

G. AULETTA - M. LECLERC - R.A. MARTÍNEZ (eds.)

BIOLOGICAL EVOLUTION: FACTS AND THEORIES

A Critical Appraisal 150 Years
After
"The Origin of Species"

With an Address of Cardinal Levada

CB2, 100,5% 235,01 - 275,01



HUMAN EVOLUTION: A BRIEF HISTORY OF THE RESEARCH SINCE DARWIN'S TIME

Giorgio Manzi

Abstract

“Light will be thrown on the origin of man and his history”: this was the single line that Charles Darwin devoted to human evolution in the *Origin of Species*, 150 years ago. Despite short, apparently incidental and innocuous, this sentence actually represented a “risky prediction”. In other words, Darwin’s claim was: whether natural selection is the basic mechanism of the origin of species, in general, there is no reason to exclude *Homo sapiens* from analogous circumstances. As a matter of fact, the debate that followed was focused on the phylogenetic relationship of our species with monkeys and apes. The circa twenty species of extinct hominids that we know at present demonstrate that Darwin’s prediction was correct: light has been thrown. At present, the science of human origin (or paleoanthropology) appears to be able to shed light not only on our evolution, but also on mechanisms and patterns of the evolution in general. This paper contains a brief overview of the most important discoveries that characterised the history of paleoanthropology until about 30 years ago; this synopsis will be followed by an introduction to current methods of research, to briefly discuss the origin of our own species.

1. Introduction

This is the story of a young interdisciplinary field of scientific investigation commonly referred to as paleoanthropology. It appeared on the scene when Darwin was developing what he called, soon after his voyage on the *Beagle*, “*my theory*” (Darwin 1837, 214). Since then, it is widely recognized that the phenomenon of evolution is ingrained on that simple, although counterintuitive and perhaps

cognitively uncomfortable, idea of natural selection shared by Charles R. Darwin and Alfred R. Wallace in 1858 (Moody 1971), then examined in great detail one year later in *The Origin of Species* (Darwin 1859). Today, whether the facts supporting the evolutionary approach to biology are many, whether many are the involved mechanisms, and many are the pertinent perspectives and approaches, the scientific theory explaining the phenomenon of biological evolution is just one, Darwin's; it represents the focus of the entire field of biology, as in the words of Theodosius G. Dobzhansky (1973, 125): “*nothing in biology makes sense except in the light of evolution.*” Thus, it is clear that speaking about theories (using the plural) is — at least in my view — scientifically incorrect, epistemologically inappropriate, and may be philosophically misleading.

This paper starts with some of Darwin's expectations on human evolution: what he did, what he did not, and what he could not foresee with respect to our present knowledge on the issue. Then we will follow a historical journey to review the most important discoveries (*Figure 1, a-f*) and some debates that have characterised the history of paleoanthropology until recent times. This overview will be closed by a brief outline of current methods of research, focused on discussing the appearance of modern representatives of the genus *Homo* — i.e., the origin of our own species: *Homo sapiens* — including aspects of investigation that Darwin could have never imagined at his time nor we could only 20 or 15 years ago.

2. Darwin's predictions

It is well known that in *The Origin of Species* — a volume of about 500 pages — only a line toward the end of the book was devoted to the origin of man and his history (Darwin 1859, 488): “*light will be thrown on the origin of man and his history.*” However, when all the 1250 copies went out of print and an intense debate started on both evolution as a phenomenon and the mechanism of natural selection that explains the phenomenon, the debate was not on orchids, chaffinches or turtles, but was focused on the relationships of monkeys and apes with *Homo sapiens*. In a sense, he was prudent because he was aware that this — the nature and origin of ourselves as a species — would have been the real target of the controversies he expected to emerge after a theoretical framework was given to the phenomenon of evolution. However, we will see how this concise and “risky” prediction was appropriate.

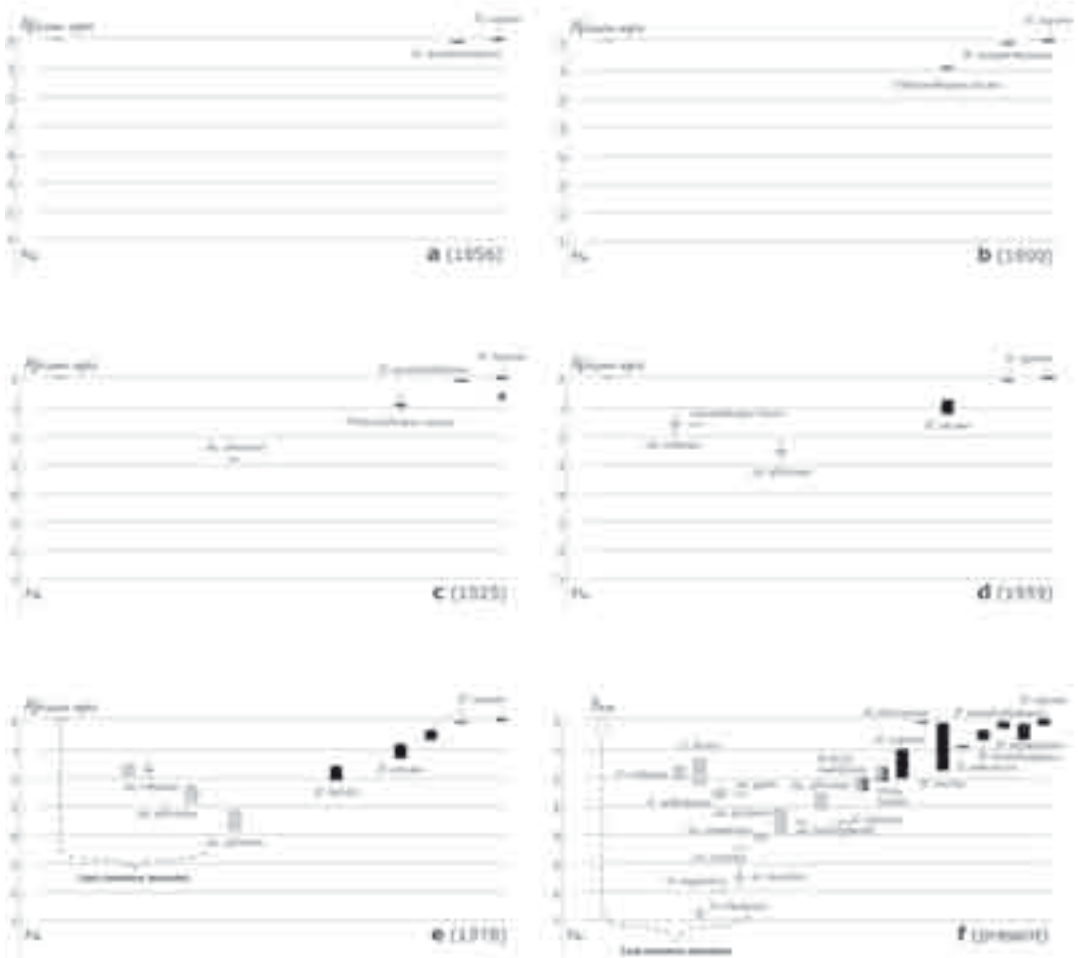


Figure 1. Our understanding of human evolution throughout the 150 years passed since Darwin's time is organized in six momentous steps. The fossil evidence known in 1856 (a) dealt only with the skeleton found in the Neanderthal, while in 1900 (b) we had many other Neanderthals, fossil representatives of our species (the “Cro-Magnons”), and the bones found in Java and ascribed to *Pithecanthropus erectus* (later included within *Homo erectus*); then, in 1925 (c), the description of the first australopithecine opened the gates of Africa to paleoanthropology; in the last one of these charts (c), the position of the species inferred after the Piltown forgery is indicated by a star. Subsequently, part of the sub-Saharan Africa became the main theatre of field endeavours, leading to special improvements in 1959 (d), with the first discovery at Olduvai, and in 1978 (e) with the description of *Australopithecus afarensis*, which followed after about 15 years that of *Homo habilis* (1964); in the same period, the contribution of the so-called “molecular clock” added an indirect evaluation of the coalescence time (still subjected to adjustments due to new fossil and genetic data) between our evolutionary lineage and those of the extant African apes. At present, the knowledge on human evolution has enhanced enormously, with the identification of about 20 species, attributed to a number of genera that include: *Sabelanthropus* (S.), *Orrorin* (O.), *Ardipithecus* (Ar.), *Australopithecus* (Au.), *Kenyanthropus* (K.), *Paranthropus* (P.), and *Homo* (H.)

It is also well known that, on the spur of the moment and with great efficacy, the controversial target of the nature and origin of our species was faced by Thomas Henry Huxley, through a volume in three parts with the eloquent title *Evidence as to Man's Place in Nature* (Huxley 1863). It is worth mentioning that this book influenced the conference read by Filippo De Filippi in Turin, which represented the official entrance of the Darwinism in Italy (De Filippi 1864).

Only after a decade will Darwin devote an entire treaty in two volumes on both the topic of human evolution and the idea of sexual selection (Darwin 1871). Other risky predictions were put forward here. I would like to draw the attention of the reader to a couple of them. It was risky, for instance, to state that Africa was our more probable homeland, in view of the great affinities of our species with gorillas and chimpanzees that, as a matter of fact, live in Africa at present (page 199). It was risky because at Darwin's time the only discoveries of human fossils were from Europe; in addition, it was also the time when other scientists were suggesting to look toward the Far East, influenced by our affinities with the orangutangs from Borneo and Sumatra. Another risky prediction was to state that the fossil record and the science of paleontology as a whole could not shed light on the process of evolution, in general, and on our origins, in particular. Too dispersed in space and time is the hard evidence represented by the fossil record, he reasoned, to be a concrete support for our comprehension of the natural history of extinct and living creatures, and the evolutionary mechanism implied in it (page 201). Fortunately, he was wrong on this point. The discoveries and achievements of paleoanthropology — just a newborn science at Darwin's time — demonstrate that he was rather pessimistic about our heuristic approach.

3. Neanderthals and Cro-Magnons

A first spot of light on human evolution, furnished by a fossil specimen, was actually there three years before the publication of *The Origin of Species*. An incomplete skeleton had been discovered by workers in a cave in the Neander valley, or Neanderthal, not far from Dusseldorf in Germany. We will not go into details here, but we may recall that the morphology of that skeleton appeared diverse in some respects from the range of variation displayed by extant human populations; thus, the extinct species *Homo neanderthalensis* was introduced into the literature (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 twentieth

century, all these discoveries had largely demonstrated that the skeleton from the Feldhofer Grotto in the Neanderthal was not an isolate enigmatic finding, but the genuine representative of an extinct human species.

Nevertheless, according to some eminent scientists (e.g. Huxley 1863; 1864), such an extinct humanity failed to represent the expected evolutionary link between the apes and ourselves, particularly in view of the large cranial volumes and big brains showed by its representatives. Conversely, this feature suggested that the Neanderthals were a collateral and partially diverging side-branch, rather than an ancestor of *Homo sapiens*. It is extraordinary to see how this view is close to what we think about Neanderthals today (e.g., Stringer and Gable 1993; Trinkaus and Shipman 1993; Harvati and Harrison 2006), given that our present conclusion is based on an extraordinary variety of data, increasingly deepened and detailed, including those on Neanderthals' DNA (see Biondi and Rickards, this volume).

Neither was it possible to consider as plausible ancestral creatures in relationships with non-human primates the so-called Cro-Magnons, the well-known fossil representatives of *Homo sapiens* that were discovered in those same decades (e.g., Broca 1868). They displayed a morphology in many respects identical to extant human populations and were the probable authors of the magnificent manifestations of prehistoric rock art. Thus, these modern-looking specimens appeared at that time (as well as today) simply as fossil representatives of our own species.

Between 1908 and 1912 there were also the discoveries at Piltdown, in England (Dawson and Woodward 1913), which were due to a well known as well as deplorable episode of forgery that I will only mention here. Nevertheless, I think it is important to recall that it represented a useful test — unintentional of course — to evaluate the potential of the emerging science of paleoanthropology to reject a false evidence, as it successfully happened in the following decades until the definitive exposure of the fraud (Weiner, Oakley and Le Gros Clark 1953).

4. The missing link

In the second half of the nineteenth century, naturalists and palaeontologists were waiting for the discovery of a definitive link between apes and ourselves, usually referred to as 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 it missed was just a ring in the chain, capable of definitively connecting the greater apes with humans. This could have fastened *Homo sapiens* to other living creatures: in a word, to nature. The German morphologist and embryologist Ernst Haeckel came also to

hypothesise the existence of such a missing link (Haeckel 1874) and to give it a name: *Pithecanthropus alalus* (that is, from Greek, “ape-man incapable to speak”).

Influenced by these ideas, the Dutch anatomist Eugène Dubois went to the Island of 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 platycephalic, with heavy brow-ridges and a receding forehead, clearly more archaic than a Neanderthal. In 1892, then, his workers found 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). It was only half a century later, that the great biologist Ernst Mayr proposed to include these fossils, together with other similar specimens found during the first half of the twentieth century in Java and China, within the genus *Homo*, representing a single species referred to as *Homo erectus* (Mayr 1950).

Now, we might consider that — while some light began to be thrown on the origin of man and his history — one of Darwin’s predictions was still waiting to be verified, given that with the Neanderthals, the Cro-Magnons, and Dubois’ *Pithecanthropus* we are still remained in Eurasia. In other words: what about Africa...?

5. 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 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 and Taylor Parker 1994, 52) However, Dart’s claim did not persuade the academic community and he was severely criticised. Many were happy 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. However, thanks to the efforts of the Scottish palaeontologist Robert Broom, between the ‘30s and the ‘40s, from the contiguous caves of Sterkfontein, Kromdraai, and Swartkrans (again near Johannesburg,

in South Africa), a number of fossil hominids came to light (Broom 1936; 1938; 1949). It was therefore possible to know the aspect of the adult individuals of *Australopithecus africanus*, giving definitive support to Dart. A different type of hominid was also discovered in some of those caves: it appeared unquestionably more heavy and robust than *Australopithecus africanus* 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, 378) that is still in use today — and suggested the existence of different contemporaneous lineages of australopithecines or, alternatively, a single evolutionary trajectory from a generalised type (*Australopithecus*) towards a more derived one (*Paranthropus*), in combination with an increasing masticatory, hence alimentary, specialization.

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 the hominids and other fossils had been 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 interesting for many researchers and open to a number of international expeditions only after the end of the '50s. It was in 1959, in fact, that a new type of hominid came 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 hominid localities. This is the site known as Olduvai gorge, a very special area along the Great Rift Valley, in Tanzania. A robust type of early hominid, similar but even more specialized than the *Paranthropus robustus* found in South Africa, was discovered there in apparent association with some kind of early stone tools. At first it was named “*Zinjanthropus*” (Leakey 1959), but now it is commonly included within the genus *Paranthropus*, as *Paranthropus boisei*.

Was this 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 answer is most probably negative and this became clearer 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 of these fossils, among other features, was the evidence expected to pertain to some kind of an earliest human, a creature still close to the australopithecines, but which could be included within our own genus: the

genus *Homo*. The debate about the taxonomic and phylogenetic status of *Homo habilis* is still open and controversial, but those and other fossils — found subsequently at Olduvai and elsewhere (see Coppens, this volume), particularly in localities around the Lake Turkana, in Kenya (e.g., Wood 1991) — are indeed there. These fossils demonstrate that around 2 million years ago (probably earlier) a new kind of hominids, ecologically interpreted as “scavengers”, were capable to produce elementary stone tools and were at an earlier stage of what we may consider the fundamental process for our evolution: that is the process of progressive increase in endocranial volume — a process usually referred to as “encephalization” (Bruner, Manzi and Arsuaga 2003).

At the beginning of the ‘70s, our knowledge about the early African hominids was broadened 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 hominid: the skeleton nicknamed and known as “Lucy” (formally AL 128-1), which was found at Hadar, Ethiopia, in 1974 (Johanson and Taieb 1976). During the same decade and subsequently, other important discoveries were made in Ethiopia, in Kenya (around the Lake Turkana), and in Tanzania, including the footprint fossil track that came to light at Laetoli, not far from Olduvai. A new species was described merging the discoveries from Hadar and Laetoli, thanks to the collaboration between Don Johanson, Tim 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 and Johanson 2004). It extended our knowledge of the australopithecines to the range between 4 and 3 million years before present. It also made clearer that these ancestral hominids were bipedal creatures, like us, but that they were more similar to apes as far as their endocranial volumes 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, with a significant increase in enamel thickness, furnishing the best evidence of features and adaptations clearly distinct from either those of the extinct and extant apes or of the genus *Homo*.

6. Phylogenetic trees

It is worth noting that a fundamental phylogenetic tree was introduced in the literature toward the end of the ‘70s, in combination with the description of *Australopithecus afarensis*, viewed as the most ancient and the most archaic fossil hominid ever discovered (as far as I know, the most refined version of this phylogeny

is that reported in Johanson and Edey's book of 1981). This scenario (see *Figure 1e*) put the new species at the origin of our evolutionary lineage, in the position of last common ancestor of both the other australopithecine and the genus *Homo*. It is also noteworthy that its geometry is very similar to what we think now — although the number of extinct species considered at that time (N=6) is almost nothing with respect to the 20 hominid taxa, or more, we recognize — showing a major divergence, at about 2.5 million years before present [compare *Figure 1f*], between the phylogenetic and adaptive trajectories of *Australopithecus* and *Paranthropus*, on one side, and that of the genus *Homo*, on the other.

With the exception of this major divergence, we may notice however that a sequential and linear pattern of evolution is the rule in such a scenario. As a model, in fact, the tree of the late '70s tends to foresee continuous and progressive anagenetic lineages, still following the gradualistic approach influenced by the “modern synthesis” of the '40s (e.g., Huxley 1942). By contrast, it is well known that during the same decade, two palaeontologists were suggesting a model (*punctuated equilibria*) that envisages a higher contribution of cladogenetic events in the course of the evolutionary process (Eldredge and Gould 1972). When applied to human evolution, this new model may imply a *bushy hominid tree* (Gould 1977a), richer in species and cladogenetic events, than those expected with the gradualistic model, which vice versa is strictly consistent with the micro-evolutionary paradigm of the synthesis.

As a consequence, according to a convinced *lumper* among my colleagues (White 2003; 1994), Gould's prediction could have pushed contemporary paleoanthropologists to “*herald each new fossil as evidence of ancient hominid biodiversity*”, advocating these claimed new species and/or new genera in support of a “*many-branched bush of diversity*” (using the words of two recognized *splitters* among my colleagues: Tattersall and Schwartz 2000, 33).

Although there can be elements of truth in White's criticism and even if the currently recognized number of species may appear as overestimated, in the last thirty years an extraordinary number of paleoanthropological discoveries has greatly expanded our understanding of the past complexity [*Figure 1f*], and has substantially confirmed Gould's prediction. Viewed from another perspective, according to a seminal paper by Ian 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. After all (...) even a subspecies has a history worthy of investigation.

Nevertheless, there are some crucial evolutionary passages until the appearance of *Homo sapiens* — including the emergence of our species, as I will briefly discuss later — that are apparently consistent with the pattern postulated by the model of punctuated equilibria.

7. Hominidae

Figure 1f describes the distribution in time of the approximately 20 species, or more, that are recognized at present by a great number of paleoanthropologists. While time is represented vertically, from 7 million years to the present, and the various bars display the chronological span of each species, these same species are disposed horizontally in a tentative order that would be indicative of both the morphological affinities between them and their respective, although hypothetical, phylogenetic relationships. Different grey tones represent different genera (or groups of affine genera): for instance we have the earliest hominids in white, australopithecines in mid-grey, and the genus *Homo* in black.

There is a side debate, at present, as far as the taxonomic status of the ensemble of genera and species represented here is concerned. It is debated in fact whether we and our extinct close relatives and ancestors should be considered a family (*Hominidae*), a subfamily (*Homininae*), a tribe (*Hominini*), or even a single genus; whether such was the case, all the species represented in *Figure 1f* should be included within the genus *Homo*, together with the two living species of *Pan* and, perhaps, also with the present genus *Gorilla* (e.g., Goodman *et al.* 1998). I do not wish to enter this debate now, but I should point out that the extended knowledge we have at present about human evolution is uncomfortably described by a restricted taxonomic approach.

Anyway, as a whole, a picture emerges that recalls the basic geometry of the phylogenetic tree put forward in the late '70s, with a major divergence at about 2.5 million years before the present, although this new representation exhibits a huge expansion in time as well as in diversity.

Obviously, crucial passages include the detachment of our lineage from the common ancestors with African apes, possibly around 6-7 million years before present or earlier, the origin of the genus *Homo* (despite a certain taxonomic incertitude, but together with the first appearance of Palaeolithic implements), slightly earlier than 2.5 million years ago, and eventually the emergence of modern humans, well established by a variety of data at about 200 thousand years before present. It is worth noting that all these crucial passages are African events.

From this general picture, it is also clear that various species were contemporaneous among them. For instance the species of *Paranthropus* were synchronic with

the earliest *Homo* species and, at least in part, lived in sympatry with them. Moreover, there were species of later *Homo* that, given their extended geographical diffusion in Africa and Eurasia, overlapped in time for long periods, being either sympatric (living in the same geographic area) or, more frequently, allopatric. Some of them greatly diverged between each other over periods of allopatry, as for instance happened for either *Homo ergaster* and *Homo erectus*, respectively in Africa and in Eastern Asia, or the sequence of chronospecies *Homo heidelbergensis* – *Homo neanderthalensis*, in Europe, with respect to their counterparts (*Homo rhodesiensis*), in Africa, which in turn led to the appearance of *Homo sapiens*.

It seems clear to me that, after the divergence from the African apes, what we know at present about the natural history of the hominids depicts a very complex history. This story strongly recalls the evolutionary pattern implied by the model of punctuated equilibria — hence, a bushy tree — rather than a simple trajectory from non-human primates to “Man”: what we might call a *ladder*, according to the Gould’s (1977a) metaphor.

8. New methods, new paradigms

In the last couple of decades, the study of the fossil record has been supported by the development of geometric morphometrics (e.g., Slice 2005). This term includes a series 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, which allows for the visualization of individual differences, as well as within or between group diversity estimates, in view of the morphology of the original specimens. Geometric morphometrics has been considered, not without emphasis, a *new synthesis* in the study of biological forms (Rohlf and Marcus 1993), since it is able to combine the description of different shapes (the field of morphology) with a rigorous numerical and multivariate approach (which is typical of morphometrics).

In addition, the utilization of electronic equipments imported from the highly sophisticated fields of both medical imagery (namely, computed tomography) and industrial imaging techniques (like microtomography or laser scanning), currently allows researchers to virtually penetrate into the intimate structure of each fossil specimen and compare it with other such specimens from an innovative perspective (e.g., Zollikofer *et al.* 1998; 2005; Spoor *et al.* 2003; Bruner and Manzi 2006; Macchiarelli *et al.* 2006). These new tools have been revolutionizing paleoanthropology in the last 20 years or so, by the development of what is commonly called

“virtual paleoanthropology” (Weber 2001). As a matter of fact, virtual representations like these, combined with geometric morphometrics when appropriate, 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. It is usually said that, in the near future (in some cases already at present), the anatomy of the fossil hominids, that usually represent rare and precious museum items, will no longer be studied on the specimens themselves but on their virtual representations.

Assisted by these new techniques and methodological improvements, and after the publication of a seminal book by Stephen Jay Gould (1977b), during the last decades we have assisted a number of successful attempts to bring human evolutionary studies towards the growing field known as *evo-devo*, which combines evolution (phylogeny) with developmental biology (ontogeny). Virtually all the morphological change we observe along evolutionary lineages reflects some modification of developmental processes; thus, 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 and 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 and Zollikofer 2001; Manzi 2003; Ramirez Rozzi and Bermudez de Castro 2004).

9. The “ontogenetic revolution”

Now, 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 and, particularly, I am referring to the pelvic inlet, the bony channel through which the large cranium of the future newborn must necessarily pass in order to come to light. A strong selective pressure should have driven the co-evolution between our pelvis morphology — which is functionally consistent with the bipedalism acquired at the beginning of the evolutionary trajectory of the hominids, let’s say between 7 and 4 million years before present — 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.

Given a number of constraints imposed by both the morphology of the pelvis of our remote ancestors, as bipedal creatures, and the selective pressure acting in favor of progressively enlarged brain and cranial dimensions, the adaptive solution probably followed an *evo-devo* template, implying a rapid change in the regulation of growth and developmental pattern. This should have led — among other non irrelevant effects — to a more premature and altricial newborn in the new species than in other “archaic” *Homo* species. It is well known, in fact, that our babies are premature, with respect to the correlation between brain dimensions and gestation lengths observed among non-human primates, and follow foetal rates of growth for another 9 months after birth or so. Viewed in this perspective, the origin of *Homo sapiens* corresponds to what I call our “ontogenetic revolution”. Such an expression 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, 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 in Africa too 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).

The origin of *Homo sapiens* — which is obviously the pivotal event in human evolution — appears in a stimulating light when viewed from this perspective. Actually, according to an *evo-devo* approach, the emergence of our species appears as a convincing example of evolution by means of natural selection, combined with a model of punctuated equilibria, which in turn postulates both the fundamental role of exaptations (in this case a big brain) and the intervention of an innovative change (in this case a new regulation of our growth and developmental pattern), occurred within a restricted and isolated population, eventually leading to a punctuated event of speciation: our speciation. This was the ontogenetic revolution of *Homo sapiens*.

Given the above scenario, 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 — at about 200 thousand years ago, 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 hominids had never experienced, including the symbolic and conceptual thought implied by Palaeolithic art expressions. A side-effect of this adaptive success was represented by the extinction of other representatives of the same genus *Homo*, as the fate of the Neanderthals demonstrates, according to the evolutionary principle of “exclusive competition” between closely related and sympatric species.

Then, the relatively rapid distribution of *Homo sapiens* across the entire planet followed. This was the prelude of the present gargantuan demographic expansion of a single species of a bipedal and highly encephalised primate that appears to me out of any natural control. We may just hope in our potential to evolve from the “cultural” viewpoint: in this perspective, science and philosophy should play their respective and relatively independent roles.

REFERENCES

- Broca P., 1868, “Sur les cranes et ossements des Eyzies”, *Bulletins de la Société d'anthropologie de Paris* 3: 350–92, 416–46, 554–74.
- Bromage T. G., Dean M. C., 1985, “Re-evaluation of the age at death of Plio-Pleistocene fossil hominids”, *Nature* 317: 525–28.
- Broom R., 1936, “A new fossil anthropoid skull from Sterkfontein, near Krugersdorp, South Africa”, *Nature* 138: 486–88.
- Broom R., 1938, “The Pleistocene anthropoid apes of South Africa”, *Nature* 142: 377–379.
- Broom R., 1949, “Another new type of fossil ape-man”, *Nature* 163: 57.
- Bruner E., Manzi G., 2006, “Digital tools for the preservation of the human fossil heritage: Ceprano, Saccopastore, and other case studies”, *Human Evolution* 21: 33–44.
- Bruner E., Manzi G., Arsuaga J. L., 2003, “Encephalisation and allometric trajectories in the genus *Homo*: evidence from the Neanderthal and modern lineages”, *Proceedings of the National Academy of Sciences USA* 100: 15335–40.
- Campbell B. G., 1965, “The nomenclature of the Hominidae”, *Royal Anthropological Institute of Great Britain and Ireland, Occasional Paper* no.22: 1–33 [Reprinted 1994 in Meikle W. E., Taylor Parker S. (eds.), *Naming our Ancestors: An Anthology of Hominid Taxonomy*, Prospect Heights, Ill.: Waveland].
- Dart R. A., 1925, “*Australopithecus africanus*: the Man-Ape of South Africa”, *Nature* 115: 195–99.

- Darwin C. R., 1837, *Notebook B [Transmutation of Species]*, in “Darwin Online”, CUL-DAR121 (<http://darwin-online.org.uk/>).
- Darwin C. R., 1859, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, London: John Murray.
- Darwin C. R., 1871, *The Descent of Man, and Selection in Relation to Sex*, London: John Murray.
- Dawson C., Woodward A. S., 1913, “On the discovery of a Palaeolithic human skull and mandible in flint-bearing gravel overlying the Wealden (Hastings Beds) at Piltdown, Fletching (Sussex)”, *Quarterly Journal of the Geological Society* 69: 117–23.
- De Filippi F., 1864, *L'Uomo e le Scimie (lezione pubblica detta a Torino la sera dell'11 gennaio 1864)*, Milano: G. Daeli.
- Dobzhansky T., 1973, “Nothing in biology makes sense except in the light of evolution”, *The American Biology Teacher* 35: 125–29.
- Dubois E., 1894, “*Pithecanthropus erectus*. Eine Menschenähnliche Übergangsform aus Java”, Batavia (Jakarta) [Reprinted 1895 in *Jaarboek van het Mijnwezen* 24: 5–77].
- Eldredge N., Gould S. J., 1972, “Punctuated equilibria: an alternative to phyletic gradualism”, in Schopf T. J. M. (ed.), *Models in Paleobiology*, New York: Freeman, 82–115.
- Goodman M., Porter C. A., Czelusniak J., Page S. L., Schneider H., Shoshani J., Gunnell G., and Groves C. P., 1998, “Toward a phylogenetic classification of Primates based on DNA evidence complemented by fossil evidence”, *Molecular Phylogenetics and Evolution* 9: 585–98. .
- Gould S. J., 1977a, *Ever since Darwin: Reflections in Natural History*, New York: Norton.
- Gould S. J., 1977b, *Ontogeny and Phylogeny*, Cambridge, Mass.: Belknap.
- Haeckel E., 1874, *Anthropogenie oder Entwicklungsgeschichte des Menschen*, Leipzig: W. Engelmann.
- Harvati K., Harrison T. (eds.), 2006, *Neanderthals Revisited*, Dordrecht: Springer.
- Huxley J. S., 1942, *Evolution: The Modern Synthesis*, London: Allen and Unwin.
- Huxley T. H., 1863, *Evidence as to Man's Place in Nature*, London: Williams & Norwood.
- Huxley T. H., 1864, “Further remarks on the human remains from the Neanderthal”, *Natural History Review (London)* 4: 429–46.
- Johanson D. C., Edey M., 1981, *Lucy: The Beginning of Humankind*, New York: Warner Books.
- Johanson D. C., Taieb M., 1976, “Plio-Pleistocene hominid discoveries in Hadar, Ethiopia”, *Nature* 260: 293–97.
- Johanson D. C., White T. D., Coppens Y., 1978, “A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of Eastern Africa”, *Kirtlandia* 28: 1–14.
- Kimbel W. H., Rak Y., Johanson D. C., 2004, *The Skull of Australopithecus afarensis*, New York: Oxford University Press.
- King W., 1864, “The reputed fossil man of the Neanderthal”, *Quarterly Journal of Science* 1: 88–97.

- Lacruz R. S., Dean M. C., Ramirez-Rozzi F., Bromage T., 2008, "Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins", *Journal of Anatomy* 213: 148–58.
- Leakey L. S. B., 1959, "A new fossil skull from Olduvai", *Nature* 184: 491–93.
- Leakey L. S. B., Tobias P. V., Napier J. R., 1964, "A new species of the genus *Homo* from Olduvai Gorge", *Nature* 202: 7–9.
- Lieberman D. E., McBratney B. M., Krovitz G., 2002, "The evolution and development of cranial form in *Homo sapiens*", *Proceedings of the National Academy of Sciences USA* 99: 1134–39.
- Macchiarelli R., Bondioli L., Debenath A., Mazurier A., Tournepeche J.-F., Birch W., Dean C., 2006, "How Neanderthal molar teeth grew", *Nature* 444: 748–51.
- Manzi G., 1991, "Braincase architectural morphology of the Neanderthal cranium from Grotta Guattari and the nature of the archaic/modern transition", *Quaternaria Nova* 1: 113–24.
- Manzi G., 2003, "'Epigenetic' cranial traits, Neanderthals and the origin of *Homo sapiens*", *Rivista di Antropologia (Journal of Anthropological Sciences)* 81: 57–67.
- Manzi G., Saracino B., Bruner E., Passarello P., 2000, "Geometric morphometric analysis of mid-sagittal cranial profiles in Neanderthals, modern humans, and their ancestors", *Rivista di Antropologia (Journal of Anthropological Sciences)* 78: 193–204.
- Mayr E., 1950, "Taxonomic categories in fossil hominids", *Cold Spring Harbor Symposia on Quantitative Biology* 15: 109–18.
- Meikle W. E., Taylor Parker S., 1994, *Naming our Ancestors: An Anthology of Hominid Taxonomy*, Prospect Heights, Ill.: Waveland
- Mellars P., Boyle K., Bar-Yosef O., Stringer C. (eds.), 2007, *Rethinking the Human Revolution: New Behavioural and Biological Perspectives on the Origin and Dispersal of Modern Humans*, Cambridge: McDonald Institute for Archaeological Research.
- Moggi-Cecchi J., 2001, "Human evolution: questions of growth", *Nature* 414: 595–97.
- Moody J. W. T., 1971, "The reading of the Darwin and Wallace papers: an historical 'non-event'", *Journal of the Society for the Bibliography of Natural History* 5: 474–76.
- Ponce de León M. S., Zollikofer C. P. E., 2001, "Neanderthal cranial ontogeny and its implications for late hominid diversity", *Nature* 412: 534–38.
- Ramirez Rozzi F. V., Bermudez de Castro J. M., 2004, "Surprisingly rapid growth in Neanderthals", *Nature* 428: 936–39.
- Rohlf F. J., Marcus L. F., 1993, "A Revolution in Morphometrics", *Trends in Ecology and Evolution* 8: 129–32
- Slice D. E. (ed.), 2005, *Modern Morphometrics in Physical Anthropology*, New York: Kluwer Academic / Plenum Publishers.
- Spoor F., Hublin J.-J., Braun M., Zonneveld F., 2003, "The bony labyrinth of Neanderthals", *Journal of Human Evolution* 44: 141–65.
- Stringer C. B., 2002, "Modern human origins: progress and prospects", *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 357: 563–79.

- Stringer C. B., Gamble C., 1993, *In Search of the Neanderthals: Solving the Puzzle of Human Origins*, New York: Thames and Hudson.
- Tattersall I., 1986, "Species recognition in human paleontology", *Journal of Human Evolution* 15: 165–75.
- Tattersall I., Schwartz J. H., 2000, *Extinct Humans*, Boulder, Col.: Westview.
- Trinkaus E., Shipman P., 1993, *The Neandertals: Changing the Image of Mankind*, New York: A. A. Knopf.
- Weber G. W., 2001, "Virtual anthropology (VA): a call for Glasnost in paleoanthropology" *The Anatomical Record (Part B)* 265: 193–201.
- Weiner J. S., Oakley K. P., Le Gros Clark W. E., 1953, "The solution of the Piltdown problem", *Bulletin of the British Museum (Natural History) – Geology* 2: 139–46.
- White T. D., 2003, "Early hominids: diversity or distortion?", *Science* 299: 1994–97.
- White T. D., Asfaw B., DeGusta D., Gilbert H., Richards G. D., Suwa G., Howel F. C., 2003, "Pleistocene *Homo sapiens* from Middle Awash, Ethiopia", *Nature* 423: 742–47.
- Wood B., 1991, *Koobi Fora Research Project – Volume 4: Hominid Cranial Remains*, New York: Oxford University Press.
- Zeresenay A., Spoor F., Kimbel W. H., Bobe R., Geraads D., Reed D., Wynn J. G., 2006, "A juvenile early hominin skeleton from Dikika, Ethiopia", *Nature* 443: 296–301.
- Zollikofer C. P. E., Ponce de León M. S., Martin R. D., 1998, "Computer-assisted paleoanthropology", *Evolutionary Anthropology* 6: 41–54.
- Zollikofer C. P. E., Ponce de León M. S., Lieberman D. E., Guy F., Pilbeam D., Likius A., Mackaye H. T., Vignaud, P., Brunet M., 2005, "Virtual cranial reconstruction of *Sahelanthropus tchadensis*", *Nature* 434: 755–59.