2003]: 1994), and to advocate that these claimed new species and/or new genera are in support of a «many-branched bush of diversity» (using the words of two convinced splitters: Tattersall, Schwartz [2000]: 33). Although there can be elements of truth in the White’s criticism and even if the currently recognized number of species may appear overestimated, in the last thirty years an extraordinary number of paleoanthropological discoveries has greatly expanded our understanding of the past complexity, and has (in our view) substantially confirmed Gould's prediction.

Nevertheless, we may consider this same topic from another perspective, according to a seminal paper by I. Tattersall ([1986]: 168):

> [...] it might well be argued that it would be better for the comprehensiveness of our understanding of the human fossil record that, if err we must, we err (within reason!) on the side of recognizing too many rather than [...] too few species units.

As a matter of fact, there are some crucial evolutionary passages until the appearance of *Homo sapiens* – including the emergence of our species (as we will briefly discuss later) – that are consistent with the evolutionary pattern postulated by the model of punctuated equilibria.

6. *New methods, new models*

In the last couple of decades, the study of the fossil record has been supported by new methods, including the fields in rapid expansion of paleogenetics and paleogenomics (e.g. Lalueza-Fox, Gilbert [2001]; Green, Shapiro [2013]), as well as the development of the numerical approach to morphology represented by the so-called «geometric morphometrics» (e.g. Slice [2005]). This term includes a number of approaches based on the multivariate statistical analysis of Cartesian coordinate data, usually (but not always) limited to landmark point locations. These include the evaluation of a mean shape and the description of variations from this, as well as within or between group diversity estimates. Geometric morphometrics has been considered, not without emphasis, a «new synthesis» in the study of biological forms (Rohlf, Marcus [1993]), since it is capable to combine the qualitative description of different shapes (morphology) with a rigorous quantitative approach (morphometrics).

In addition, the use in paleoanthropology of electronic equipments imported from 3D laser scanning or other advanced medical/industrial imagery (computed tomography, microtomography) and even more sophisticated imaging techniques (synchrotron light tomography), currently allows researchers to virtually penetrate into the intimate structure of each fossil specimen and compare it with other such specimens from a really innovative perspective (e.g. Zollikofer *et al.* [1998], [2005]; Spoor *et al*. [2003]; Bruner, Manzi [2006]; Macchiarelli *et al.* [2006]).

In the last couple of decades, these new tools represented an effective revolution, with the development of what is commonly called «virtual paleoanthropology» (Weber [2001]). Images produced by electronic equipments combined with geometric morphometrics have opened a number of new possibilities for the analysis of the fossil record, including: a) the virtual extraction and reconstruction of anatomical elements, with the possibility to correct plastic distortions; b) the analysis of inaccessible internal and small-sized structures; c) the modelling of biomechanical properties, of the ontogenetic process, of evolutionary changes; etc. In the near future and, in some cases, already at present the anatomy of the fossil specimens, usually rare and precious findings, are no longer be studied directly, but on their virtual representations.

Combined with these new techniques and methodological improvements in the study of morphology, we have assisted to a number of successful attempts to bring human evolutionary studies towards the growing field of the *evo-devo* (after Gould [1977b]) approach, which combines evolution (phylogeny) with developmental biology (ontogeny). The assumption is that any morphological change we observe along evolutionary lineages reflects modifications of the developmental process. For instance, we may ask when and how the modern human pattern of growth and development appeared (Moggi-Cecchi [2001]). A number of studies have demonstrated that the australopithecines, and possibly the earliest species of the genus *Homo* too, had a growth and developmental pattern similar to those of extant great apes (Bromage, Dean [1985]; Zeresenay *et al.* [2006]; Lacruz *et al.* [2008]). Moreover, although debated (see, e.g., Macchiarelli *et al.* [2006]), there are researches strongly suggesting that even late representatives of the genus *Homo*, like the Neanderthals, did not have an ontogenetic pathway identical to ours (e.g. Ponce de León, Zollikofer [2001]; Lieberman *et al*. [2002]; Bruner *et al.* [2003]; Manzi [2003]; Ramirez Rozzi, Bermudez de Castro [2004]; Gunz *et al*.[2010]).

7. *The ontogenetic revolution*

There is an anatomical district, where our pattern of growth and development deeply interacts with the process of encephalization that has characterised the evolution of the genus *Homo*. This anatomical district is the pelvis, particularly the pelvic inlet: the bony channel through which the large cranium of the future newborn must necessarily pass in order to come to light (e.g. Arsuaga [2012]). We may assume that a strong selective pressure should have driven the co-evolution between pelvis morphology – which is functionally consistent with the bipedalism acquired at the beginning of our lineage, between 7 and 4 million years ago and further developed subsequently – and the process of encephalization, which started with the emergence of the genus *Homo* and followed an exponential increase during the last 2 million of years (Fig. 2).

Given a number of constrains imposed by both the morphology of the pelvis of our remote ancestors, as bipedal creatures, and the selective pressure acting in favour of progressively enlarged brains and related cranial dimensions, human adaption followed an *evo-devo* template during the last 2 million of years or so, implying changes in the regulation of growth and development. This should have led – among other non irrelevant effects – to a more premature and altricial newborn in the modern species than in other "archaic" representatives of the genus *Homo*. Our babies born in fact "premature" with respect to what is expected from the correlation between brain dimensions and gestation lengths observed among non-human primates. Thus, in our species, foetal rates of growth follow for another several months after birth. Viewed in this perspective, the origin of *Homo sapiens* corresponds to what one of us (GM) had called an «ontogenetic revolution».

This echoes the observation that the encephalization process followed different trajectories along the various evolutionary lineages of the genus *Homo* (Bruner *et al.* [2003]). As a matter of fact, despite the expansion of brain and cranial dimensions was a process shared by *Homo erectus* in Eastern Asia, *Homo neanderthalensis* in Europe, and the ancestors of *Homo sapiens* in Africa, this process neither followed the same evolutionary modalities nor led to the same evolutionary destinies (e.g. Manzi [1991], [2003]; Manzi *et al.* [2000]). Particularly, the Asian and European lineages had a tendency to maintain an archaic architecture of the braincase, similar in many respects to the putative early *Homo* ancestors from Africa, and eventually went extinct. The same model was preserved also in Africa until about 200 thousand years before present, when this architecture sharply changed with the appearance of modern humans (e.g. Lieberman *et al.* [2002]; White *et al.* [2003]), while populations preserving an archaic-looking cranial shape – such as, for instance, the Neanderthals – still persisted elsewhere.

When viewed in this perspective, the origin of *Homo sapiens* – which is obviously the pivotal event in human evolution – appears now in a stimulating light. Actually, according to an *evo-devo* approach, the emergence of our species is a convincing example of cladogenetic evolution (i.e. a genuine speciation), advocating both the fundamental role of exaptation (in our case a big brain) and the intervention of an innovative change (in our case a new regulation of growth and developmental patterns), which may occur within a restricted and isolated population, as postulated by the «punctuationist» perspective (Eldredge, Gould [1972]), eventually leading to an event of allopatric speciation. This scenario represents the ontogenetic revolution from which *Homo sapiens* probably emerged.

From different sources of data (e.g. Stringer [2002], Mellars *et al.* [2007]), we know at present that modern humans appeared in Africa – more probably in eastern Africa – around 200 thousand years before present, when in Europe the Neanderthals were still at an early stage of their evolution. We also know that *Homo sapiens* started soon a worldwide diffusion, driven by a cultural potential that previous and penecontemporaneous hominids had never experienced, including the symbolic and conceptual thought implied by Palaeolithic art expressions (Fig. 3).

A side-effect of this adaptive success was represented by the extinction of other representatives of the same genus *Homo*, as demonstrated for instance by the fate of the Neanderthals, according to the evolutionary principle of "exclusive competition" between closely related and sympatric species. The rapid distribution of *Homo sapiens* across the entire planet followed. This was the prelude of the present demographic expansion of a single species of a bipedal and highly encephalised primate that appears to us out of any natural control. For the future, we may only hope in our potential to evolve from the cultural viewpoint: in this perspective, science and philosophy should play their respective and relatively independent roles.

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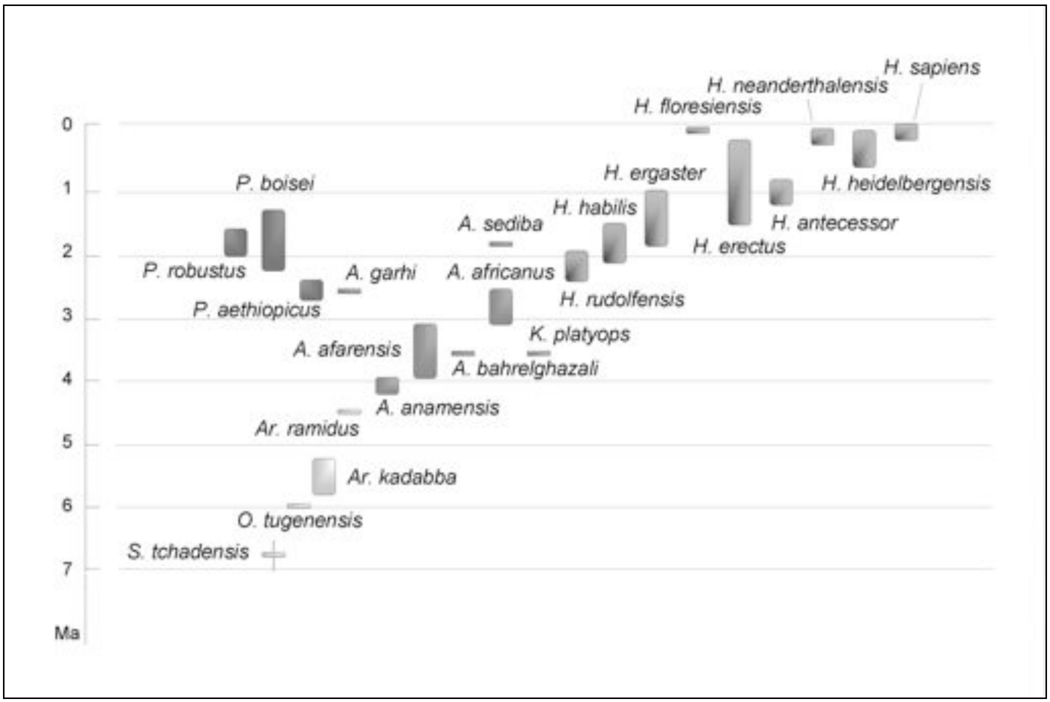

Figure 1 – At present, our knowledge on human evolution includes 23 species, distributed along the last 7 million of years (Ma) and attributed to a number of genera, i.e.: Sahelanthropus (S.), Orrorin (O.), Ardipithecus (Ar.), Australopithecus (A.), Kenyanthropus (K.), Paranthropus (P.), and Homo (H.). The fossil evidence is distributed above according to the year of the first description of each species, whereas the graph below suggests some phylogenetic relationships.

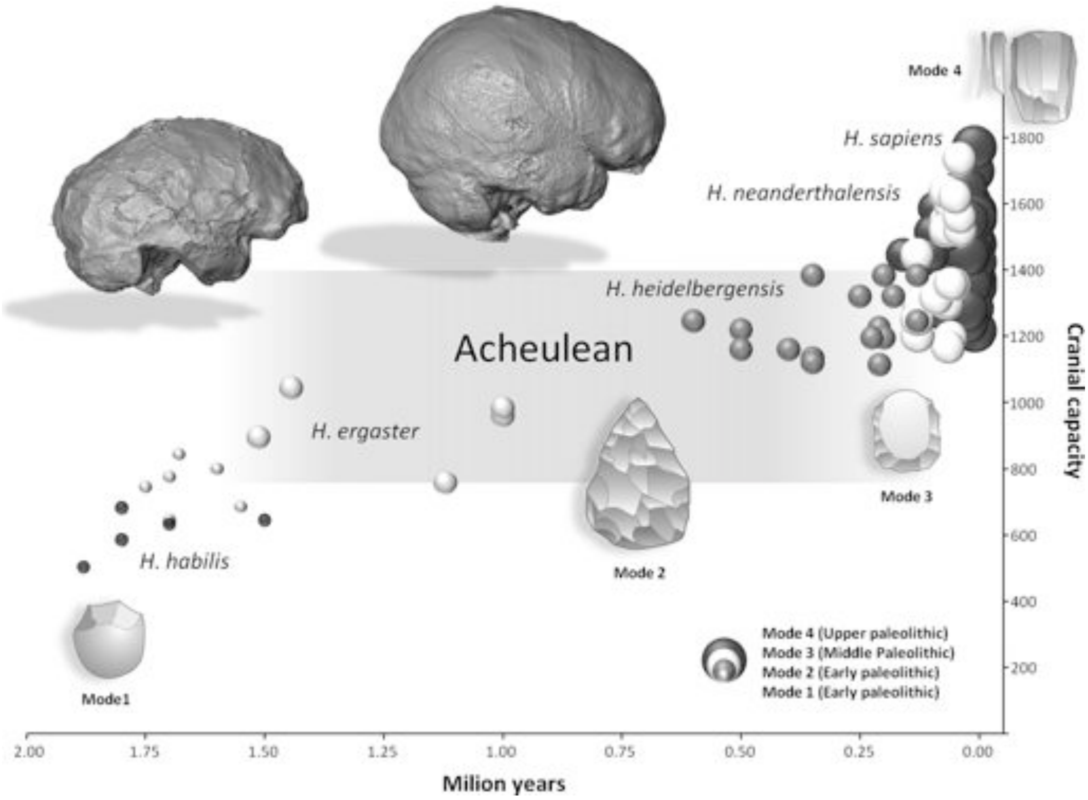

Figure 2 – The expansion of brain volumes, or "encephalisation", during the evolution of the genus *Homo* follows an exponential growth, but this is (at least in part) a side-effect of the intersection between the chronologies of different species and a rather general trend, while it must be remarked that each regional lineage tends to follow a peculiar pattern of encephalisation. At the same time, the increasing in complexity of the lithic industries (technological "Modes" of the Paleolithic) are only apparently associated to this curve; however, it is clear that different species (represented by shades of gray) are associated with more than one technological horizon (dimensions of the spheres). In addition, much of human evolution is covered by the Acheulean (Mode 2 of Lower Paleolithic), representing a sort of prolonged stasis in contrast with the rather continuous process of brain expansions. Data from Holloway et al. (2004).

Figure 3 – Aesthetic perception and expressions of symbolic thought across time in *Homo sapiens*: just a naïf suggestion.