Fifty years of Debate on the Origins of Human Bipedalism

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Introduction

Special attention has been paid to bipedalism because of its importance in the evolution of mankind. However, this important feature is often poorly explained or understood, due to preconceived ideas concerning our origins. How did this mode of locomotion emerge in our family? For more than a century, scientists focused on morphological comparisons between modern apes and humans trying to find an anatomical link between ape and human locomotion. This was reinforced when Plio-Pleistocene hominids were found in Africa (from 1924 onwards). Two major questions persisted: were our ancestors good bipeds in the same way as modern humans, or were they still spending time in the trees? To understand the evolution of a locomotor behaviour, it is crucial to take into account the environment. In parallel, faunal and floral researches were developed as early as Dart's times leading to hypotheses such as the "East Side Story" (Coppens, 1983). The framework was nevertheless generally restricted to Plio-Pleistocene times and did not take into account the great depth of geological time. The explosion of fossil hominoid discoveries in the 1990's gave impulse to prospect the Miocene sediments which resulted, in 2000, in the discovery in Kenya of the 6 million years old *Orrorin tugenensis* the earliest known bipedal hominid, which seriously challenged the date for the dichotomy of apes and humans (Senut et al., 2001). This find was followed in 2001 by two others, *Ardipithecus kadabba* in Ethiopia (Haile-Selassie, 2001)and *Sahelanthropus tchadensis* in Chad (Brunet et al., 2002; Beauvilain, 2003) both of which are claimed to be bipeds. At the same time, the idea of a knuckle-walking ancestor returned to the front of the scene, but the fossil evidence does not seem to support this hypothesis. From a behavioural aspect, field studies by primatologists yielded crucial evidence concerning ape locomotion which allowed refinement of previous results. The history of hominid bipedalism is a multifaceted story combining anatomical, chronological and environmental studies. Without doubt, it will continue to be debated. However, today, a picture of the ancestor seems to emerge: an arboreal hominoid, with an erect trunk that would have lived at the end of the Middle Miocene in a tropical environment.

Before 1960

In medical circles, the bipedal mode of locomotion has been widely researched as early as Ancient Greek times. Not only were medical doctors interested in human anatomy; but also artists have been inspired as early as Leonard de Vinci in the XVth century who meticulously drew the skeleton and the muscles. During the XVIth century, modern anatomy was born with André Vésale. At the end of the XVIIth century, Edward Tyson, the founder of comparative anatomy was the first anatomist to compare the anatomies of the chimpanzee and humans and concluded that the morphology of the ape was closer to humans than to that of other primates. However its stature is quite different from humans. Bipedalism was considered to be a distinctive feature of *Homo* by Linné in 1758 in *Systema Naturae*. Later, Blumenbach (1779), following Buffon (1766), named the order of Bimanes. Lamarck, 1809 was the first naturalist to formulate a hypothesis on the origin of bipedalism in the history of mankind. He suggested that a quadrumanous creature living in trees became bimanous on the ground following the disappearance of the trees. Despite the fact that his impressive work is rarely quoted in papers dealing with the origins of bipedal locomotion, he is actually a precursor in the field pointing out the links between the evolution of mankind and the environment. "If one or another race of quadrumanes, especially the most perfect among them, by force of circumstances or by any other cause, lost the ability to climb in the trees and to grasp branches with its feet as with its hands, for hanging therein, and if generation after generation the individuals of this race were forced to use their feet solely for walking and ceased to use their hands as feet, without doubt, following the observations pointed out in the previous chapter, these quadrumanes would in the end be transformed into bimanes and the big toe would cease being separated from the other toes, their feet serving purely for walking" (translated). Subsequently, Darwin (1856), Huxley (1863), Haeckel (1868), focused on the relations between apes and humans and the similarities between the two. In this comparative framework, most of the studies from the late XIXth

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century and early XXth century resulted in identification of a good prototype for the ancestral hominid which could be represented by some modern taxa, and as a result bipedalism was considered to be a major feature defining humanity. The major hypotheses were varied 1) arboreal origins, 2) terrestrial origins including 3) a quadrupedal arboreal animal, 4) a brachiator, 5) a knuckle-walker or 6) a vertical climber (see Tuttle, 1977 for an historical overview). The best models were provided by modern apes such as *Pan, Pongo* or *Hylobates*. But the same models were used for different reasons: *Pan* was retained as a suspensor-brachiator by Keith (1923) or Gregory (1930), and among the modern apes, some authors opposed arboreal behaviour and terrestrial behaviour. In a comprehensive analysis based on pedal morphology, Morton (1935) supposed that the foot of the ancestor was intermediate between *Gorilla Pongo* and *Homo*. All these studies were mainly based on modern primates and to a certain extent scholars were looking for an intermediate stage between an ape-like creature and humans, leading to a reinforcement of the erroneous idea of a "missing link".

Bipedalism is a complex phenomenon which has been widely studied in modern and fossil animals from anatomical, comparative, biomechanical, cognitive, palaeontological aspects, robotics, etc.., but bipedalism has sometimes been misinterpreted or poorly explained. In the animal kingdom, many vertebrates can move and/or stand bipedally such as birds, dinosaurs and several non-human mammals, but they are different from primates. With the development of field researches on living apes, it became obvious that bipedalism was not restricted to humans, but was widely expressed in primates. This led some scientists to reject bipedalism as a marker of humanity. However, the differences in human and non-human bipedalism are reflected in the skeletal morphologies in relation to occasional or obligatory behaviour. Humans are the only primates that can walk on two legs for long distance and for a long time. Moreover, bipedal gait was shown more recently to be less energy-consuming than quadrupedal movement (Ishida, 1991; Sockol et al., 2007; Steudel, 1995). In more recent studies, it has been shown that having short lower limbs in hominids is more costly in terms of locomotion (Steudel and Tilkens, 2004). Human bipedalism is thus pertinent for defining the earliest stages of human evolution.

In the past 50 years, the development of field researches on modern primates and fossil hominids, a better understanding of the geo- and biochronology, the new approaches in studies in locomotion led to new scenarios of hominid origins. Challenging new fossil discoveries were made resulting in new interpretations of our deepest origins and of bipedalism in particular. This is why in this article I will mainly focus on the palaeontological evidence. After the discovery in 1924 of the Taung child in South Africa (Dart, 1925), most of the debates were concentrated on the Plio-Pleistocene hominids. The Taung specimen was frequently discussed (found in Africa and not in Asia, and it was a child) as it challenged the establishment which, at the time, considered the ancestor to have lived in Asia. Because it supported Darwin's hypothesis of an African origin for humans, it was a major breakthrough in the study of human evolution, as this creature could have been bipedal in ancient times.

In the early 1920's, the specimens of *Pithecanthropus erectus* from Java were the oldest known ancestor which exhibited a bipedal skeletal morphology (Dubois, 1994) associated with a less human-like skull. When Taung child was found, it appeared to be cranially more human than previously expected; it could have been bipedal as shown by the anteriorly displaced foramen magnum (a feature considered to be crucial for determining the propensity to bipedalism in fossil hominids). In fact, when comparing an ape and a human skull, it is obvious that the foramen magnum is generally posteriorly situated in the ape. The first evaluation of the position of the foramen magnum is due to Le Gros Clark (1955), but he cautiously noted in his book (*The Antecedents of Man*), that even if the foramen magnum is more anteriorly positioned in humans, this position is variable between dolichocephalous and brachycephalous skulls and he suggested that locomotion is not the only factor for causing an anterior position.

In the late 1930's, several adult or sub-adult remains of *Australopithecus africanus, Paranthropus crassidens, P. robustus* (Broom, 1938; Broom, 1949, Broom and Robinson, 1950, 1952) were found in different sites such as Sterkfontein, Swartkrans, Kromdraai) including postcranial elements which confirmed that these early hominids were bipedal, but not in exactly the same way as in humans. However, it was suggested that if the Australopithecines were bipeds as reflected in the anatomy of the lower limbs, the upper limb would have been similar to that of humans. This happened to be wrong, but as a result the researches were focused on the lower limb.

The sixties: if you are an ancestor, your skeleton must be humanlike

In 1960, a new early man, *Homo habilis*, was discovered at Olduvai Gorge in Tanzania in the same site which had yielded the remains of *Zinjanthropus boisei* in 1958 (Leakey, 1959; Leakey et al., 1964). The material consisted of two parietal fragments, a fragmentary mandible and partial hand and foot. These last elements suggested that the hand was human-like and the foot that of a biped (Leakey et al., 1964). Original studies by Washburn (1963) regarding the evolution of human behaviour led to the hypothesis of a knuckle-walking stage between brachiation and bipedalism. This image was prominent for some time, but the fossil evidence did not support the theory. In a comparative study of Plio-Pleistocene hominid postcranials, Napier (1964) concluded that early hominids were bipeds, and showed that *Australopithecus africanus* was more human-like in its skeleton than *Paranthropus robustus*. These differences could have been related to the difference in environments: *Australopithecus* inhabited a more open savannah than *Paranthropus*. In 1967, Napier, concluded *"An environment neglected by scholars but one far better for the origins of man is woodland savanna, which is neither high forest nor open grassland"* (p. 52). But it reinforced the fact

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that more studies were necessary on fossils which resulted in a definition of humankind which was not only based on skull, brain and teeth but also had to involve locomotor behaviours. The 1960's were also a major time for the search for hominid fossils in Africa and several expeditions were launched, such as the Omo International Research Expedition which led to the discovery of some postcranial elements of Plio-Pleistocene hominids.

The Seventies: Lucy, a new model for bipedalism

The seventies were particularly rich and challenging for the study of human evolution.
Two major facts were of importance in the study of fossil locomotion. First, the book by John Robinson (1972) on the locomotor apparatus of the fossil hominids was the first comprehensive analysis of early hominid postcranial bones. He backed up Napier's work by showing that *Australopithecus africanus* was more human-like in its bones than were the robust Australopithecines. Secondly, fieldwork in the Awash Basin led to the discovery at Hadar of the famous Lucy skeleton (3.2 Ma old), which was named *Australopithecus afarensis* (Johanson et al., 1978). This was a major breakthrough in the field: for the first time in the study of human evolution an almost complete skeleton of an early hominid was available for study, the proportions of body could be estimated, and the locomotor behaviour could be assessed from the entire skeleton. However despite the great number of bones present, preliminary studies of the skeleton led to opposing results (see Stern, 2000 for an overview). Some scholars pointed out a mixture of arboreal climbing and terrestrial bipedalism in the locomotor repertoire (Senut, 1978, 1981; Senut and Tardieu, 1985; Schmid, 1983; Susman et al. 1984, Stern and Susman, 1983), whereas others suggested a full adaptation to bipedalism considering that the high variation in the features could match the variation seen in modern humans (Lovejoy, 1978). Soon after the preliminary studies, two major hypotheses emerged: either A. afarensis was a highly dimorphic hominid taxon fully adapted to bipedal locomotion; or it consisted of two different hominid taxa which co-existed, 1) an Australopithecine being bipedal and arboreal and 2) a more advanced and a fully bipedal large-sized taxon. These divergent views were widely disputed at several meetings, but up to now, the debate is not closed (see bibliography in Senut, 1992). The AL 333 site (more recent than that of Lucy) is the core of the problem as we cannot be sure that all the specimens collected there came from the same level. If the more morphologically advanced specimens came from upper strata, then, the systematic issue of A. afarensis would be easier to resolve. More recently, several anthropologists suggested that a diachronic variation could explain the morphological variation in these hominids, but there is still no consensus among the colleagues. Lucy is probably one of the most studied hominid skeletons, but there is no consensus regarding its position in the hominid phylogenic tree. It exhibits some ape-like and some human-like features, but the polarity

status is generally difficult to establish and preconceived ideas have predominated. It was assumed generally without any demonstration (up to recent times), that apes were primitive and that therefore ape-like features were primitive (White, 1982, White and Suwa, 1987; Leakey and Walker, 1997). However, chimp-like features exhibited in Lucy were not recorded in Miocene hominoids and were present only in modern chimpanzees and gorillas and for some of them in orang-utans. As a matter of fact, these features appear to be most probably derived in the African apes. In the late seventies, the development of research on pygmy chimpanzees led to another major trend in the study of the origins of bipedalism, which culminated in the "Pygmy chimp theory" proposed initially by Zihlman and co-authors (1978). Lucy was often represented as a morphological intermediate between chimpanzees and humans.
Another major discovery was made in the mid 1970's in Tanzania where hominid footprints were excavated at Laetoli (3.6 to 3.8 Ma) (Leakey and Hay, 1979). The footprints showed the evidence of an arch, the points of pressure were hominid-like, but the big toe was slightly divergent. It was at the time considered that the footprints were made by *Australopithecus afarensis*. Again, some scientists considered the prints to be human-like (Day and Wickens, 1980) or more ape-like (Deloison, 1991) with arboreal adaptations. The main problem resides in the fact that there is some overlapping of the tracks and most scientists focused on one or two prints only. Subsequent detailed studies based on a statistically comprehensive sample of modern Amerindians by Tuttle and co-authors (1991) showed that the features described as Australopithecine-like at Laetoli could actually be accommodated in modern humans who walk bare-foot and indistinguishable from those of *Homo sapiens* and could not be attributed to *Australopithecus afarensis* on the basis of pedal morphology (Tuttle, 1996). The possibly human aspect of the footprints was confirmed later (Senut, 2006). If the prints cannot be attributed to *Australopithecus afarensis*, then another hominid species was present in East Africa in the mid-Pliocene, as suggested in the 1970's by Senut (1978, 1981). But who walked at Laetoli 3.8 million years ago? It is not possible to conclude for the time being, but it might be considered that *Praeanthropus africanus* could be a good candidate (Senut, 1996).
During the seventies, numerous functional and biomechanical studies were performed on modern primates in order to understand bipedalism, and vertical climbing was considered to be an ancestral condition for hominid bipedalism (Fleagle et al., 1981). It was based on the idea that some muscles were efficient in climbing adaptations and in bipedalism.
Another aspect of fossil locomotor adaptations was given more attention in the seventies: the environmental studies. To obtain a comprehensive picture of human evolution, environment had to be taken into account, an idea which was put forward by Coppens and Howell in the Omo Research Expedition in Ethiopia as early as the late 1960's. The palaeoenvironments at Hadar have been studied in great detail by vertebrate palaeontologists, invertebrate

palaeontologists, palynologists and a picture emerged of an environment which was not dry and/or arid, but in which trees were present (Bonnefille and Vincens, 1985). It was a major contradiction to the usual belief that hominids emerged in a savannah-like environment.

The idea took root that bipedalism emerged in a more wooded environment.

1980's, the race for *Homo habilis*

A striking discovery was the *Homo habilis* skeleton (OH 62) found at Olduvai, 1.8 Ma old (Johanson et al., 1987). In this fragmentary skeleton, none of the long bones is complete, but the specimen was attributed to *Homo* based on maxillo-dental comparisons with OH 24, KNM ER 1813 and KNM ER 1470. However, the status of the East African specimens has been widely challenged and to accommodate the new Olduvai remains in the variation of *Homo habilis* as appreciated at the time, we had to increase the variability of the features. OH 62 is a gracile skeleton with the size and proportions of Lucy. The postcranial feature have been said to be Lucy-like despite the fact that detailed comparisons of the long bones are not possible due to their fragmentary aspect (left proximal femur, right proximal tibial shaft, right radial and ulnar fragments). It was suggested that it might represent a third lineage in East Africa, a gracile one which paralleled A. *africanus* from South Africa (Senut, 1987). More recent work on this material suggests that it could be an early habiline which already displayed long legs but retained primitive brachial proportions (Haüsler and McHenry, 2004). More recent data (Ruff, 2009) suggest that femoral and humeral strength proportions are out of the human variation and falls in the chimpanzee variation. However, in all the studies, it is assumed that this skeleton belongs to *Homo habilis*, an attribution based on comparisons with the South African specimen Stw 53, which is considered to be a representative of *Australopithecus africanus*.

The same problem applies to KNM ER 3735, a fragmentary skeleton from Koobi Fora in Kenya (Leakey et al., 1989), also considered to belong to *Homo habilis*. However, its humeral morphology recalls that observed in KNM ER 739 from Koobi Fora attributed to *Australopithecus boisei* and represents a smaller version (Senut, 1978).

The attribution of these fossils was assumed on the basis of cranio-dental features, supposedly more pertinent for taxonomy, but the variability of such features is still not clear today. This approach is reductionist and shadows the evidence given by the postcranial bones which often appear to be more useful for systematics.

At the same time, Coppens at a Vatican meeting in 1981 formalized his "East Side Story" which explained the distribution of modern apes and humans in relation to the development of the East African Rift. The divergence between African apes and humans would have taken place in East Africa 8 to 10 million years ago in relation with the formation of the Rift which created a climatic barrier (Coppens, 1983, 1986). A Miocene hominoid population was thus separated: the one in the Eastern part of the rift

became adapted to more open environments and evolved into hominids and the one remaining in the West which was already adapted to forested environment, evolved towards to African apes, *Pan* and *Gorilla*. If the geographic aspect of the hypothesis is the most debatable, it remains that the impact of the Rift on the environments and the timing of events have since been confirmed, the eastern Rift being less humid than the Western Rift 6 to 8 million years ago (Pickford et al., 1993, Senut and Pickford, 1994; Senut, 2006). During the same years, detailed analysis of the fauna and the flora of the Plio-Pleistocene hominid sites were done which resulted in the organisation of an international meeting of the Singer Polignac Foundation in Paris, held in 1982. The results were that early hominids did not live in an open, savanna-like environment, but more probably lived in a wooded savannah (Colloque Singer-Polignac, 1985). The arboreal adaptations of our ancestors fitted well with the environmental data.

1990's: new postcranial evidence

In 1990, an international meeting was organized at the Singer-Polignac Foundation in Paris on the origins of bipedalism (Coppens and Senut, 1991); all aspects of bipedalism were discussed, but again no consensus was reached. Up to 1994, anthropologists focused their studies on Plio-Pleistocene hominids; the oldest widely accepted evidence of hominids was around 4 million years with specimen such as the Kanapoi humerus (Patterson and Howells, 1967; Senut, 1979) which was allocated to *Australopithecus* by the discoverers and to *Homo?* (Senut, 1979) and later to *Praeanthropus africanus* (Senut, 1996). A proximal humerus from Mabaget Formation has also been considered as an early hominid (Pickford et al., 1983), but the morphological evidence was not sufficient to allocate this fragmentary humerus to a hominid *sensu stricto* (Senut, 1983). The Lukeino lower molar (6 million years old) was not generally considered to be a hominid despite its clearly hominid morphology (Pickford, 1975).

Two other specimens were also candidates for early hominids: the Mabaget mandibular fragment from the Tugen Hills (Hill, 1985) around 5.1 Ma old and the Lothagam fragmentary mandible (Patterson et al., 1970) dated originally at around 7 Ma, but which is younger in age (ca. 4.7 Ma) (McDougall and Feibel, 1999).

In 1994, White and his team announced the discovery of the oldest known "hominid", *Australopithecus ramidus* (White et al. 1994), later attributed to a new genus *Ardipithecus* (White et al., 1995). Its bipedalism was assumed on the basis of the position of the foramen magnum. However, the cranial bone is so fragmentary, that the determination of the position of the occipital foramen is not clear and the total length of the skull could not be estimated as the skull was crushed. Several postcranial elements were briefly described in the same paper, but the evidence for bipedalism is poor and not convincing, as we will see later.

Several months later dental and postcranial remains were found at Kanapoi (Walker et al., 1995), among which a
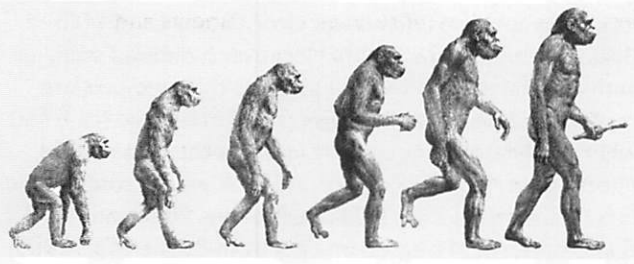
Figure 1. Linear evolution from a quadruped to a biped hominoid (after Time Life) 1970

Figure 2. Poster of the International Congress in Forli (1996) depicting a descent from tree. The quadrupedal stage is not necessary, but the impact of the quadrupedal evolution has still a lot of influence.

tibia in two pieces exhibits a clear hominid morphology, confirming previous work on the humerus from the same site. Despite the modern aspect of some of the bones, and acknowledging the presence of two different anatomical groups, the authors allocated all the material to a new taxon, Australopithecus anamensis, of which new material was found at the end of the 1990's (Leakey et al., 1998, Ward et al., 1999). The study of a fragmentary carpal bone led some authors to hypothesize knuckle-walking adaptations in the wrist joint (Ward, 1999).

Also in 1995, Sterkfontein in South Africa yielded an associated pedal skeleton with a divergent big toe (Clarke and Tobias, 1995). Although the degree of divergence is debated, the foot morphology clearly evidences climbing adaptations in this hominid. Less than a decade later, the rest of the skeleton was found showing a mixture of climbing and bipedal adaptations (Clarke, 2003).

Then, in the mid-nineties, more evidence supported the fact that early hominids were bipedal, but were also adapted to an arboreal environment. Several papers were presented at the "Preistoria e Protostoria Congresso Mondiale" in Forli (Italy) in September 1996. The idea of an arboreal origin was no longer heretical: it was actually depicted on the official poster of the meeting. However, a quadrupedal stage was drawn, but it is not necessary for understanding how bipedalism evolved. But the mediatic impact of Rudy Zallinger's illustration in the book by Howell (1970) was so strong that many anthropologists still accept a quadrupedal, knuckle-walking stage in the evolution of our locomotion, despite the poor evidence.

The 3rd Millenium

Most anthropologists were convinced that the earliest hominids would be found in the Pliocene, in accordance with the molecular data; it was thus considered useless to search the Miocene sediments in Africa. But some palaeontologists were motivated to look deeper in time in order to understand the origins of our lineages, and it became clear as early as the mid-1980's that it was necessary to focus researches on Upper Miocene sediments. It resulted in the discovery in 2000 by a Franco-Kenyan team of a 6 million years old hominid, Orrorin tugenensis (Senut et al., 2001) in the Tugen Hills (Kenya). This was highly criticized in the scientific and mediatic worlds, mainly because it challenged the established ideas based on molecular data. Anthropologists were not prepared to accept this old age, and even commented that these remains belonged to a chimpanzee. This would have been just as exciting because at the time we did not know of any fossil chimpanzee. However, detailed analysis of the postcranial remains demonstrates that Orrorin was a biped in a manner different from that of Australopithecines (Pickford et al., 2002; Galik et al., 2004).

The thumb phalanx is also morphologically human-like, and suggests the ability for precision grips (Gommery and Senut, 2006). If the femur and the thumb phalanx are human-like, the proximal phalanx and the humerus exhibit arboreal features (Senut et al., 2001). The hominid status and the bipedalism of Orrorin have been confirmed in independent studies of the femur and of the thumb phalanx (Richmond and Jungers, 2008; Almécija et al., 2010). Orrorin was still climbing trees, which is probably a pertinent adaptation considering its body size of ca 48 kgs. (Nakatusakasa et al., 2007). Based on a comparative analysis of more than 50 modern primates (including monkeys and apes) and of the young adult femur, Orrorin would not have been smaller than 1.10 m and not taller than 1.37m. Trees were probably places to escape predators, to sleep and to feed. In the Lukeino Formation, a large sample of fossil leaves was found (Senut, 2006) which suggest that the environment 6 million years ago consisted of a dry evergreen forest with some more forested patches (Bamford et al., submitted). The fauna support this reconstruction with the presence of Strepsirhine primates (Pickford, this volume), water chevrotains, impalas, colobine monkeys, a small forest-dwelling giraffe, arboreal civets, frugivorous bats, etc…Extensive deposits of travertines

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have been identified which yield snails, vegetation, and sometimes mammals. These recall the situation observed today in Lake Bogoria where petrified plants, bones or even rocks embedded in the travertine can be found in the vicinity of hot springs. The alkaline aspect of the water led to these petrifications and is evidenced in the Lukeino Formation, 6 million years ago.

The discovery of *Orrorin* thus challenged the established ideas: the divergence between apes and humans was older than estimated by the molecular evidence, bipedalism evolved in a more humid environment than thought; bipedalism was associated with climbing adaptations but was not identical to the human repertoire.

This discovery gave the incentive to other scientists to look into the Miocene, because a few months later the discovery of supposedly hominid fossil remains, *Ardipithecus kadabba* from Ethiopia was published (Haile Selassie *et al.*, 2001) in strata the age of which is between 5.2 and 5.8 Ma old. The evidence for bipedalism was assumed from a proximal pedal phalanx which resembles Lucy's. But the evidence is poor: a facet on the anterior aspect of the foot. However, this facet is also present in *Proconsul nyanzae* (Walker *et al.*, 1987). Lucy was an arboreal climber and a biped and it is difficult on the basis of an isolated phalanx to support clear bipedal adaptations in *Ardipithecus kadabba*. Moreover, the phalanx does not come from the older levels, but from Amba which is the youngest deposit (ca 5.2 Ma) (Senut, 2006). Later a distal humerus was found but its morphology is not hominid-like: it recalls slow climbers such as modern *Pongo*. There is still debate about the *Ardipithecus kadabba* material. The same year the discovery of a fossil hominid skull 2000 km away from the Eastern Rift in Chad was announced. This was formalized a year later in the publication of *Sahelanthropus tchadensis* supposed to be 6 to 7 Ma old, on the basis of flawed faunal analysis (Brunet *et al.*, 2002). A reconstruction of the skull was proposed in 2004 (Zollikofer *et al.*, 2005) which shows that the foramen magnum was anteriorly displaced. However, the reconstruction has been challenged and suggested that the skull might represent an early member of the gorilla lineage (Senut, 2005; Wolpoff *et al.*, 2002, 2006; Pickford, 2005). But previous studies on bipedal adaptations in primates (including humans) demonstrated that the position of the foramen magnum varies in relation not only to locomotion, but also to brain expansion (Biegert, 1963). When its position is studied in a large sample of modern humans and chimpanzees, there is a strong overlap of the data (Schaeffer, 1999). It is difficult to conclude from an isolated skull what is the value of the mean. Among fossil hominids, it has been shown that the foramen was even more anteriorly positioned in Australopithecines, despite the fact that they are not better adapted to erect bipedalism than modern humans are (Aiello and Dean, 1990). Another problem concerning *Sahelanthropus* is its age: initially, it was announced on the basis of the faunal analysis to be 6 to 7 Ma old. This date was supposedly confirmed by an Al/Be analysis of the sediments which yielded an age comprised between 7.2 and 6.9 Ma (Lebatard *et al.*, 2008). However, the skull was collected from the surface of the sediments and

its stratigraphic position is not clear (Beauvilain, 2003; Beauvilain and Watté, 2009). Moreover a detailed study of anthracotheres from the site suggests that two taxa are represented: one species suggests a Pliocene age (ca 5 Ma) whereas the other is generally found in the basal Upper Miocene (ca 10 ma) (Pickford, 2008). A recent study of the fossil giant otters from Dikika, a Pliocene Ethiopian site (Fig. 5 in Geraads, 2011, based on data from Peigné *et al.*, 2008) also indicates a possibility that a younger fauna (Pliocene) is represented at Toros-Menalla. The age of the hominoid material remains uncertain.

In the 2000's, new techniques, new fieldwork led to the re-interpretations of previous fossils and the development of technical researches. In 2004, Bramble and Lieberman showed in a study on the energetics of walking that humans were born to run and that early hominids might have been adapted to running. But, it is difficult to match these results with the fossil evidence, because the body size and the limb proportions would not have been efficient for these hominids. In 2006, an international meeting organized in Kyoto gathered together several specialists of locomotion, palaeoenvironments and the Miocene (Ishida *et al.*, 2006). Various adaptations to bipedalism in modern and fossil primates were considered using for example modern macaques trained to walk on two legs, and debates took place on the renewed idea of the presence of a knuckle-walking stage in the origins of bipedalism (Richmond *et al.*, 2001) or a climbing stage in the ancestors of hominids. The discovery in 2006 of an Australopithecine child in 3.4 Ma deposits at Dikika in Ethiopia confirmed the arboreal adaptations in early hominids (Alemseged *et al.*, 2006). The scapula in particular shows a clear resemblance to that of gorilla. However, early hominids exhibit a scapular morphology close to that of *Pongo* (Vrba, 1979; Senut, 1978) and it would be interesting to compare the Dikika material with the Asian ape.

In the mid 2000's, Crompton and his team revived the idea that the locomotion of the orang-utans was a good model for understanding the origins of hominid behaviour (Thorpe *et al.*, 2007). In a biomechanical demonstration, he showed that *Pongo* was the only ape to possess a fully extended knee and was bipedal in the trees in the wild. He concluded that a generalist hominoid living in the trees could have evolved into a bipedal terrestrial hominid, or a terrestrial knuckle-walker (such as African apes), or remained adapted to a fully arboreal life. These results supported the hypothesis erected by Stern in 1975. The ancestral hominid could have been arboreal and terrestrial. In 2009, another biomechanical study of the wrist in modern apes led to the same conclusions (Sockol *et al.*, 2009).

At the end of the 2000's, a series of papers was published on the skeleton associated with the remains of *Ardipithecus ramidus* first described in 1994. The authors came to the conclusion that *Ardipithecus ramidus* was bipedal (White *et al.*, 2009; Lovejoy *et al.*, 2009). However, most of the features which can be studied do not reflect such adaptations. The pelvis was completely crushed (resembling a "Road kill" according to White) and it was reconstructed as a hominid, and effectively the result is that it looks like

a pelvis of *Australopithecus afarensis*. The foot is certainly the most striking element as it shows a clear adaptation to grasping with its highly divergent big toe and there is no evidence of an antero-posterior plantar arch.

The hands have curved metacarpals and phalanges which suggest an arboreal life. The distal thumb phalanx does not resemble that of humans, or Australopithecines, or *Orrorin*, but it looks more like that of apes, with a reduced distal tuft, a narrow shaft and the development of the flexor muscles. However, no comparisons were made despite the fact that all the data were already published and available. But what appears the most surprising is the reconstruction of the vertebral column which exhibits the 4 curvatures usually seen in humans, whereas only a cervical vertebra and a fragmentary dorsal vertebra are preserved. Finally, when considering the stature, the femur was reconstructed like that of a modern human, slender, elongated, a reconstruction which is not supported by the massive shaft. Moreover, because the extremities are not preserved, it is difficult to support the human reconstruction! The arms are not preserved; it is also difficult to assume *a priori* a human-like morphology. In fact, the anatomy of the forearm with a large interosseous space and a strongly curved radius suggests the presence of strong, well developed pronator and supinator muscles, as observed in modern African apes. In conclusion, I do not think that *Ardipithecus ramidus* is a bipedal hominid, but more certainly represent an ancestral form of African ape, maybe a palaeochimpanzee, a view already suggested in 1994 on the basis of the dental anatomy. However, the publications have been so much mediatised, that scientific debate has been occulted. It is sad that scientific debate cannot take place today; these fossils have been so widely publicised that the results became a truth propagated by the media and not in a clear, open scientific debate.

In 2010, a partial hominid skeleton found in 2005 in 3.6 Ma old strata at Woranso-Mille was published (Haile-Selassie *et al.*, 2010) confirming adaptations to bipedalism in another specimen of *Australopithecus afarensis*. But, if the authors suggest that the scapula is human-like, the same comment applies here as for the Dikika child and it would be interesting to compare the specimen with *Pongo* scapulae.

Recent discoveries

The most surprising discovery of the last decade was made at Malapa in South Africa, in two million year old deposits: two partial skeletons of a new species of Australopithecine, *Australopithecus sediba* (Berger *et al.*, 2010). The specimens consist of a fragmentary skeleton of a young boy and several remains of an adult female. They exhibit a mixture of human and australopithecine features in their skeleton. They were clearly bipedal, but retained some climbing features. The hand is particularly interesting as it presents a long thumb (when compared with the other digits), a carpo-metacarpal morphology close to that known in Australopithecines, but a clearly human-like scaphoid. Do these skeletons represent an intermediate stage between *Australopithecus* and *Homo* (in this case, that would imply

two different, parallel evolution in East and South Afirca) or do they already belong to the *Homo* lineage? The important aspect of these discoveries is that they comprise rather complete material and they can yield a lot of information about the variability of the skeleton and of bipedalism in a two million year old hominid. How do they compare to the other East African hominid species such as *Australopithecus afarensis*, *A. anamensis*, *A. garhi* and the early *Homo*? Were there several adaptations to bipedalism 2 million years ago? How were they different? Without any doubt, these questions will raise a lot of debates in the next years.

We already know that other forms of bipedalism existed in the past with *Oreopithecus bambolii* from the Upper Miocene of Tuscany. Since its discovery in 1958, the skeleton of *Oreopithecus* has fuelled many debates: was it a bipedal animal on the line to humans or was it an arboreal ape? (Hürzeler, 1958, Straus 1963). In the mid-1990's, the study of a new pedal specimen from the same site led to the conclusions that it was a biped, but not in a hominid way (Köhler and Moyà-Solà, 1997). The foot does not exhibit the double arch specific to humans and possesses a highly divergent big toe, but different from that of extant apes.

The biomechanical studies of the bones and the different axes show that when the foot was on the ground it was positioned in a mortise-like manner. But being bipedal does not mean that it was not arboreal. In fact, it was capable of moving as easily in the trees as on the ground (Rook *et al.*, 1999). It was living in an insular environment where rare predators were mainly piscivores. *Oreopithecus* filled all the vacant primate niches and was well adapted to arboreal life with its long grasping upper limbs as to life on the ground.

Conclusions

The history of hominid bipedalism appears complex and to understand how this mode of locomotion emerged, we must not focus exclusively on the Plio-Pleistocene hominids and modern African apes. On the basis of discoveries in the last decade, we conclude that the dichotomy between apes and humans took place around 10 million years ago, maybe slightly earlier (Pickford and Senut, 2005; Suwa *et al.*, 2006; Kunimatsu *et al.*, 2007; Pickford *et al.*, 2009). We must concentrate the research efforts on the Miocene period which witnessed the rise of the early hominids (the term being taken in its reduced sense). Most Early Miocene and Middle Miocene apes were adapted to arboreal environments and it is logical to emphasize that in its first expression bipedalism was associated with a great deal of arboreal adaptations.

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Figure 1. Linear evolution from a quadruped to a biped hominoid (after Time Life) 1970 (to include p.9)

Figure 2. Poster of the International Congress in Forli (1996) depicting a descent from tree.The quadrupedal stage is not necessary, but the impact of the quadrupedal evolution has still a lot of influence (to include p. 13)