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# Palaeoanthropology and the Evolutionary Place of Humans in Nature

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Palaeoanthropology, the study of the fossil evidence for human evolution, remains a highly contested field. New discoveries are continuously being used to promote alternative models as well as to propose new candidates for our ultimate ancestor. The fossil evidence has increased over the years, and has been supplemented (and often challenged) by molecular data drawn from living people and the great apes. As recently as the 1980s, palaeoanthropologists proposed that human roots stretched back into the Middle Miocene, between 17 and 8 million years ago. Then the earliest true hominids or human ancestors became the South African australopithecines, who are less than 5 million years old. Now there appears to be a tremendous variety of early humans at all stages of their evolution. Along with this new research on the basal hominids has been a renewed interest about what it means to be *Homo sapiens*. Molecular and fossil data shows that Africa was also our homeland, and that all people today are descended from a small founder population in existence there between 50,000 and 200,000 years ago.

Every human society has stories about their past, myths and legends that explain who they are, and how they came into being. These accounts are conditioned by history and experience, and the collective behaviors that anthropologists study as part of culture. What we call "science" offers explanations, which can also be conditioned by cultural values, attitudes and beliefs (Cartmill, 1993, 2003; Landau, 1991; Lewin, 1987). But science is separated from story telling and myth, one is told, because it is done within a framework that requires empirical evidence that can be supported or falsified. In many so-called hard sciences, assumptions can be tested experimentally. Variables are defined, placed in certain situations, and then their interactions can be directly observed. Alter the variables and the result may or may not change. The historical sciences are different. What is being studied is the past, something that has already happened, which cannot be recreated in nature or in a laboratory. Rather than worrying about "physics envy" (Gould, 1981, p. 113), some historical sciences are beginning to learn how to live within these restrictions.

Palaeoanthropology is one of these historical sciences. It is the multi- and interdisciplinary study of human origins and evolution. The facts in palaeoanthropology are fossil human bones and their context in time and space. These are generally referred to as hominids or hominins, common names for the Linnaean biological Family Hominidae or Tribe Hominini, respectively. This distinction depends on how one sees our closest living nonhuman relatives, the African apes. Originally placed in Family Pongidae, along with the orangutan (genus *Pongo*), chimpanzees (*Pan*) and gorillas (*Gorilla*) are genetically more similar to humans, something that should be reflected in taxonomy. So many classifications only distinguish African apes and humans at the tribal levels, just above the genus.

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Others restrict the term Hominidae and hominid for humans, a convention which will be followed here.

In the 1960s, F. Clark Howell proposed the creation of a field that would examine human evolution from all perspectives. He used the term palaeoanthropology to describe the field research he was doing west of the Omo River in southern Ethiopia. Howell, Richard Leakey from Kenya, and Camille Arambourg from France led an international team investigating human evolution in the Shungura Formation, a composite geological sequence spanning the past 4 million years (Coppens et al. 1976). This was done through detailed geological mapping of sedimentary rock exposures and subsequent field collecting of fossils and archaeological (past cultural) remains. Ancient plant and animal remains, as well as sediments, provided palaeoenvironmental data. Changes in types of mammals over time were used for dating (biostratigraphy), as was the measurement of radioactive decay of isotopes in volcanic deposits above or below the fossil bearing layers (Deino et al. 1998; Ludwig & Renne 2000). The goal of palaeoanthropology was to understand the pattern of human evolution in its broadest context. Some researchers felt that Howell was trying to justify his large, expensive field projects, since unlike some of his students (most notably, Donald Johanson), he never made the "big score" which defines public success as a palaeoanthropologist, the discovery of new and more ancient early hominids. But this approach provided the framework for the best modern field research.

The study of human evolution has a relatively recent history. The first fossil remains, the European Neandertals, were only identified as such in the mid 19th century (Bowler, 1986, 1989). The first ancient African hominids, the australopithecines, were discovered in the 1920s (Dart, 1925); the most recent species, *Sahelanthropus tchadensis*, was defined in July 2002 (Brunet et al. 2002). But ideas about our past extend back to the beginnings of recorded history. There has been a long debate about the nature of human nature, which is not restricted by academic discipline. What is it that makes humans different from animals (Cartmill, 2001, 2002)? How did humans become the dominant group, the masters of all they can see? Various features have been proposed as the prime mover: the soul, our large brain, the capacity for critical reasoning and thinking, technology and other aspects of material culture, language and communication, and culture in general, learned behavior shared by people as members of a society. Are these aspects of human behavior a product of heredity or social environment or both? When did aspects of social or cultural behavior become important? There is a range of opinions, but for fields like sociobiology (Wilson, 1975) and evolutionary psychology, even learned behaviors are ultimately the products of basic biological needs, subject to natural and sexual selection in the same way as inherited traits. At some point in our past, we were nonhuman animals; when did we start to change and why? For some researchers, the answer was easy. Once humans developed cultural systems, biology became irrelevant.

This paper deals with the fossil evidence of the earliest stages of human evolution, as currently understood. From an insider's perspective, it describes the basic facts that are generally accepted by most researchers, but even these are subject to interpretation in different ways. There have been major shifts in perspectives about early human evolution in the last three decades, and it is possible that others will occur in the next few years. This article also attempts to place the debate about the evolution of humans and their behavior within a historical perspective. Basic ideas still supported today predate the recognition of the fossil record, and the fossils themselves are often ignored in debates about what happened and why. What is probably the major concern at present is more troubling: the lack of certainty about interpretation. As more and more fossil species and even genera are defined, their evolutionary relationships remain unknown.

## Historical Perspectives

If one goes back to the early 1800s, Western Europeans had a clear explanation of where humans had come from, and how their history had unfolded. The Biblical record of creation recorded in the Book of Genesis was taken as literal truth. It even provided a guide to when these remarkable events had occurred. By adding up the generations of "begats," who fathered whom, and by using other historical sources, James Ussher (1581-1656), the Anglican Archbishop of Armagh, calculated the date of the creation of the earth. For Ussher, it was the night preceding Sunday October 23, 710 in the Julian calendar, or 4004 BC in our own (Rudwick, 1976, p. 70), a fact printed ever since in the margins of the authorized (or King James) version of the Bible (Daniel, 1975, p. 27). Bishop Dr. John Lightfoot took this one step further. He put creation at 9:00 am, October 23, 4004 BC. This was the first day of the Trinity term at Cambridge University. Since Lightfoot was the Master of St. Catherine's College, and Vice-Chancellor of Cambridge University (Daniel & Renfrew 1988, p. 10), it put his university in synch with the divine. While 4004 BC was initially proposed as the age of the earth, for some it later became the age at which humans were created (Barber, 1980, p. 281).

The fields that would now be recognized as biology, geology and palaeontology were initially developed within a framework of natural theology. In order to understand God's purpose in nature, one collected and studied natural phenomena. A typical example of natural theology was William Paley's (1743-1805) work of the same name (Paley, 1802). In it, he argued that plants and animals have structures that enable them to survive and propagate. Since these structures were so elaborate, they could not be due to chance, and must have had a Creator. Such ideas still exist, under the rubric of "intelligent design" (Ruse, 2003). For Paley, the first purpose of a study of nature was to teach us that God exists; the second was to illustrate God's attributes (Barber, 1980). While the heyday of natural theology was the 18th century, in England it got a boost from the Earl of Bridgewater in the early 19th century. In his will, he left a sum of £ 8000 for books "on the power, wisdom, and goodness of God, as manifested in the Creation", works which became the Bridgewater Treatises. In 1833, the authors were chosen by a committee whose members were the President of the Royal Society, the Archbishop of Canterbury and the Bishop of London (Barber, 1980, p. 219). One was the leading British geologist, a man who also happened to be Dean of Westminster, William Buckland (1784-1856). Buckland was named Oxford University's Reader in Mineralogy in 1813 and Reader in Geology five years later. In his inaugural lecture as the Reader in Geology, published as *Vindiciae Geologicae; or the connection of geology with religion explained*, Buckland concluded that

> In all these [geological and palaeontological phenomena] we find such undeniable proofs of a nicely balanced adaptation of means to ends, of wise foresight and benevolent intention and infinite power, that he must be blind indeed who refuses to recognize in them proofs of the most exalted attributes of the Creator (Buckland in Hallam, 1989, p. 42).

This position might seem quaint today, but, by virtue of his authority, Buckland also played a major role in the rejection of the indisputable palaeontological and archaeological evidence for remote human antiquity (Grayson, 1983; Van Riper, 1993). He was working at a time when there was increasing evidence that was not compatible with the 6000 years offered by Biblical history. The discovery of fossils of earlier life forms led to a belief in the existence of earlier earths; these had all passed away as a result of catastrophes, to be replaced by a new creation (Rudwick, 1976, p. 133). Noah's flood could have been a historical account of the last of these catastrophes. As they were documenting the evidence for an extended earth history, geologists were uncovering stone tools in association with large extinct mammals. These dated to the Pleistocene ice age, then known as the "diluvium", the sediments of the flood that gave their name to the period itself. The stones were clearly tools, as many were similar to those used by contemporary non-Western peoples, hinting that Europe too had experienced a period before the emergence of civilization. But since most of these artifacts were found on the surface, or eroding out of banks of sediments, it could always be argued that the association with truly ancient fossils was spurious. One of the most famous examples deals with a skeleton that Buckland discovered in 1820 at Paviland Cave (Figure 1) or Goat's Hole, Wales (Aldhouse-Green, & Pettitt, 1998; Grayson, 1983). Along with extinct animals, the burial was found 15 cm beneath the surface of cave floor and was associated with red ochre and bone and ivory jewellery. It was assumed to be female because of the jewellery, and became widely known as the "Red Lady of Paviland" (Grayson, 1983, p. 65). Buckland concluded that the skeleton was a postdiluvial intrusion; the cave, "having either been used as a place of sepulture in early times or resorted to for refuge by the wretches that perished in it, when the country was suffering under one of our numerous military occupations" (Buckland in Daniel, 1975, p. 37). The remains of an early British camp nearby threw "much light on the character and date of the woman under consideration; and whatever might have been her occupation, the vicinity of a camp would afford a motive for residence, as well as the means of subsistence, in what is now so exposed and uninviting a solitude" (Buckland in Grayson, 1983, p. 67). Far from being an early prostitute, the red lady turns out to be a male from the Upper Palaeolithic and is approximately 18,500 years old (Aldhouse-Green, & Pettitt, 1998).

The continued puzzling association of ancient remains with supposedly recent people was solved with the excavation of Brixham or Windmill Hill Cave near Torquay in southwest England (Daniel & Renfrew, 1988). A committee was formed to oversee the 1858 excavations, composed of leading British geologists. They were careful to state that they were not trying to solve the question of the establishment of human antiquity per se, but were exploring the site "with a view toward the solution of certain geological problems" (Grayson, 1983, p. 179). Some stone tools were found along with many ancient fossil mammal bones. These were

***Figure 1.*** Selected Hominid Sites in Europe

discovered under a layer of travertine or flowstone, which had cemented the deposits in place and confirmed their proper association and antiquity (Grayson, 1983; Daniel, 1975). By 1859, the year of the publication of the *Origin of Species* (Darwin, 1859), scientists had generally concluded that humans had lived in Europe well before the beginnings of recorded history. In this new climate, Sir John Evans, one of the founders of Palaeolithic or "Old Stone Age" archaeology, concluded that "this much appears to be established beyond doubt, that is a period of antiquity remote beyond any of which we have hitherto found traces, this portion of the globe was peopled by man" (in Daniel, 1975, p. 61)

## Taxonomy and the Place of Humans in Nature

It was within this premodern scientific framework that Carl von Linné, better known as Carolus Linnaeus (1707-1778), created the system of biological classification that, with some modifications and many additions, is still in use today. For Linnaeus (1758), the basic unit of life was a species. Species were defined on physical features, and were grouped into higher and higher categories or taxa, including Genus, Family, Superfamily, Order, and, ultimately, Kingdom. Variation within a species was considered unimportant. An archetype or typical representative of a species was the base line against which all other members of the group were compared. Like other natural philosophers, Linnaeus believed that species had been created by God, and had a fixed, unchanging and invariable form. The tenth edition of Linnaeus's *Systema Naturae* (Linnaeus, 1758) became the standard reference work for all subsequent biological classification, and continues as such today. As God had created, so Linnaeus had classified ("Deus creavit, Linnaeus disposuit;" Barber, 1980, p. 55). Linnaeus was innovative in his method, but also in his perception of humanity and human nature. He created the species

*Homo sapiens* with only the words "know thyself." This maxim has been attributed to many ancient Greek philosophers, most notably Socrates. But it was also carved in the temple at the Oracle of Delphi (Wilkins, 1979). He also placed humans within the Order Primates, along with lemurs, lorises, tarsiers, monkeys, and apes. This was a biological group to be sure, but had to be the most important one, if it contained humans. He also defined geographic races using a strange combination of physical features, temperament, dress, and behavior. For example, while *Homo sapiens europaeus* were "white, serious, strong" and "ruled by laws," Asians were "yellow, melancholy, greedy" and "ruled by opinion," and Africans were "black impassive, lazy … crafty, slow, foolish" and "ruled by caprice" (Marks, 1995, p. 50).

For Linnaeus, there was no question; humans were animals who belonged in a biological group with other animals, the primates. But their exact relationship with primates was subject to question, even when a fossil record of the order started to accumulate. The Linnaean method of classification was flexible, so it could also include fossil species, including early hominids. In the last two decades, as more and more fossil hominids have been defined in a positive orgy of splitting (Table 1), the question remains. What made us different from our closest living animal relatives? But a new question has arisen, and has almost replaced the first one. What makes *Homo sapiens* or "anatomically modern" humans human? What makes them us, different from other fossil hominids? Was there some important threshold or boundary that we had to cross before we could be truly human? Did this threshold involve anatomical and/or behavioral changes (Chazan, 1995; Ingold, 1995)? If so, what were they, and what caused them to develop? Finally, if many hominid species had existed, some lasting over a million years, why did we survive when other hominids did not (Tattersall, 2000)?

Even with a substantial fossil hominid record, some early assumptions remain intact. There is the issue of a "cerebral rubicon"; how big did the brain need to be before it belonged to a true human? Surely a large brain meant modern intelligence, something of clear importance in our history. This was a major concern partly due to the discovery in the early 20th century of a fragmentary skull, mandible (lower jaw), and isolated canine tooth at Piltdown, England (Millar, 1972; Weiner, 1955). Classified as *Eoanthropus dawsoni* or Dawson's dawn man (after its discoverer), the skull was indistinguishable from that of living humans, but the tooth and mandible had more in common with apes. Piltdown was estimated to be early Pleistocene in age, based on associated fossil mammal species. With a cranial capacity of approximately 1070 cc, overlapping with the smallest living humans, it supported the theory that brain had led the way in human evolution. As a result, only fossil hominids with large brains could really be like us.

In Darwin's (1859) *Origin of Species*, he offered an explanation for the diversity of life, both past and present. It could be applied to humans, although the co-discoverer of natural selection, Alfred Russel Wallace, was determined to view the human brain as the product of a divine creation. Called "descent with modification," Darwin's theory argued that individuals in a species vary. Most of these variations are neutral, but some give an advantage in the struggle for existence while others do not. As a result of the process of natural selection, only a few

Table 1
*Valid Hominid Genera, Species and Subspecies and when they were Defined.*

| Genus | *Sahelanthropus* |
|---|---|
| Species and Subspecies | *Sahelanthropus tchadensis* (2002) |
| *Ardipithecus* | *Australopithecus* |
| *Ardipithecus ramidus ramidus* (1994, 2001)<br>*Ardipithecus ramidus kaddaba* (2001) - reassigned to *Ardipithecus kadabba* (2004) | *Australopithecus anamensis* (1994)<br>*Australopithecus afarensis* (1978)<br>*Australopithecus bahrelghazali* (1995)<br>*Australopithecus africanus* (1925)<br>*Australopithecus garhi* (1999) |
| *Kenyanthropus* | *Orrorin* |
| *Kenyanthropus platyops* (2001)<br>*Kenyanthropus rudolfensis* (2001) = *Homo rudolfensis* | *Orrorin tugenensis* (2000) |
| *Paranthropus* | *Homo* |
| *Paranthropus boisei* (1959)<br>*Paranthropus aethiopicus* (1985)<br>*Paranthropus robustus* (1938) | *Homo habilis* (1964)<br>*Homo rudolfensis* (1976)<br>*Homo erectus* (1891)<br>*Homo ergaster* (1975)<br>*Homo antecessor* (1997)<br>*Homo heidelbergensis* (1908)<br>*Homo neandertalensis* (1864)<br>*Homo sapiens* (1758)<br>*Homo sapiens idaltu* (2003) |

individuals survive to adulthood and are able to reproduce successfully. They pass all of their variations, including the favorable ones, on to future generations, and eventually lead to new species. Darwin envisioned this process as slow and continuous, as predicted by uniformitarian principles (of observing the present to understand the past).

> There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, while this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved (Darwin, 1859, p. 490).

The lack of transitional forms between species was explained as a product of an imperfect geological record. If this record had been continuous, one would see a gradual change from the parent to the daughter species. Darwin also could not explain the source of morphological variation, and how it was transmitted from one generation to the next. It would take ideas like that of punctuated equilibria (Eldredge & Gould, 1972; Gould & Eldredge, 1977) in the 1970s to explain the former, and the development of genetics to deal with the latter.

It would be a quarter of a century after the discovery of genuine ancient hominid fossils, the earliest australopithecines in South Africa, that Piltdown was revealed to be a fraud - a combination of a Romano-British skull with a modern orangutan jaw. As a result, the South African australopithecines were finally accepted. But not without a struggle; "not until Broom and Robinson recovered a partial skeleton of *Australopithecus africanus* (Sts 14) in 1947 did a doubting world accept that the earth was once inhabited by human bipedal pinheads" (McHenry, 1986, p. 178).

## Human Evolution: Facts and Models

The study of human evolution, palaeoanthropology, remains a very contentious discipline, in which every single pronouncement seems to be challenged by others. Horrobin (2001, p. 39) hit a sore spot when he recently suggested that a group of specialists in human evolution should be referred to as "a quarrel of palaeoanthropologists." In order to contribute something new, one either has to find a new fossil species, or say something new about fossils that have already been discovered. This is supposed to be an objective process, but as Tuttle (1988) reminded us a few years ago, palaeoanthropology is a curious science, where one's public profile and discoveries are often more important than one's specific research problem. As is true for other kinds of palaeontology, the facts are the fossils and their position in time and space; everything else seems to be someone's opinion. These opinions could influence taxonomy or classification. In turn, they affect the phylogenies built upon them, the models of how species and genera are related through time from ancestors to descendants. Even cladograms, the models produced by applying phylogenetic systematics or cladistics (Hennig, 1966), are subjective orderings of inferred relationships. They organize taxa on shared derived (innovative) characteristics; this is the currently preferred method of systematics. Once students of palaeoanthropology understand this, great debates boil down to discussions among various field and laboratory researchers over the significance of the fossil record. Constant claims for revolutions in interpretation of these fossils seem to be overblown, but occasionally turn out to be accurate. Since there are only so many fossils to go around, one either has to find others, or say something new about the ones that have already been discovered.

In order to understand the pattern and process of human evolution, fossils must be placed in their proper context in time and space. The age of such fossils can be determined using a number of methods. East Africa has become the paramount place for early hominid research in large part due to geological accident. As the Great Rift Valley formed in the Miocene, erosion of the emerging highlands and deposition of sediments into low lying lake basins led to the rapid burial of organic material. Subsequent uplift, due to tectonic activity, led to the exposure of fossil bearing deposits dating to the Pleistocene (between 10,000 and 1.8 million years ago), Pliocene (1.8 to 5 million years ago) and Miocene (5 to 25 million years ago) Epochs. Most fossils are found through surface survey as they erode out of exposed sediments and rocks. These exposures show layers of sedimentary rocks sandwiched by volcanic ash or lava layers. The latter are datable using techniques like potassium argon ($^{40}K$ / $^{40}Ar$) or argon/argon ($^{40}Ar$ / $^{39}Ar$) that measure radioactive decay from one isotope to another. Volcanic rocks are heated at the time of formation and lose whatever argon they originally contained. Since the rate of decay is known, the amount of argon can give a date when the volcanic layer was deposited (Deino et al. 1998; Ludwig & Renne 2000; Wintle, 1996). Employing the general principles of stratigraphy, fossils from sedimentary layers below a dated volcanic deposit would be older, while those above it would be younger. The chemical composition of the volcanic rocks can also be identified and correlated over wide distances, providing the basis for a master geological framework. For example, in the Shungura Formation at the Omo River in southern Ethiopia, a sequence more than 700 m thick has been developed using these methods, even though each individual rock outcrop samples only a fraction of it. Dating is aided by biostratigraphy. Many mammals underwent rapid change and diversification at the same time as early hominids, including suids (pigs), antelopes, and elephants (Harris & White, 1979; White & Harris, 1977). They act as index fossils for dating places without a history of volcanism, such as the South African australopithecine sites.

Based on current knowledge, the earliest hominids are found in Africa and date to the Late Miocene (between 8 and 5 million years ago). In order to be classified as hominids, they must show evidence of morphological changes for bipedal locomotion, upright walking on two hind legs. This is generally accepted as the minimum requirement for a specimen to be placed in the hominid family. But other than this, the oldest forms are extremely ape-like (Tables 2 and 3). Using comparative morphology palaeoanthropologists hypothesize that the last common ancestor was more ape-like than human-like, and the earliest hominids generally follow the ape pattern in all but their skeletal adaptation for locomotion. There are no fossils known that can be directly linked to the living African apes, nor any that could be considered representative of the last common ancestor between them and humans. Researchers distinguish the first members of our own genus, *Homo* (Wood, 1992), by their large brains (relative to overall body size). Fossils of early *Homo* first appear in Africa around 2.5 million years ago. Around the same time, the first archaeological sites can be detected; these are identified by the presence of flaked stone tools in fine-grained sediments (sands or silts), in a context where such rock would not occur naturally. It is possible that protohominids and early apes used some basic tools, as chimpanzees do today (McGrew, 1992), but these were in perishable, organic materials that leave no fossil evidence.

Models of human origins preceded the discovery of fossil remains that could be used to test them. As David Pilbeam (1980, p. 262) was one of the first to notice, "our theories have said more about the theorists than they have about what actually happened." In many studies, "the theories are unconstrained by fossils; they are fossil-free or in some cases even fossil proof ... Yet we all thought the fossils were contributing a great deal" (Pilbeam, 1980, p. 267) to the debates about human origins. The first reports of early hominids described material excavated in 1924 from breccia deposits at the Taung limestone quarry in South Africa (Figure 2). A child's face, mandible and fossilized brain or endocast were embedded in natural cement, along with other mammal fossils. Described by Dart (1925), they were named *Australopithecus africanus*, or the "southern ape from Africa". Dart was puzzled by the small brain of this individual, but as a neuroanatomist, argued that its lobes and fissures were organized as in humans, not apes. The child had a small canine, and a foramen magnum (literally "the big hole" in the base of the skull where it balances on the vertebral column) oriented for upright posture, and presumed bipedal locomotion. Adult versions of the same species were eventually discovered at Sterkfontein near Johannesburg and elsewhere, and confirmed Dart's controversial diagnosis. On faunal correlation with East Africa, it is assumed that these australopithecines lived between 2.5 and 3 million years ago.

***Figure 2.*** Selected Hominid Sites in Africa.

In a world where Piltdown was the model for early humans, Dart felt the need to emphasize the cultural achievements of his australopithecines. Even if they had small brains, he thought they had the capacity for hunting and cultural behavior. He noticed that many of the mammal bones recovered from the same deposits were broken in specific ways. Examining the fracture patterns, he concluded that australopithecines had processed them for food and then used the bones as tools for hunting in increasingly dry savanna environments (Dart, 1953, 1957). Dart's killer apes, with their osteodontokeratic or "bone-tooth-horn" culture were a typical product of early palaeoanthropological thinking. These models saw hominids as the principal actors, directly responsible for their own evolution (Willoughby, 1991), the first step along an inevitable line of killing and progress which led to global colonization, but also to numerous global conflicts. The fossil and the archaeological records were both examined for the first sign of uniquely human traits. As hominids developed these traits, they became more like us: bipedal locomotion, tool manufacture, more complex social life, language and intelligence. In contrast, more recent models see hominids as just part of the African fauna, passively responding to environmental change in the same way as many other mammalian species. For Coppens (1994), the tectonic uplift of the central African mountains during the Miocene split the range of the last common ancestral population. Those that became chimpanzees and gorillas stayed on the wetter, west side, while those who became human evolved in the east, which became increasingly arid over time. Vrba (1993, 1996) noted that the adaptive radiation of hominids in the Pliocene and Pleistocene parallels that of many other African mammals. Stanley (1992, 1996) argued that once early bipedal hominids appeared, they could only develop larger brains relative to body size once they became fully terrestrial. This happened around 2.5 million years ago, with the onset of the ice ages of the Pleistocene and the expansion of grasslands or savannas in Africa. For later humans, Potts (1998a, 1998b) argues for a compromise, what he labels variability selection: hominids responded to the increasing intense cycling of the ice ages over the last million years by remaining flexible in behavior. While other species disappeared, somehow they managed to keep going.

## Anthropoids, Hominoids, and Hominids

Humans belong to the Order Primates and Suborder Anthropoidea, as originally defined by Linnaeus. Composed of New World and Old World monkeys, apes and humans, anthropoids exhibit some shared skeletal features. The mandible is fused into a single bone at the midline or symphysis. The frontal, the bone of the forehead, is also joined along the midline at the metopic suture, and the orbits (eye sockets) are cup like and enclosed in behind the eye. This distinguishes them from the other primate suborder, the Prosimii or prosimians, with only a bar of bone behind the eye (Martin, 1990). All living and fossil apes and humans belong to the Superfamily Hominoidea. Like other mammals, they have four kinds of teeth; from the middle of the mouth back on each side, top and bottom, these are the incisors, canines, premolars and molars. Old World monkeys, the Cercopithecoidea, and hominoids (apes and humans) both have the same number of each tooth type on each side of the mouth, giving them a dental formula of 2.1.2.3. This gives the total number of 32 teeth when counted and multiplied by four. For purposes of identification, individual teeth are numbered relative to the midline of the row. The first incisor is I1, with a superscript ($I^1$) for the upper or maxillary tooth, and a subscript ($I_1$) for the lower or mandibular incisor. A hominoid with 2 incisors, 1 canine, 2 premolars, and 3 molars would have a lower jaw tooth row numbered $I_1$, $I_2$, $C_1$, $P_3$, $P_4$, $M_1$, $M_2$, and $M_3$. Notice that the premolars are numbered $P_3$ and $P_4$. Numbers are calculated with reference to the proposed primate ancestor from the early Cenozoic around 65 million years ago; it had a dental formula of 3.1.4.3. If teeth are lost over evolutionary history, they were the ones on either side of the canine. As a result, a primate with only two premolars has a P3 and a P4; New World monkeys, with three, have a P2, P3, and P4.

On their lower molars, hominoids have 5 cusps or high points, with fissures in between. The deepest fissures form a Y pattern, with the bifurcation opening up towards the cheek or buccal side. This is the Y5 or Dryopithecine cusp pattern, named after fossil apes first found near Paris in the 1830s. It can be easily distinguished from the bilophodont molars of the cercopithecoids, where pairs of cusps have joining ridges, and the tooth is shaped like a figure eight. Living hominoids tend to have long arms relative to their leg length, and use them as the primary means of locomotion: brachiating like Tarzan for gibbons (*Hylobates*) and siamangs (*Symphalangus*), slow climbing and suspension for orangutans, and knuckle walking for the African apes, chimpanzees and gorillas. Humans, being bipedal, are the exception, but we retain the shoulder and upper arm structure of our climbing relatives. While there are fossil hominid skeletal remains from the Miocene, palaeontologists have little idea what the last common ancestor of African apes and humans looked like or how it moved.

Living apes and humans can be easily distinguished by dental characteristics (Table 2). African apes have thin dental enamel on their molars, while humans and orangutans have thick enamel. The shape of the tooth row or dental arcade forms a U in living apes, with the corners at the canines, and parallel tooth rows behind. Living humans have a parabolic dental arcade. Many early hominids and Miocene apes have a U shape, while some exhibit a V, compressed at the front of the mouth. Modern apes tend to have large, protruding canine teeth. As a result, there is a diastema or gap between the upper canine and second (or lateral) incisor, as well as between the lower canine and the first premolar. One of the most diagnostic dental features is the shape of this $P_3$. Since it hones or rubs against the upper canine, its shape is associated with canine size. Living humans have a nonsectoral $P_3$, a tooth with two cusps of more or less equal size. Living apes have a sectoral $P_3$, with a single large cusp, a cone shaped tooth that resembles a canine. Some early hominids such as *Ardipithecus ramidus*, have the same pattern, while others (*Australopithecus afarensis*) have a semisectoral $P_3$, with a large cusp on the cheek side of the mouth, and a shelf of bone and incipient second cusp on the tongue or lingual side. The latter would be considered more derived towards the modern human condition than the former.

The fossil record includes hominoids that exhibit a number of these traits, but it is case of mixing and matching at random (Table 3). There is no fossil hominoid which resembles a living ape in all respects, either dentally or skeletally. As a result, defining a hominoid as an ape or human is especially difficult. The oldest "hominoid," in other words, an anthropoid with a Y5 dental pattern, is *Aegyptopithecus zeuxis* from the Jebel Quatrani Formation at the Fayum in Egypt, dating to around 35 to 33 million years ago (Simons, 1995). *Aegyptopithecus* appears to have been an arboreal quadruped, shaped much like a modern monkey. It may have had a tail, something seen in no modern hominoid, and it had a long projecting snout like a dog. It is one of many anthropoids found at this locality, now described as early forms that existed prior to the divergence of hominoids and cercopithecoids (Klein, 1999).

The next oldest dental hominoids come from East Africa near Lake Victoria and Lake Turkana and date to the Early Miocene between 25 and 16 million years ago. They are composed of many isolated teeth, partial jaws, along with some postcranial bones (bones from the skeleton apart from the skull and mandible). About six genera have been defined, all of which have the Dryopithecine Y5 lower molar pattern. *Proconsul*, one of the earliest and best known, has thin dental enamel, and limbs of equal length, like modern monkeys. Early Miocene hominoids are extremely variable, but come from a restricted area, associated with tropical forest or woodland habitats.

Table 2

*Time and Space Distribution of Fossil Hominoids and Hominids.*

| | |
|---|---|
| Age | 0 to 1 million years old – *Homo sapiens*, *Homo sapiens idaltu*, *Homo neandertalensis*, *Homo heidelbergensis*, *Homo antecessor*, *Homo erectus* |
| | 1 to 2 million years old – *Homo ergaster*, *Homo erectus*, *Homo rudolfensis*, *Homo habilis*, *Paranthropus robustus*, *Paranthropus boisei* |
| | 2 to 3 million years old – *Homo rudolfensis*, *Paranthropus aethiopicus*, *Australopithecus garhi*; *Australopithecus africanus* |
| | 3 to 4 million years old – *Australopithecus afarensis*, *Australopithecus anamensis*, *Australopithecus bahrelghazali*, *Kenyanthropus platyops*, |
| | 4 to 5 million years old – *Ardipithecus ramidus*, Sterkfontein Member 2 "*Australopithecus*" |
| | 5 to 6 million years old – *Ardipithecus kadabba*, *Orrorin tugenensis* |
| | 6 to 7 million years old – *Sahelanthropus tchadensis* |
| | 5 to 16 million years old – Miocene apes in Eurasia and Africa |
| | 17 to 25 million years old – Miocene apes in Africa only |
| Location | Worldwide today – *Homo sapiens* |
| | Europe and Middle East - *Homo sapiens*, *Homo neandertalensis*, *Homo heidelbergensis* |
| | Europe - *Homo sapiens*, *Homo neandertalensis*, *Homo heidelbergensis*, *Homo antecessor* |
| | East and Southeast Asia - *Homo sapiens*, *Homo heidelbergensis*, *Homo erectus* |
| | East Africa – *Homo sapiens, Homo sapiens idaltu*, *Homo heidelbergensis*, *Homo erectus* / *Homo ergaster*, *Homo habilis*, *Homo rudolfensis*, *Paranthropus boisei*, *Paranthropus aethiopicus*, *Australopithecus garhi*, *Australopithecus afarensis*, *Australopithecus anamensis*, *Kenyanthropus platyops*, *Ardipithecus ramidus*, *Ardipithecus kadabba*, *Orrorin tugenensis* |
| | South Africa – *Homo sapiens*, *Homo heidelbergensis*, *Homo erectus*, *Homo ergaster*, *Homo habilis*, *Paranthropus robustus*, *Australopithecus africanus*, Sterkfontein Member 2 "*Australopithecus*" |
| | Chad - *Sahelanthropus tchadensis*, *Australopithecus bahrelghazali* |
| Associated Environments | Tropical Forest – *Ardipithecus ramidus*, *Ardipithecus kadabba* |
| | Mixture of Habitats – *Australopithecus afarensis* (Hadar); *Australopithecus bahrelghazali*; *Kenyanthropus platyops*; *Sahelanthropus tchadensis* |
| | "Open" Woodland – *Orrorin tugenensis*; *Australopithecus anamensis*; *Australopithecus afarensis* (Laetoli) |
| | Grassland – Sterkfontein Member 2 "*Australopithecus*", *Australopithecus garhi*, all early African *Homo* |

Table 3

*Anatomical Characteristics of Fossil Hominids.*

| | |
|---|---|
| Anatomical coverage | Teeth, mandible and/or maxilla (=jaws) – Most Miocene apes; *Australopithecus bahrelghazali*<br>Teeth, jaws, face and skull – *Sahelanthropus tchadensis*; *Kenyanthropus platyops*, *Australopithecus garhi*, *Homo sapiens idaltu*<br>Teeth, jaws, some postcranial (body) bones – *Australopithecus anamensis*, *Ardipithecus ramidus*; *Ardipithecus kadabba, Orrorin tugenensis*, *Homo erectus*, most *Homo heidelbergensis*<br>More or less completely known - Sterkfontein Member 2 "*Australopithecus*", *Australopithecus afarensis*, *Homo neandertalensis*, *Homo sapiens*, some *Homo ergaster* and *Homo heidelbergensis* specimens |
| Limb Proportions | Ape like (long arms and short legs) - Sterkfontein Member 2 "*Australopithecus*", *Australopithecus afarensis*, *Homo habilis*<br>Human like (short arms and longer legs) – all members of genus *Homo* except for *Homo habilis*<br>Unknown – *Ardipithecus ramidus*, *Ardipithecus kadabba*, *Orrorin tugenensis, Australopithecus bahrelghazali*, *Sahelanthropus tchadensis*, *Kenyanthropus platyops*; *Australopithecus garhi*, *Homo rudolfensis* |
| Locomotion | Knuckle walking – modern African apes<br>Bipedalism – modern humans; all members of genus *Homo*, *Orrorin tugenensis*, *Australopithecus anamensis*<br>Bipedal, but retains climbing abilities – *Australopithecus afarensis*, Sterkfontein Member 2 "*Australopithecus*"<br>Unknown - *Ardipithecus ramidus*, *Ardipithecus kadabba*, *Australopithecus bahrelghazali*, *Sahelanthropus tchadensis*, *Kenyanthropus platyops*, *Australopithecus garhi* |
| Brain Size Relative to Overall Body Size | Small (Modern ape condition) – all early hominids except those listed below as "unknown"<br>Intermediate – *Homo habilis*<br>Large (Modern human condition) – members of the genus *Homo* other than *Homo habilis*<br>Unknown - *Ardipithecus kadabba*, *Australopithecus bahrelghazali, Orrorin tugenensis* |

Table 3 (cont.)
*Anatomical Characteristics of Fossil Hominids.*

| | |
|---|---|
| Face | Prognathic (juts out)– Sterkfontein Member 2 "*Australopithecus*", *Australopithecus anamensis*, *Australopithecus africanus*, *Australopithecus garhi*, all *Paranthropus*, early members of genus *Homo*<br>Orthognathic (flat) – *Sahelanthropus tchadensis*, *Kenyanthropus platyops*, later members of genus *Homo*<br>Unknown - *Ardipithecus ramidus*, *Ardipithecus kadabba*, *Orrorin tugenensis*, *Australopithecus bahrelghazali* |
| Dental Arcade | U shaped (modern ape condition) – Some Miocene apes, most early hominids<br>V shaped – Some Miocene apes<br>Parabolic (modern human condition) – most later members of genus *Homo*<br>Unknown - *Orrorin tugenensis*, *Australopithecus bahrelghazali*, Sterkfontein Member 2 "*Australopithecus*" (not yet reported) |
| Canine / $P_3$ complex | Small canine and non-sectoral lower first premolar (modern human condition) – *Australopithecus africanus*, *Australopithecus garhi*, all *Paranthropus* species, all members of the genus *Homo*<br>Intermediate sized canine and semi-sectoral lower first premolar – *Australopithecus afarensis*, *Australopithecus anamensis*, probably *Orrorin tugenensis*<br>Large canine and sectoral lower first premolar (modern ape condition) – *Ardipithecus ramidus*, *Ardipithecus kadabba*<br>Unknown - Sterkfontein Member 2 "*Australopithecus*", *Australopithecus bahrelghazali* |
| Enamel thickness | Thick (Modern human and orangutan condition) – all hominids except for *Ardipithecus*<br>Thin (Modern African ape condition) - *Ardipithecus ramidus*, *Ardipithecus kadabba* |
| Sources of information for Tables 2 and 3 | Andrews, 1995; Asfaw et al. 1999; Begun, 1992, 1994, 2003, 2004; Brunet 2001; Brunet et al. 1995, 1996, 2002; Clarke, 1998, 1999, 2002; Clarke & Tobias 1995; Dart, 1925; de Heinzelin et al. 1999; Haile-Selassie, 2001; Haile-Selassie, Asfaw et al. 2004; Haile-Selassie, Suwa et al., 2004; Jablonski et al. 1998; Johanson & White, 1979; Johanson et al. 1978, 1982; Kimbel et al. 1994; Leakey & Harris, 1987; Leakey et al. 1995, 1998, 2001; Lieberman, 2001; Moya Sola & Kohler, 1996; Partridge et al. 2003; Patterson, 1967; Pickford & Senut, 2001; Senut et al. 2001; Stewart & Disotell, 1998; Sussman et al. 1985; Vignaud et al. 2003; Ward, 2002; Ward et al. 1999, 2001; White, 1980a, 1980b; White et al. 1993, 1994, 1995, 1999, 2003; WoldeGabriel et al. 1994, 2001; Wolpoff et al. 2002; Wood, 1992, 2002 |

The first apes outside of Africa are found in similar habitats from the Middle Miocene, around 16 to 17 million years, onwards. At this time, a land bridge developed where Africa and Eurasia meet today, and apes are among the African animals that dispersed using extensive, continuous, rainforests (Begun, 1992, 1994; Jablonski et al. 1998). Many Eurasian mammals appear in Africa for the first time and vice versa, examples of a great faunal interchange which provides an important biostratigraphic marker. A wide variety of hominoid genera soon appear, including *Dryopithecus*, *Pliopithecus* and *Ouranopithecus* in Europe and *Sivapithecus* in Asia (Begun, 2003). All are known primarily from jaws and teeth, and show a mixture of traits. One of the few postcranial fossils, a partial skeleton from Can Llobateres, Spain, shows adaptation for suspension and swinging (Moya Sola and Kohler, 1996). A Late Miocene ape from Italy, *Oreopithecus*, may have structural adaptations for bipedalism, but also exhibits long arms relative to leg length (Rook et al. 1999). At the end of the Miocene, 5 to 6 million years ago, conditions worldwide became much cooler. More seasonal environments appear, and the rainforests are greatly reduced in extent. A critical event in hominoid evolution at this time is the Messinian salinity crisis (Hsu, 1983; Krijgsman et al. 1999; Duggen et al. 2003; McKenzie, 1999), when the Mediterranean Sea dried up and was replaced by a desert. The disappearance of the tropical rainforests of Eurasia and Africa led to the extinctions of many apes. It may also be responsible for the adaptive radiation of Old World monkeys. With smaller body sizes and much shorter life spans, monkeys might have successfully outcompeted apes in drier habitats. But recently, some Miocene palaeontologists have proposed that European or Eurasian hominoids returned to Africa to become the ancestors of living African apes and hominids (Begun, 2003; Jablonski et al. 1998; Kordos & Begun, 2001, 2002; Stewart & Disotell, 1998).

Explaining the diversity and evolutionary history of Miocene apes has always been problematic due to their widespread distribution. Simons and Pilbeam (1965) offered the first modern classification, since the "Miocene hominoid fossil record was in something of a mess" (Pilbeam, 1986, p. 295). Most of the fossils consisted to fragmentary jaws and teeth, and these had been assigned to many different taxa. Over 50 species and 25 genera were reduced to two main subfamilies: the Dryopithecinae, ancestral to modern apes and the Ramapithecinae, ancestral to hominids/humans. The second subfamily was named for *Ramapithecus*, known from upper jaw fossils from the Siwalik Hills in Pakistan (Lewis, 1934). It exhibited human like dental traits including small canines and incisors, thick dental enamel, and a presumed parabolic dental arcade. As was the case for australopithecines and later hominids, the molars were square, with low crowns and flat chewing surfaces. As a result, it was assumed that *Ramapithecus* was bipedal and probably tool using. More discoveries of complete jaws revealed that *Ramapithecus* was different from both living apes and humans; like other Miocene apes, they had a V shaped dental arcade, extremely narrow at the front. Simons and Pilbeam's model of two groups of Miocene apes held until palaeontologists started arguing that there were dental similarities between *Ramapithecus* and another Asian hominoid genus, *Sivapithecus* (Andrews & Tekkeya, 1980). Then a *Sivapithecus* face was discovered in the Siwaliks, Pakistan (specimen GSP 15,000) that was remarkably similar to a modern orangutan (Pilbeam, 1982). Along with remains from Pasalar, Turkey, it became clear that *Ramapithecus* was not a hominid at all. Enamel thickness was now felt to be the primitive or ancestral condition for great apes, since it was shared by orangutans and humans, but not by African apes. By 1982, researchers were forced to conclude that no Miocene hominoid was directly linked to any living form, let alone to humans. The next oldest fossil that was human-like was less than 5 million years old, the earliest australopithecines. Surprisingly, this conclusion had already been reached a decade earlier by geneticists who were studying living primates (Goodman, 1963; Sarich, 1971; Sarich & Wilson, 1967).

## The Molecular Clock: An Alternative Perspective

By the early 1960s, molecular biologists were testing some basic methods to determine relationships between animals. By current standards, these methods were extremely primitive. Goodman (1963) created a hominoid evolutionary tree using blood serum proteins. The intensity of immunological responses by one species to the injected blood proteins of another could be used to identify how close the two were in evolutionary terms (Pilbeam, 1986). Goodman noted that African apes and humans were very similar, but accepted the interpretation of *Ramapithecus* as a Middle Miocene fossil hominid, dating to between 8 and 12 million years ago. As a result, the last common ancestor of African apes and humans had to be older than predicted by molecular data. Goodman mistakenly concluded that the rate of molecular evolution had significantly slowed down in this lineage.

Sarich and Wilson (1967; Sarich, 1971) took this approach one step further. They developed methods to quantify immunological reaction strengths more easily, and to quantify the differences between pairs of species (Pilbeam, 1986). They used serum albumin, a protein composed of about 570 amino acids that is found in both humans and African apes. They purified albumin from a number of primate species and injected the samples into rabbits. The rabbits develop antibodies to the proteins, and the resulting product was tested against a series of primate albumins. The degree of reaction gives a measure of similarity. If two albumins are identical, they yield an immunological distance or ID of 0; the more different, the larger the ID value. Sarich and Wilson applied Kimura's (1983) concept of neutral mutation, the idea that parts of the genome have no apparent function only change as a result of mutation. These mutations occur at a fixed rate through time, providing a molecular clock dating evolutionary events. Sarich proposed to date the time of divergence using the formula, ID = kt, where k is a constant and represents the rate of molecular change, and t is the time of divergence. A human to chimpanzee reaction gave an ID of 7, human to rhesus macaque 32, and human to a spider monkey 58 (Sarich, 1971). A value for k was calculated using an estimated 100 units of immunological distance for 60 million years of Cenozoic mammalian evolution. An ID of 100 = k (60 x $10^6$), so k equals 1.67 units ID per million years of separation, or 0.83 units per million years per lineage. This put the human: chimpanzee date of divergence at 4.19 million years (7 units of ID with 1.67 units per million years). Orangutans have diverged around 7-8 million years ago, gibbons 10 to 12 million years, and Old World monkeys diverged from apes 23 million years ago (Sarich, 1971). This fit the fossil evidence quite well, as long as *Ramapithecus* was not a hominid. Sarich concluded that "to put it as bluntly as possible, I now feel that the body of molecular evidence on the *Homo* - *Pan* relationship is sufficiently extensive that no one no longer has the option of considering a fossil hominid specimen older than about 8 million years as a hominid *no matter what it looks like*" (Sarich, 1971, p. 321; italics in original). Not only was he challenging the validity of a Middle Miocene hominid, he was telling palaeontologists that their interpretation of fossils was dead wrong.

DNA hybridization techniques (Sibley & Ahlquist, 1984, 1987) put humans closer to chimpanzees than either was to gorillas. DNA samples from two organisms are combined, then heated in order to determine how long it takes to break the bond between them. The result gives a measure of similarity, as closer related organisms will have a stronger bond than less related ones. Newer methods, including direct sequencing of DNA, confirm the genetic closeness of chimpanzees and humans, while in terms of their skeletal structure, chimpanzees and gorillas are more closely related (Bailey, 1993). Studies of mitochondrial DNA, organelles outside the cell nucleus that convert sugar into energy, as well as Y chromosomes point to great within-group genetic diversity for African apes, something absent in living humans (Gagneux et al. 1999; Ruvolo, 1997; Kaessman et al. 1999, 2001; Stone et al. 2001). If this diversity of forms marks the time since populations within a species last had a common ancestor, the genetic homogeneity of humans today suggests they we have a relatively short evolutionary history (Cann et al. 1987). This is something first unknowingly detected by Lewontin (1972) when he studied blood group frequencies in living human populations worldwide. He was attempting to measure the biological significance of human "races," but found that most variation was between individuals, not geographically separated populations. As a biological concept, race had little validity, a conclusion that continues to be supported today (Brown & Armelagos, 2001).

So what does the fossil evidence actually offer to those who wish to understand human evolution? Geneticists from Sarich (1971) to the proponents of mitochondrial "Eve," our African last common ancestor (Cann et al. 1987; Wilson & Cann, 1992) argue that they can give a better picture of human evolution than palaentologists. But most of the variation they examine has developed in the last 50,000 years. It is impossible to see the great diversity of fossil hominids, if modern humans are the only source of information.

## Are There Too Many Taxa? The Earliest Hominids

The rest of this paper will briefly review the current state of knowledge about fossil hominids, information that is summarized in Tables 2 and 3. But be aware that our perceptions of this evidence change almost monthly as new species and genera are reported. The facts are the fossils in time and space; interpretations are legion. The first early fossil hominids were classified as *Australopithecus africanus*, using the Taung child's skull, mandible and brain endocast (Dart, 1925). The first adult version was from Member 4 at Sterkfontein and was originally classified as *Plesianthropus transvaalensis* by Robert Broom (1936; Broom & Schepers, 1946). It took until the 1950s for the australopithecines to be accepted as early hominids. By then, hundreds of fossils had been recovered from a number of dolomite caves filled with breccia, and more have followed. The most notable was the 1998 discovery of an almost complete skeleton from Member 2 at Sterkfontein

(Clarke & Tobias, 1995; Clarke, 1998, 1999, 2002; Partridge et al. 2003), previously believed to be too old to contain hominid remains. South African fossils are classified as *Australopithecus africanus*, *Paranthropus robustus*, or as early *Homo* (specifically, *Homo habilis*). All are bipedal, with *Homo* having the largest brain. *Australopithecus africanus* and *Paranthropus robustus* are distinguished on facial and dental features. Members of the robust species have larger premolars and molars, and enlarged facial and cranial attachments for chewing muscles. In East Africa, similar forms (*Paranthropus boisei* and *Paranthropus aethiopicus*) can be as old as 2.5 million years, but most are between 2.0 and 1.0 million. The gracile australopithecines, such as those from Taung and Sterkfontein, are between 3 and 2.5 million years old.

Ironically, by the time the South African australopithecines were recognized as early hominids in the 1950s, spectacular East African fossil finds had supplanted them. New sites, located in the rift valley, contained similar fossils but these were associated with easily datable volcanic ash or lava layers. Until the mid 1970s, the fossil record in East Africa repeated the time sampled in the South African caves. This would soon change, as more and more, older and older, hominids were discovered and classified. The first of these, and still the most important, is *Australopithecus afarensis* (Johanson & White, 1979; Johanson et al. 1978, 1982). This species was defined in 1978/79 for material from Hadar in the Afar Triangle of Ethiopia, and Laetoli in northern Tanzania. The quantity and quality of fossil remains recovered from the Hadar is unprecedented. They include AL 288-1, the "Lucy" skeleton that is about 40% complete, as well as the "First Family" which represents about 13 individuals, children and adults. The Hadar fossils are around 3.25 million years old, while the Laetoli ones, mainly jaws and teeth, are between 3.6 and 3.8 million (Leakey & Harris, 1987; Leakey et al. 1976; White, 1980b). Laetoli was recognized as a fossil hominid site by Kohl-Larson in the 1930s; Mary Leakey conducted research there in the 1970s, and uncovered three sets of hominid footprints in a volcanic ash horizon (Day & Wickens, 1980; Hay & Leakey, 1982; Leakey & Hay, 1979; White, 1980a; White & Suwa, 1987). More bones were later found at the Maka locality in the Middle Awash of Ethiopia; these are intermediate in time, around 3.4 million years old (White et al. 1993, 1999). More complete crania were reported in the mid 1990s, when about 53 new specimens were described, adding to the approximately 250 specimens recovered in the 1970s (Kimbel et al. 1994, p. 449). With almost complete body coverage, *Australopithecus afarensis* is the best-known species this side of the European Neandertals. One could now talk about populations and functional morphology. All fossils were described as belonging to a single species, with great deal of sexual dimorphism (difference in body size by sex), although this has recently been challenged (Reno et al. 2003). They were bipedal with extremely small brains, in the modern chimpanzee range. The easiest way to describe them is as resembling apes from the waist up and humans from the waist down. Specimens whose limb proportions are known show extremely long arms and short legs; this is the opposite of what is seen in living and recent human populations. Despite the quantity of information, or perhaps because of it, there has been a longstanding debate about just how bipedal *Australopithecus afarensis* was. For Lovejoy (1988; Lovejoy et al. 1988; Ward, 2002), they were better at it than us today, as females did not have the secondary structural changes in the pelvis to birth a large brained baby. On the other hand, Stern and Susman (1983; Susman et al. 1985) focused on the long arms and curved hands and feet, and argued that their primary mode of locomotion was climbing and hanging, while they were bipedal on the ground. For them, "diminutive (30+ kg), small-canined, non-tool-using hominids are not likely to have been fully terrestrial" (Susman et al. 1985, p. 184).

Up until the mid 1990s, *Australopithecus afarensis* was the only truly ancient human. But since then a bewildering number of hominids have been defined, each apparently older than the last (Table 1). They seem to come in bunches. When a research team names a new species, another group soon follows with their own. Over the last couple of years, even new genera were defined as the search for the "missing link" or last common ancestor continued unabated. One of the first was *Australopithecus bahrelghazali*, from the Bhar el Ghazal region of Chad (Brunet 2001; Brunet et al. 1995, 1996). From Koro Toro near Lake Chad, this single find of a fragmentary mandibular symphysis was the first hominid found outside of South and East Africa. The most recent, and oldest, discovery comes from a nearby site at Toros-Menalla. Classified as *Sahelanthropus tchadensis* (Brunet et al. 2002; Vignaud et al. 2002; Wood, 2002), it is composed of a cranium, a fragmentary mandible and some isolated teeth, 6 specimens in total (Wood, 2002, p. 133). It is dated to between 6 and 7 million years ago by faunal or biostratigraphic comparison with North and East Africa. Is it a hominid or an ape (Wolpoff et al. 2002)? In this time range, in the absence of bones from the hips and lower limbs, it is impossible to tell. It is described as human on facial features, its jaw and small canine with apical wear. The molars exhibit enamel thickness that is intermediate between living apes and humans (Wood, 2002, p. 134; Brunet et al. 2002:145,151). Some features make it like an ape and are shared with many other early hominids: a small brain and the shape of the back of the cranium. But the skull and face are reminiscent of *Kenyanthropus* and early *Homo*, especially the ER-1470 skull from the east side (also known as Koobi Fora) of Lake Turkana in northern Kenya (Brunet et al. 2002). *Kenyanthropus platyops* (Leakey et al. 2001; Lieberman, 2001) includes a number of fossil specimens from Lomekwi in the Nachukui Formation in the west side of Lake Turkana. Specimens assigned to *Kenyanthropus* include a distorted cranium, a temporal, 2 partial maxillae or upper jaws, isolated teeth, plus two earlier mandible fragments (Leakey et al. 2001). These are estimated to be around 3.5 to 3.3 million years old, and are associated with other mammals found in open grasslands and forests (Leakey et al. 2001).

Another new species is *Australopithecus anamensis* (Patterson 1967; Leakey et al. 1995, 1998; Leakey & Walker 1997, Andrews 1995; Ward et al. 1999, 2001), from Kanapoi and Allia Bay, south and east of Lake Turkana respectively. The two Kanapoi localities are dated to 4.1 and over 3.5 million years ago, while Allia Bay is estimated to be 3.9 million years old (Andrews, 1995). The hominid sample includes a proximal tibia (the area below the knee), a distal humerus (area about the elbow), as well as a number of upper and lower jaws and isolated teeth. It combines an australopithecine face and teeth with postcrania like those of later *Homo* (Andrews, 1995, p. 556). *Australopithecus anamensis* is associated with dry, possibly open, wooded or bushland environments, with gallery forest along rivers (Leakey et al. 1995).

*Ardipithecus ramidus* (White et al. 1994, 1995; WoldeGabriel et al. 1994) comes from Aramis in the Middle Awash region of Ethiopia, not far from Hadar.

To date, there are 17 specimens described, including 1 cranial base fragment, 1 mandible fragment, teeth, and three left arm bones (radius, ulna, and humerus) from a single individual. These are dated by ($^{40}$argon/$^{39}$argon) to between 4.4 and 4.2 million years ago. According to their discoverers, these exhibit a mixture of ape and hominid traits (White et al. 1994). The more apelike features include a large canine and completely sectoral $P_3$. Unlike any other hominid candidate, *Ardipithecus* shows thin dental enamel, only seen in modern African apes. Indeed, it is described as the "most apelike hominid ancestor known" (White et al. 1994, p. 312). The case for *Ardipithecus* being a hominid is not strong, as they are also associated with true tropical forest conditions. The bottom of the skull contains a foramen magnum that is placed forward; therefore it is argued that it came from a bipedal creature. But many apes show more or less upright body posture, so this is not conclusive. The other hominid like feature is said to be its incisor like ("incisiform") canine.

This species was redefined in 2001 as *Ardipithecus ramidus ramidus* when another sub-species was created, *Ardipithecus ramidus kadabba* (Haile-Selassie, 2001; WoldeGabriel et al. 2001). The latter is dated between 5.54 and 5.77 million years old. It is composed of 11 specimens from 5 separate localities in the Middle Awash, representing 5 or more individuals (WoldeGabriel, 2001). These specimens are much more fragmentary; they include a right mandible fragment, some postcranial remains, bones and isolated teeth. The lower canine is described as incipient incisiform, even more like an ape than that of *Ardipithecus ramidus ramidus* (WoldeGabriel, 2001). Six more teeth were recently described, and led the investigators to reclassify it as a new species, *Ardipithecus kadabba* (Haile-Selassie, Suwa et al. 2004).

*Orrorin tugenensis* is defined on 13 specimens, representing a minimum of 5 individuals (Pickford & Senut 2001; Senut et al. 2001). They are from the Lukeino Formation at Kapsomin in the Tugen Hills of central Kenya, and are estimated to be around 6 million years old. Fossils include two left femora (thigh bones), a distal humerus, a proximal hand phalanx and some isolated teeth. The incisors, canines, and lower $P_4$ are described as ape like, but the molar enamel is thick (Senut et al. 2001). The femora and humerus are 1.5 times larger than those of Lucy, similar in size to a modern female chimpanzee (Senut et al. 2001). They are clearly from a bipedal human, but one who, like *Australopithecus anamensis*, has apelike face and dental features.

In the last few years, a number of candidates for the earliest hominid have been proposed. *Sahelanthropus* is the oldest and most recently defined; it is really at the limit of how old a hominid can be, according to calculations based on the molecular clock. In addition, it is possible that the adoption of cladistics promotes splitting of fossils into more and more individual taxa, as only single derived traits are needed to define a new clade. In his editorial published along with the description of *Sahelanthropus*, Wood (2002, p. 134) argues that it represents "the tip of the iceberg of taxonomic diversity during hominid evolution 5 to 7 Mya," an astounding and unnerving statement to anyone who has to teach this material.

Along with a growing interest in the patterns and processes of evolution, catastrophism is making a comeback as an explanatory framework (Benton, 2003). Once derided as the refuge of supporters of the Biblical account of Genesis like Buckland, modern catastrophism gained support when Alvarez and his colleagues argued that a meteorite impact 65 million years ago led to extinction of many Mesozoic life forms, including dinosaurs, ammonites, and microscopic creatures like Foraminifera (Alvarez et al. 1980). The discovery of the impact crater, at Chixulub in the Yucatan peninsula of Mexico, has just about confirmed this theory (Hildebrand et al. 1991). It is possible that catastrophism has had a major role to play in various stages of human evolution including the end of the Miocene, reducing the amount of hominid diversity to our present, biologically homogeneous species (Willoughby, in press).

Palaeoanthropology continues to be subject to multiple and ever changing interpretations. Much of what students and professionals learn is contradicted a few years later. Some fossils are immediately accepted as hominids, only to be dismissed decades later (Lewin, 1987). This can been seen in the fate of *Ramapithecus*, and in current discussions about the origin of *Homo sapiens*. With the mapping of the human genome, molecular researchers may claim to have the upper hand in understanding our past. They have even been able to extract genetic material from some fossil hominids (Krings et al. 1997), but these are only from the latest time periods. The bulk of molecular work is being done on living individuals. What about the specialists in the fossils? There is awareness of, but increasing insecurity about, the pattern of early hominid origins, and little known about the processes involved. The most unnerving idea is the possibility that bipedalism was not unique to early hominids, that it was shared with the last common ancestor of African apes and humans. Why does this form need to be more ape like than human? If proto-hominids were bipedal, it would explain one glaring problem, why we have never found any African ape fossils from the Late Miocene or Pliocene. The answer would be that actually we have, but we have called them all hominids, rather than apes.

Finally, there is no evidence of hominids with modern body size and proportions until around 1.7 million years ago, well after the appearance of the first members of the genus *Homo* (Wood, 1992). The species, named *Homo erectus* or *Homo ergaster*, is best represented by a nearly complete skeleton from Nariokotome on the west side of Lake Turkana in Kenya (Walker & Leakey 1993). It was not fully adult, but may have been quite tall (Klein, 1999, p. 291), although this can be challenged (Ohman et al. 2002). At around 880 cc, its brain size was bigger than anyone before, but still much smaller than living humans with an average of 1350 cc and range from 1000 to 2000 cc in volume. It is probably not surprising that the first hominids dispersed out of Africa into Asia around the same time, as seen in the fossils of the same age from Dmanisi in Georgia (Gabunia et al. 2001).

## What Do We Actually Know?

Palaeoanthropologists, like other scientists, are beginning to become more aware of the context of their research. While it has been argued that no one lets the facts get in the way of a good theory, the facts (fossils) do continue to have a significant role to play. Without them, there would be no idea of the complexity of hominid evolution, as the other line of evidence, DNA, only helps us to understand our own species and its relationships with other living primates. Can those who study fossil humans say much about human nature? It really depends on what is meant by "nature." Psychologists talk about human behavior being a product of nature and nurture, inheritance and socialization. But even they know that these two presumed opposites interact over the life of an individual. The fossil hominid record gives us a relatively good picture of the evolution of the human skeleton. The first hominids evolved in Africa over 5 million years ago; they were extremely small in body and brain size. It is not until around 2.5 million years ago that any form with a bigger than average brain appears; these hominids belong to the genus *Homo*, as we ourselves do today. The first evidence of material culture, the beginnings of the archaeological record, can be traced back almost as far. Simple flaked stones are found in association with modified animal bones, in fine grain sands or silts where they would not occur naturally. But some chimpanzees, those from the Tai forest in the Ivory Coast, regularly transport and use stones as hammers to crack open nuts, and many other chimpanzee populations employ tools in subsistence activities (Boesch & Boesch 1983; Mercader et al. 2002). Both members of the genus *Homo* and stone artifacts appear when it is getting cooler and drier throughout Africa; this is a sign of the onset of the global glacial cycles we still live in today. Archaeologists and palaeontologists generally agree that the next major stage in human evolution occurred with the dispersal of *Homo erectus* / *Homo ergaster* out of Africa starting around 1.7 million years ago (Rightmire, 1990). By 200,000 years ago, when the first members of *Homo sapiens* appeared in Africa, there were different species of humans throughout Eurasia. It is only with the second out of Africa migration, after 50,000 years ago, that our own species spread north and replaced these others, probably without any interbreeding. It is in this context that the first real archaeological transition occurred. Labeled the creative explosion (Pfeiffer, 1982) or human revolution (Mellars & Stringer 1989), it is said to be the product of the first people who were truly modern in all respects (Klein 1992, 1995). Their African ancestors were anatomically the same as living people, but archaeologically indistinguishable from their archaic cousins elsewhere (Willoughby, 2000). How they became human in both biology and behavior remains the other great palaeoanthropological question (Willoughby, in preparation). It is this question that I have tried to address in my own research (Willoughby, 2000, 2001).

## Biological and Behavioral Modernity

A number of new dating techniques were first applied to hominid sites in the late 1980s; these include electron spin resonance (ESR), thermoluminescene (TL), optically stimulated luminescence (OSL) and uranium series (Wintle, 1996). They provide age estimates for sites beyond 40,000 years ago, the effective limit of radiocarbon or $^{14}$C dating. Up until this time, the only materials that could be dated were those within the radiocarbon time span, or alternately those associated with the Middle Pleistocene and earlier volcanic sequences. When applied to sites associated with *Homo sapiens* fossils, it became clear that anatomically modern humans were present in Africa by 200,000 years ago (Stringer & Andrews, 1988), and in two places in the Levant, the Mugharet es Skhūl and Jebel Qafzeh prior to 100,000 years ago (Akazawa et al. 1998). This was at a time when other kinds of humans were present elsewhere: Neanderthals in Europe and late *Homo erectus* in East Asia. Meanwhile, the developers of the molecular clock had examined living human mitochondrial DNA variation and concluded that the last common ancestor for all of us today was African as recently as 100,000 or 200,000 years ago (Cann et al. 1987). In no time, palaeoanthropologists interested in the origins of modern humans were proposing that the earliest *Homo sapiens* were indeed African, but had not left Africa until after 50,000 years ago (Stringer & Andrews, 1988). When Skhūl and Qafzeh were occupied, the Levant was an environmental extension of Africa; around 70,000 years ago, after glacial conditions were re-established, Neanderthals migrated into the Levant and replaced them (Akazawa et al. 1998). It is not until after 50,000 or even 40,000 years ago, that the "Out of Africa 2" migration occurred. Genetically, all of us today can trace our ancestry back to these African populations, not to the Neanderthals or anyone else in Eurasia at the same time.

What was worse, these "anatomically modern" Africans were creating artifacts and archaeological sites indistinguishable from those of their Neanderthal cousins in Europe. These Middle Palaeolithic sites (or Middle Stone Age in Africa south of the Sahara) contain a variety of shaped flake stone tools divided into a few types: points, notches, scrapers and denticulates. While some of these sites exhibit evidence of intentional burials, there is little other sign of behaviors typical of contemporary or historic hunter-gatherer peoples. Clearly these people were skeletally "people like us" (Ingold, 1995), but this is the only thing that distinguishes them from any other contemporary population.

When found outside of Africa after 40,000 years ago, such people are usually associated with Upper Palaeolithic archaeological industries that are striking in the variety of their innovations. New features include tools made on parallel-sided flakes (blades); more evidence of curation of tools, saving them for repeated and future use; use of new materials for tool production, including bone, ivory, and antler. There is evidence of personal adornment or, jewelry, the first portable art ("Venus" or female figurines, as well as those portraying Pleistocene animals), parietal art consisting of cave painting and/or engraving, and long distance transport of raw materials and finished tools through trade, exchange and information networks. At any one time, there is also a great amount of regional variation in stone tool assemblages. This may reflect stylistic or ethnic identity; people who choose to make their tools in the same distinctive ways probably learned from the same teachers (Willoughby, 2001). Humans begin to specialize in hunting one or two animal species, and fish or shellfish begin to be used. Sites appear to increase in size, and are more structured, as special areas are reserved for particular activities. Burial sites with grave goods appear or become more complex. People expand into new territory, previously unoccupied by humans, such as Siberia, the Americas and Australia (Mellars, 1991; Bar-Yosef, 2002).

The combination of these traits is argued to represent the emergence of "behavioral modernity," the products of people who were truly human in all respects, not just in their anatomy. Why, then, are not Middle Palaeolithic/Middle Stone Age Africans doing these things, if they were essentially human in their biology? In other words, why is there such a gap between the beginnings of anatomical modernity and the onset of this Upper Palaeolithic behavioral modernity? Richard Klein (1992, 1995, and 1998) offers the most popular explanation. For him, the development of modern anatomy was not enough. He proposes that around 50,000 years ago, human brains were somehow reorganized to allow for multitasking, and the emergence of symbolic behavior. This led to the development of complex language and cognitive behaviors, and produced the cultural or creative explosion (Pfeiffer, 1982) associated with the beginnings of the Upper Palaeolithic. Many specialists in the evolution of language (for example, Lieberman, 1998) and cognitive neuroscience (Pinker, 1997) favor this explanation. Some support is also offered by the identification of a mutation in the FOXP2 gene. A single amino acid mutation on one strand of the double helix is the cause of specific language impairment, a pathology that results in significant problems with speech, but not mental deficiency (Lai et al. 2001). The problem may be caused by a defect in the formation of the speech centers of the brain while a fetus is still in the uterus. Given that this was the first gene shown to have any role in language development, the evolutionary geneticists tried to sequence it in a number of mammal species (Enard et al. 2002). In the millions of years since mice and apes had a common ancestor, there has been only one amino acid change. Within the Order Primates, there was also little sign of mutation. But since the split of African apes and us, there have been two mutations on the human side, and these are associated with the emergence of modern humans between 50,000 and 200,000 years ago. Clearly something new happened, something that might have become fixed in later humans through natural selection. The cost of this change is the disease, but could the benefit be the development of new ways of thinking and behaving?

Klein is convinced that there was a key neurological change around 50,000 years ago that enabled the cultural revolution of the Upper Palaeolithic. It also gave these early Africans an unbeatable advantage and led to their dispersal worldwide at the expense of all other contemporary hominid species. Other Africanist archaeologists feel that Middle Palaeolithic/MSA people were already modern in all ways (for example, McBrearty, & Brooks 2000; Henshilwood et al. 2001; Willoughby, 2001). They have documented the presence of many new kinds of technologies and behaviors. But Klein feels that these are lucky accidents, or the result of mixing of later and earlier archaeological deposits.

The “failure” of Middle Palaeolithic/MSA Africans to become behaviorally modern humans as soon as they became anatomically modern is either a key research question or a remnant of the priority of Europe in palaeoanthropological research. But their restriction to Africa until less than 50,000 years ago may have a simpler explanation than Klein is willing to accept. Studies of variation in mitochondrial DNA (Gagneux et al. 1999) and Y chromosome sequences (Stone et al. 2001) point to the lack of real significant variation in humans while African apes have a great deal. If this variation reflects the amount of time since our split from a last common ancestor, the subsequent evolutionary history of apes and humans has been surprisingly different. Many geneticists think that these early African modern humans went through one or more periods of bottlenecking or almost extinction (Harpending et al. 1993) prior to the “Out of Africa 2” migration.

What could have caused this episode or these episodes of stress? Specialists on past environments note that the late Pleistocene was characterized by increasing intensity and frequency of glacial and interglacial oscillations (Potts, 1998a, 19989b). In Africa, glacial stages are marked by long periods of dry and cold conditions; the equatorial rainforests may have almost disappeared while deserts expanded (Hamilton, 1976, 1982). Another contributing factor may be the eruption of the volcanic Mount Toba in Indonesia between 68,000 and 73,000 years ago (Wintle, 1996, p. 1313). This eruption remains one of the largest explosions in the Cenozoic Era, the last 65 million years. Some researchers (Ambrose 1998; Rampino & Ambose 2000) have proposed that this eruption may have led to a "nuclear winter" scenario similar to that which led to the massive extinctions of dinosaurs and many other animals that marked the start of the Cenozoic (Alvarez et al. 1980).

Whatever else we know about these earliest African *Homo sapiens*, however "modern" they were in their anatomy or even in the behavior, it is clear that there was little really special or new about them. How they survived to become the founder population for all of us today is a question that remains to be answered. Over the last 6 to 7 million years, the fossil record shows us that there were a bewildering number of hominid species (Tattersall, 2000). We are the sole survivors of a long process of change. Bipedalism, large brains, a symbolically based cultural adaptation – all must have played some role in our remote history. But it may really have been an accident that allowed small populations of African modern humans to be the ultimate ancestors of all of us living today.

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