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(1868-1945)

EVOLVING PRIMATES:
A PALAEOLOGIST'S VIEW
OF HIS TRIBE

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INTRODUCTION

Human evolution, palaeoanthropology, human origins, hominid paleobiology, human palaeontology, human evolutionary studies. Is there any other field of research that has more labels to describe itself, even though they all covers largely the same ground? This diversity in self-identification is at least in part rooted in the perspective and approach of the researcher or research group. One can look back in time, mapping the evolutionary trajectory of modern humans as a unique species, and encountering 'incidental side branches' along the way. Alternatively, one can investigate the origin and radiation of a primate group, with the minor point that this group happens to have only one surviving branch today: modern humans. In practice this distinction may not always be as clear-cut, but it does inform some of the important debates and alternative interpretations found in the study of human evolution past and present.

Another unique element of studying our own evolutionary history, as opposed to that of other mammals, is the impact of its broad appeal to both students and the wider public. Numerous large-scale undergraduate courses in human evolution are taught worldwide, and these benefit from a concise and consistent narrative, rather than an ever changing landscape of new facts, hypotheses and interpretations. Meanwhile, the media tend to prefer not to confuse their readership with subtleties and uncertainties when presenting the latest findings, whilst loving a controversy, 'big' personalities making strong statements, and the frequently reported notion that textbooks have to be rewritten.

Here I will first explore some broader topics to give a context to the study of human evolution, trying to take the more palaeontological perspective of humans as 'just another primate'. With humans and their extinct relatives being known as 'hominins'

(from the tribe Hominini; see below), I therefore prefer the term 'hominin evolution' over 'human evolution' to stay away from the more philosophical question what 'human' means, and to which species it might apply. Subsequently I will review one of the more complex phases of hominin evolution, the origin and early radiation of the genus *Homo*, and discuss how progress has been made recently based on new fossils, new information extracted from fossils old and new, and novel analytical methods to assess the evidence. Overall the focus will be on Africa, as the continent that witnessed the origin and first two-thirds of the evolutionary history of hominins. What I will not provide here is a comprehensive overview of our current understanding of that history; for that I refer to Bernard Wood's 31st Kroon Lecture (Wood, 2009).

STUDYING HOMININ EVOLUTION

Vertebrate palaeontological research is unusual in the sciences in that the essential evidence, the fossils, come to us in a more or less random way. Yes, we go out looking for them, being well-informed about the local geology and distribution of previous finds, but ultimately it all depends on whatever erodes out of the rocks, or is exposed in a particular cave or quarry. In other words, although we can and should examine the existing fossil record based on carefully designed hypothesis testing, the primary evidence itself cannot really be acquired 'on demand', unlike the circumstances when studying extant biology. Nevertheless, we are not completely at the mercy of random events. Before trying to make sense of fossils, or before even finding one, a number of issues can be considered that predictably set the limitations of what can be achieved when reconstructing the evolution of a species or a group of species. Some of these issues may seem obvious when presented this way, but not infrequently they get ignored.

A first point is that it is unlikely that all extinct species of a particular taxonomic group will ever be discovered as fossils. This understanding alone makes that any reconstructed evolutionary tree can only be an approximation. In the case of hominin evolution it is difficult to estimate how many species may have existed in the past because today only one survives. That this is not representative is clear from the fact that about 50,000 years ago there were at least four contemporary species (*Homo sapiens*, *H. neanderthalensis*, *H. floresiensis* and the Denisovans). Unfortunately, this relatively recent species diversity is itself affected by the unknown rate at which species are represented in the fossil record, and can thus not be used to estimate the number of extinct species throughout hominin evolution. In contrast, for species groups with many extant representatives it is possible to model how many extinct species have existed, based on certain assumptions about the process of evolution. This estimate can be compared with the known number of extinct species, thus giving a rough idea of how well the current fossil record samples the past. This exercise has been done for primates and the conclusion was that only about 3% of all extinct primates species are currently known (Martin, 1991). The impact of such a low sampling rate on how we interpret the fossil record is modelled in Figure 1. It will be obvious that the reconstructed phylogeny is a poor representation of the actual events. Of course, hominin evolution played out over less than half the period of time shown in Figure 1, and for the largest part in an area that is geographically constrained (i.e. Africa). Hence, here the 3% will probably be too low an estimate, but the concept that we will always be limited in our ability to discover the 'true' evolutionary tree nevertheless applies.

A major reason for a poor species sampling rate of the fossil record is that fossils are only discovered under a relatively rare and special set of circumstances. First, a species must have lived in the area. Second, the right environmental conditions must have existed so that skeletal remains were buried and could fossilize. Third, the right conditions must exist today so that a

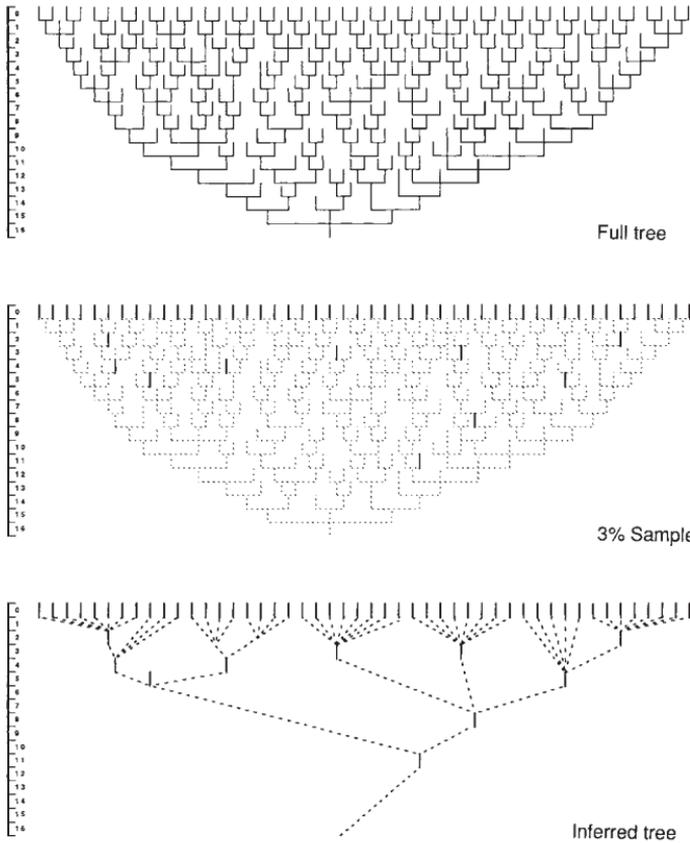


Figure 1. Hypothetical evolutionary tree leading to 48 extant species (Full tree). Each species has a standard survival time of 1 million years. To represent a hypothetical 3% of extinct species that are known from the fossil record 10 species have been randomly selected (3% Sample). The reconstructed tree based on the 3% sample is a poor representation of the actual tree (Inferred tree). The origin of the group is underestimated when based on first known species, and many ancestor-descendant relationships are reconstructed incorrectly. Source: Martin (1991, Figure 2).

fossil can resurface. Fourth, the area must be visited by people interested in fossilized bones, so that the resurfaced specimens are collected and interpreted. In practice this means that in Africa the Plio-Pleistocene sites that produce hominin fossils are largely restricted to the Eastern Rift Valley and to cave sites in southern Africa (Figure 2). In the former the original conditions of rapid sedimentation at lake margins and river systems made fossilization possible, and tectonic activity leads to the necessary erosion that exposes the bones. Limestone caves are well-known for preserving bone. They function as natural traps or carnivore lairs, the eroding limestone and calcite deposits provides the right sedimentary environment for fossilization, and commercial mining in particular results in the initial discovery of fossils.



Figure 2. Map of Africa with the main Plio-Pleistocene sites where hominin finds have been made. The large number of sites in the Afar region, the Turkana Basin, and the Sterkfontein Valley are shown as approximation only. Source of map: www.geocurrents.info.

One look at the geographical distribution shown in Figure 2 will make it clear that the sites with hominin fossils are concentrated in only a tiny fraction of the African land surface. Concluding that hominin evolution specifically and exclusively took place in eastern and southern Africa can therefore only be a misconception, in my view. Nevertheless, the notion has come up at times, for example as part of the ‘East Side Story’ (Coppens, 1994), with hominin evolution east of the Rift separated from great ape evolution in the west, and in the proposal that fossils found in Malawi indicate that there was a specific ‘corridor’ for dispersal between eastern and southern faunas (Schrenk et al., 2002). Large parts of Africa lack the Plio-Pleistocene fossil record that is a prerequisite to detect hominin presence in the area. In this situation absence of evidence cannot be seen as evidence of absence. Most prominent perhaps is the Congo Basin. Its rainforest provided a rich environment for primates, and the historical process of climate-related expansions and contractions created isolated habitats along the edges that promote allopatric speciation. From this perspective one can perhaps even think about the Eastern Rift and the southern caves as ‘marginal’ to the main show. A perfect example that hominins lived in many more places than where their fossils are mostly found came with the unexpected discoveries in the desert of Chad of *Australopithecus* fossils at 3.6 million years ago (Ma) and *Sahelanthropus* fossils at 7 Ma (Brunet et al. 1995, 2002, 2005; Lebatard et al, 2008), thousands of kilometers away from the nearest sites in the Rift Valley (Figure 2). And still, a recent article on early hominin evolution and climate nevertheless starts with the statement “Current evidence suggests that all of the major events in hominin evolution have occurred in East Africa” (Maslin et al., 2014, p. 1).

It is not only the geographical distribution of fossil evidence that is discontinuous and fragmented, but this also applies to the temporal distribution. Even in places where abundant hominin fossils are found these are usually restricted to specific time intervals. Sedimentary rock layers representing other periods of times may be completely absent because they were never formed

at the time, or have eroded away. Or if they are present and do produce a rich mammalian fauna hominins can still be absent altogether or extremely rare. A good example can be found on the eastern side of Lake Turkana. Abundant hominin fossils are known from the time period of between 2.1 and 1.4 Ma, representing *Paranthropus boisei* and multiple species of *Homo* (Wood, 1991). Moreover, fossils of a single hominin species, *A. anamensis*, are known from a site dated to 3.9 Ma (Ward et al., 2001). However, no sedimentary layers are known from between 2.1 and 2.5 Ma, and although sediments around 3 Ma have produced abundant and well-preserved mammalian fossils only a few hominin fragments have ever been found (Wood, 1991), despite several field seasons of prospecting.

A good example of how an uneven temporal distribution of discoveries can bias our interpretation of the fossil evidence is the notion of a major radiation of hominin taxa around 1.9 million years ago (“The most profound period for hominin evolution”, Shultz & Maslin, 2013, p.1). Yes, the first appearance dates of *P. boisei*, *H. rudolfensis*, *H. habilis* and perhaps *H. erectus* all fall between 1.9 and 2.1 Ma, but this is most likely an artefact of the absence of evidence from the preceding time period. Older fossils attributable to *Homo* and *Paranthropus* are known from Ethiopia, the western side of Lake Turkana and Malawi but these are more fragmentary and difficult to assign to specific species (Kimbel et al., 1997; Prat et al., 2005; Schrenk et al., 1993; Suwa et al., 1996; Villmoare et al., 2015). Hence, the actual radiation of early *Homo* species will have occurred well before 2.0 Ma (Villmoare et al., 2015; Spoor et al., 2015). Moreover, *P. boisei* may have gradually evolved from *P. aethiopicus* from at least 2.5 Ma (Kimbel, 2015).

One reason it may sometimes appear that not much progress is made in the study of hominin evolution is the phenomenon that the more we know the more difficult it gets. Life is simple when you have only a few species; two or three distributed in time provide a nice linear model of evolution. As more species are discovered the complexity increases and the relationships

become more confusing, even though it will provide a better representation of the past. After all, it is the nature of evolution that more evidence will eventually lead to difficulty in distinguishing separate lineages soon after speciation has happened, even if morphological change is thought to be mostly rapid at this point, rather than slow and gradual. For example, the recently described LD 350-1 mandible from Ethiopia has been identified as the earliest evidence of the *Homo* lineage at 2.8 Ma, based on dento-mandibular features that subtly, but consistently differ from the well-known morphology seen in *Australopithecus afarensis* (Villmoare et al., 2015). Hence, the origin of our lineage is not characterised by a major and dramatic shift, but by small markers indicating that speciation had likely taken place. By all means and purposes the individual originally owning this early *Homo* mandible would have looked like *Australopithecus* with a few, seemingly insignificant differences. It is only because we infer with hindsight that this represented the beginning of a new lineage that we see this as important. And of course particularly important because that lineage eventually happened to have our own species as one of its branches.

Distinguishing species close to speciation is even more problematic if it concerns a potential ancestor – descendant relationship, and the change may have been gradual. Apart from the relationship between *P. boisei* and *P. aethiopicus*, mentioned above, a good example in hominin evolution is the relationship between the eastern African species *A. afarensis* (3.8 – 3.0 Ma) and *A. anamensis* (4.2 – 4.0 Ma). In the teeth and jaws *A. afarensis* shows a clear trend of morphological change over time (Kimbel et al, 2006), and fieldwork at Woranso-Mille (3.6–3.8 Ma) has produced fossils that are intermediate between *A. anamensis* and earliest *A. afarensis*, and are difficult to classify as one or the other (Haile Selassie et al. 2010). Hence, the teeth and jaws appear to show a pattern of gradual (anagenetic) change, although it is possible that the discovery of more complete cranial fossils of *A. anamensis* will nevertheless reveal a clear speciation event.

With this emphasis on things we do not know, those that will perhaps never be known, those that bias our perception, and those that make our life difficult it may seem that I take a pessimistic view of our current knowledge of hominin evolution. In fact, I am rather positive about what has been achieved over the last decades. In contrast to the cliché still heard sometimes, the hominin fossils discovered thus far do not just fit in a shoebox, and the hominin record is arguably a good deal better than for many other mammalian groups. And so it should be, given the substantial amount of tax payers money that has gone into worldwide exploration. Likewise there is little truth in the idea that speculating researchers have wildly different ideas about the interpretation of these scrappy bones. Professionalization of our field is marked by increasing numbers of internationally well-connected researchers who tackle their work systematically and in detail, addressing properly formulated hypotheses. Consequently, a broad consensus has emerged about the overall pattern and trends of hominin evolution, as we know it from the fossil record. At times it may not seem that way, but this is because we look at the evidence in increasing detail, and good science is marked by critically testing and retesting the ideas and conclusions of our peers. In all, that broad consensus will likely be a valid representation of those parts of hominin evolutionary history that can be known at present, including the emergence of our own species, but we should be realistic and know that it is not the full picture.

CLASSIFICATION OF HOMININS (OR HOMININANS)

Before looking at some practical research it is important to review some issues that are at the heart of hominin palaeontology, and can be a major cause of confusion when the latest research findings are presented in the broader setting of media reports or intro classes at university. This concerns the way modern humans and their extinct relatives are classified among other primates, and how species can be defined, recognised and grouped. The

classification of species and groups of species may sound like a pastime for nerds, but it is the essential foundation of studying most aspects of biology. Species are the units of the evolutionary process, and how species are grouped expresses their joint origins. In the case of us humans it very much concerns the question of how we relate to our wider biological primate context, and the great apes in particular.

Consulting textbooks of the previous century will show that humans and their extinct relatives are referred to as 'hominids' the vernacular of the family Hominidae. Our closest relatives, the great apes, are jointly grouped as Pongidae, or pongids for short (Figure 3a). This classification very much reflected the special place we humans gave ourselves among the higher primates. From the 1960s onwards molecular evidence, initially from proteins and subsequently from DNA, has demonstrated that this interpretation is incorrect. In fact, humans are closest related to chimpanzees and bonobos, jointly they are closest related to gorillas, and jointly these humans plus African apes are closest related to orang utans. Nowadays it is a well-accepted principle that classification should reflect phylogeny or the evolutionary relationships of groups, and as a consequence the names among humans and great apes have changed. Humans and their extinct relatives are now most commonly referred to as 'hominins', the vernacular of the tribe Hominini (Figure 3b). The African apes and humans are named as Homininae, and all great apes plus humans as Hominidae. It took a while for 'hominins' and 'hominin evolution' to become the established terms, and even these days a few colleagues continue to use 'hominids' in the traditional sense.

A problem with the now broadly accepted 'new' classification is that it does not fully resolve the relationship between humans and African apes. In particular, the closest relationship between humans and chimpanzees is not represented by a group name or taxonomic rank (Figure 3b). In sophisticated morphological studies of the hominids (i.e. humans and great apes) it is

increasingly desirable to be able to describe what specific features characterize each of the evolutionary groupings, including the one that exclusively combines humans, chimpanzees and bonobos (see e.g. Stoessel et al., 2016). Hence, from a scientific perspective it is justified to revise the classification once more, to bring it in line with our best understanding of how humans and great apes are related. Following Andrews & Harrison (2005) the necessary changes include combining humans, chimpanzees and bonobos in the tribe Hominini, chimpanzees and bonobos in the subtribe Panina, and humans with their extinct close relatives in the subtribe Hominina (Figure 3c). The vernacular of the latter thus becomes ‘homininans’, and what I am discussing here is ‘homininan evolution’ or ‘homininan palaeontology’.

I have no illusion that the most appropriate classification will be widely adopted very soon, and I can see some of my colleagues, journalists, and members of the interested public roll their eyes at the prospect. Changing ‘hominids’ to ‘hominins’ was confusing for quite a while, and to this day needs to be explained at times. Changing again and now to ‘homininans’ seems a near-impossible proposition, given the need to introduce a rather awkward name to the wider community, the accumulated levels of confusion, and the prospect to once again adjust textbooks and university courses. So why do I even bring this up? Why bother with these finer points of classification? Because it brilliantly illustrates that the study of our evolutionary past is constrained by factors other than good scientific practice. If the topic was rodent or carnivore evolution there would be little problem adjusting the classification to the latest insights of how species are related. Or to give a practical example, now that it is well-understood that whales and dolphins evolved from even-toed ungulate ancestors it is widely accepted that their long-established classification needed to change. As counterintuitive as it may seem, these hyperspecialised aquatic creatures are now subsumed in the order Artiodactyla, sometimes known by the new name Cetartiodactyla (Asher & Helgen, 2010). Classification is just a tool to bring order based on the latest phylogenetic evidence. It would be best

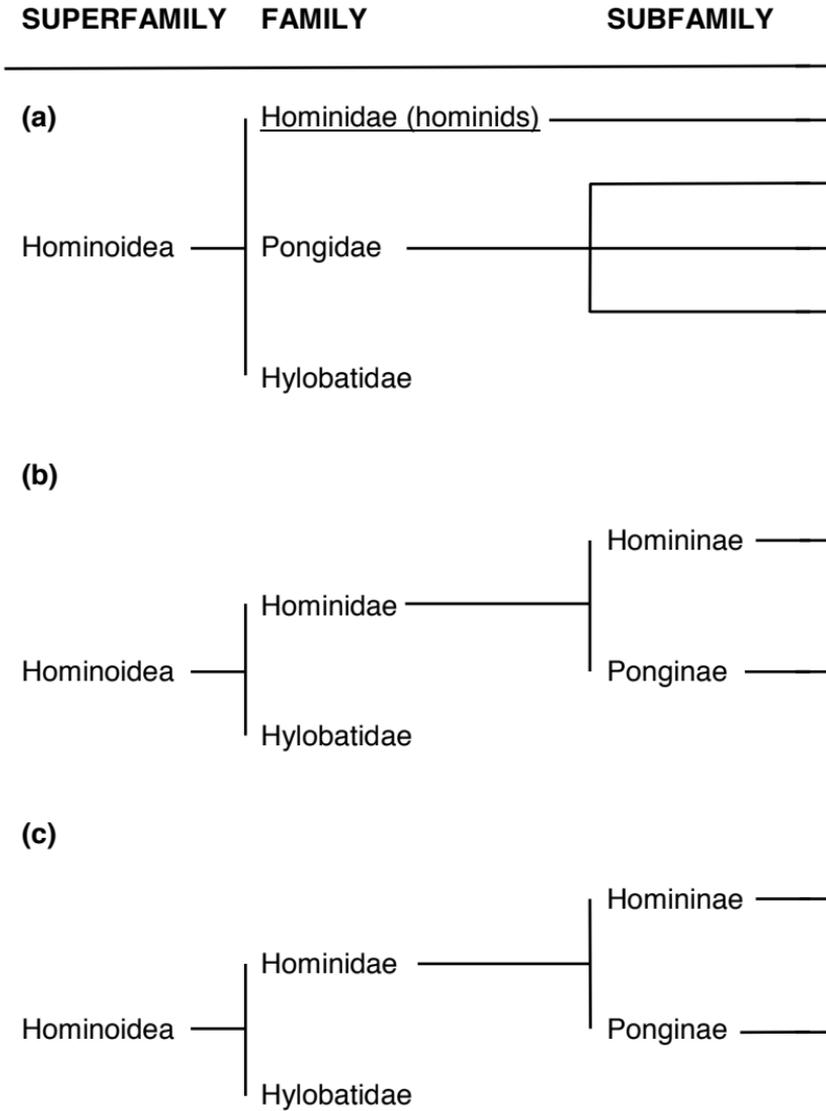
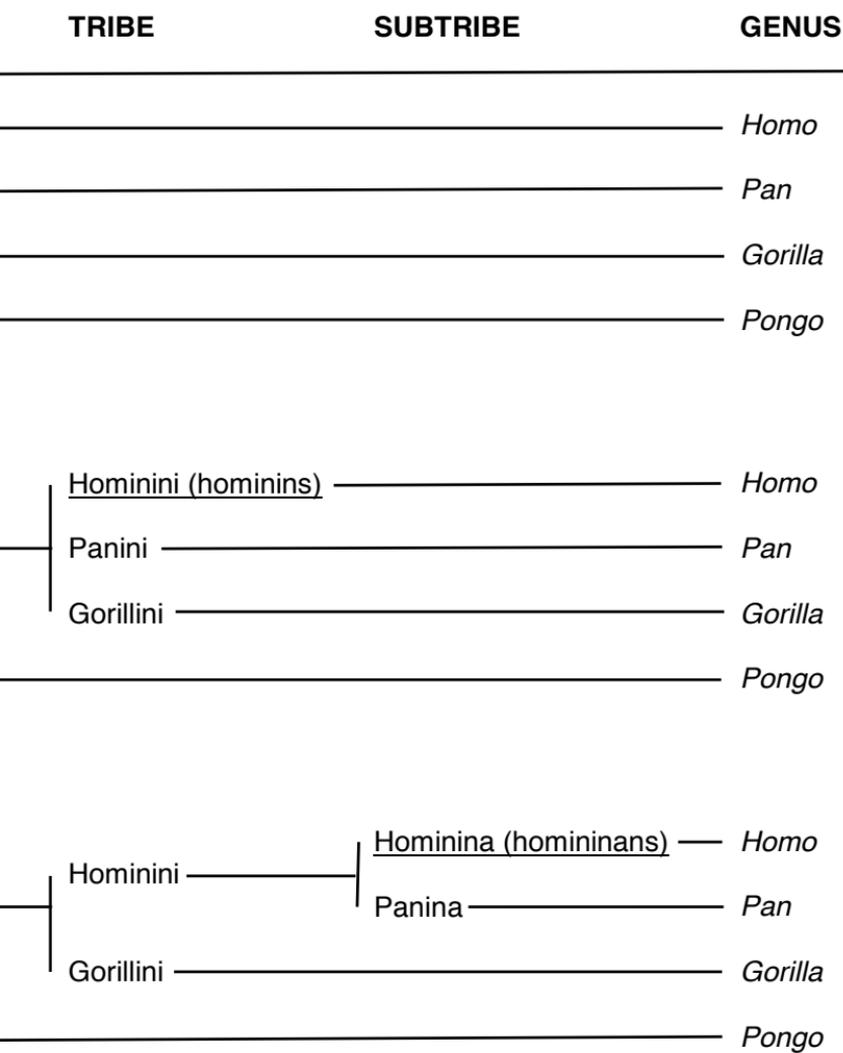


Figure 3. Classification of extant hominoids. (a) The traditional taxonomy which contrasts humans and the great apes. (b) A taxonomy which recognises the close genetic link between humans and African apes. (c) A taxonomy which recognises the degree of genetic relatedness



between all genera of humans and great apes. Humans and their extinct relatives are known by the vernacular of hominid, hominin and homininan, respectively (underlined). The hylobatids are not specified beyond family level.

to apply this principle here too, but for now I will surrender and stick with 'conventional' hominin evolution.

If species are the units of biological evolution, and the basis of classification it is worthwhile to consider for a moment what species are. After all, the naming of a new species in hominin palaeontology tends to be perceived as a special occasion, usually followed by a mixed response of those who agree and those who see this as a misguided interpretation of variability in an established species that exaggerates diversity. A good starting point is to see how primatologists and other zoologists who deal with extant taxa approach the species concept, as they tend to have the full organism, genetic makeup, behaviour and population structure at their disposal (see Groves, 2014ab for reviews). Many of us will have grown up learning that a species is a group of interbreeding populations that do not naturally interbreed with other such groups. This definition, known as the biological species concept, is problematic when such groups do not come into contact with each other in natural circumstances, because how can one tell if these groups interbreed? For living populations that is a matter of geographical separation, but for extinct ones there is a likely separation in time as well. Instead the phylogenetic species concept is now frequently used. It states that a species is a separate evolutionary lineage, and the smallest group of populations which has fixed heritable differences from other such groups (Groves, 2014b). Importantly, species should be seen as scientific hypotheses that must be testable by examining the defining characteristics. Following from this approach there has been a trend towards recognising former subspecies as species. Hence, based on consistent and heritable differences the western and eastern gorillas are nowadays recognised as separate species, and so are the orang utans from Borneo and Sumatra. DNA analyses have often led the way, but more sophisticated morphological analyses frequently confirm the molecular evidence. The phylogenetic species concept can be applied in palaeontology, but the power to resolve species differences is obviously limited as only skeletal morphology can be analysed, with the exception of occasional preservation of genetic material.

Whereas species are a biological reality as individuated evolutionary lineages, any classification above the species level is less well-defined. Apart from other possible criteria, the one essential requirement of any higher category, such as genus, tribe, or family, is that it should be monophyletic, a grouping that contains all of the descendants of their most recent common ancestor (Wood & Collard, 1999). Interestingly, this rule is manifestly broken in conventional hominin classification, as it has been consistently found that the genus *Australopithecus* is not monophyletic (Strait & Grine, 2004). Figure 4 shows hominin relationships based on the sharing of recently evolved morphological features (a cladistic analysis). Whereas *Paranthropus* and *Homo* form monophyletic groups (clades), this is not the case for *Australopithecus*; the descendants of its common ancestor also includes species of the genera *Kenyanthropus*, *Paranthropus* and *Homo*, making it paraphyletic. This situation can be resolved by placing *A. anamensis*, *A. afarensis* and *A. garhi* in different genera, so that only *A. africanus* retains its original genus name. In fact, the genus name *Praeanthropus* is already available for the species *Pr. afarensis* (Strait & Grine, 2004), but new genus names would have to be proposed for the others. Nevertheless, despite the widespread recognition that *Australopithecus* currently functions as a paraphyletic ‘wastebasket taxon’ (*ibid.*) there is great reluctance to take action. Naming a new genus in hominin palaeontology appears to be perceived not as a routine procedure to follow the modern rules of taxonomic classification, but as an emotionally charged deed that rocks humanity’s genealogy. It should be noted that an alternative is available for having a large number of generic names to maintain monophyly in hominin taxonomy: all species could simply be included in the genus *Homo* (Groves, 2012). This idea is equally provocative as proposing several new genus names, and so the less than desirable status quo is maintained. In part this resignation may follow from the lingering intuitive perception of *Australopithecus* and *Homo* as evolutionary grades or stages that humans went through on their journey to modernity, rather than as technical names of monophyletic clades. When it comes to the classification of

humans and their relatives, whether at the level of tribe, subtribe or genus, humans are still not considered ‘just another primate’ and exceptionalism continues to play a role.

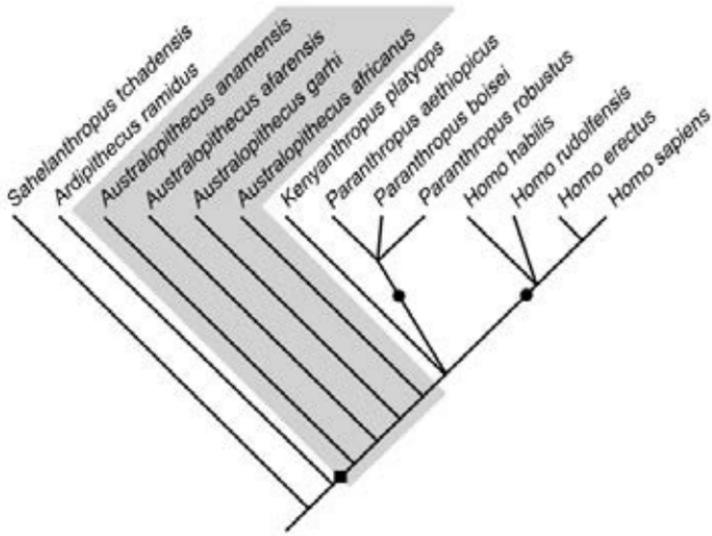


Figure 4. Cladogram showing the relationship between hominin species, as found by Strait & Grine (2004) based on craniodental characters. Uncertain relationships are represented by branching points of multiple species (polytomies). Homo and Paranthropus are monophyletic clades, which contain all the descendants of their most recent common ancestor (black circles). In contrast, Australopithecus (grey area) is paraphyletic because the descendants of its common ancestor (black square) also includes species of the genera Kenyanthropus, Paranthropus and Homo.

SORTING FOSSILS

Primary research in vertebrate palaeontology tends to involve a number of consecutive steps. First, an attempt is made to recognise species in a collection of fossils, based on similarity or difference between individual specimens, including the type specimens of established taxa. Second, the evolutionary (phylogenetic) relationships between species are investigated, these days most commonly based on cladistic analyses which distinguish between derived and primitive characters. Third, the elements of time and geography can be added to come up with an evolutionary tree that includes the known time span of species, their likely phylogenetic relationships, and patterns of dispersal. Fourth, the biology associated with morphology and evolutionary change is investigated, by assessing aspects such as growth and development, mastication, dietary preferences, foraging strategies, habitat selection, locomotor behaviour and modifications of the brain and sensory organs. Establishing a concrete link between such characteristics and the morphological differences that distinguish species is often difficult, not least because the latter may be affected by random genetic drift as much as by selection and functional adaptation (Ackermann & Cheverud, 2004). Nevertheless, these steps form a feedback loop, because better understanding the underlying biology informs the definition of 'good' characters for use in species recognition. For example, morphology can be identified that is particularly prone to convergent evolution, and is thus not informative with respect to evolutionary relatedness.

Here I will discuss a case study that concerns the first, and essential step of trying to sort fossil specimens and make associations with the holotypes of established species. It mostly concerns the relationship between *Homo habilis* and *Homo rudolfensis*, and deals with the question whether these are indeed separate species, and if so, how they can be recognised and which key specimens should be attributed to each. Of course there is nothing new about attempts to assess the status of *H. habilis* and *H. rudolfensis*,



Figure 5. The Homo habilis holotype OH 7, including a partial mandible, partial parietals and hand bones. Photo by John Reader.

but progress has been made in several ways. New fossils have been found, new aspects of morphology have been identified as diagnostic and novel analytical methods have been developed.

But first a bit of historical background. The species *H. habilis* was first described in 1964, based on discoveries by Louis and Mary Leakey and their team a few years earlier at Olduvai Gorge, Tanzania (Leakey et al., 1964). The type specimen, Olduvai Hominid 7 (OH 7), is a partial mandible, two fragmentary parietal bones, and associated hand bones (Figure 5). The fossils are dated to 1.8 Ma. OH 7 and some others, named as paratypes, were described as a new species because they were found to be more derived in morphology than *A. africanus*, but not as derived as *H. erectus*. This intermediate position especially applied to estimated brain size and molar size. In the ensuing years a lively debate developed which centred on the question whether there was indeed enough ‘morphological space’ for a species that was intermediate between *A. africanus* and *H. erectus* (see Tobias, 1991 for a detailed review). However, it was not until the early 1970s that the debate about the earliest members of the *Homo* lineage moved on, triggered by a number of spectacular discoveries on the eastern side of Lake Turkana made by the Koobi Fora Research Project, led by Richard Leakey.

During the 1972 field season a large number of cranial fragments were discovered, which were painstakingly and skilfully puzzled together by Meave Leakey and Alan Walker, to form the well-known specimen KNM-ER 1470. The cranium has a rather larger cranial capacity than found in *Australopithecus*, and the face is remarkable flat in appearance (Figure 6). In the following years more important specimens were found that are now assigned to *Homo*. Prominent among these are the crania KNM-ER 1813 and KNM-ER 3733. The latter is clearly attributable to *H. erectus* (or *Homo ergaster* for some), but KNM-ER 1813 is overall less derived than that species, and characterised by a smaller cranial capacity and a more prognathic face than KNM-ER 1470 (Figure 6). Jointly these latter two specimens, KNM-ER 1813 dated to

~1.86 Ma (Feibel et al., 2009) and KNM-ER 1470 to 2.06 Ma (Joordens et al., 2013), took centre stage in ongoing debates about the early evolution of the genus *Homo*. Importantly, KNM-ER 1470 was made the type specimen of a new species *H. rudolfensis* (see Wood, 1999 for a discussion of the circumstances).

The core questions that arose were whether KNM-ER 1470 and KNM-ER 1813 represent one or two species, and if there were two, what these should be called. Some maintained that the morphology of the two fossils falls within normal variation of a

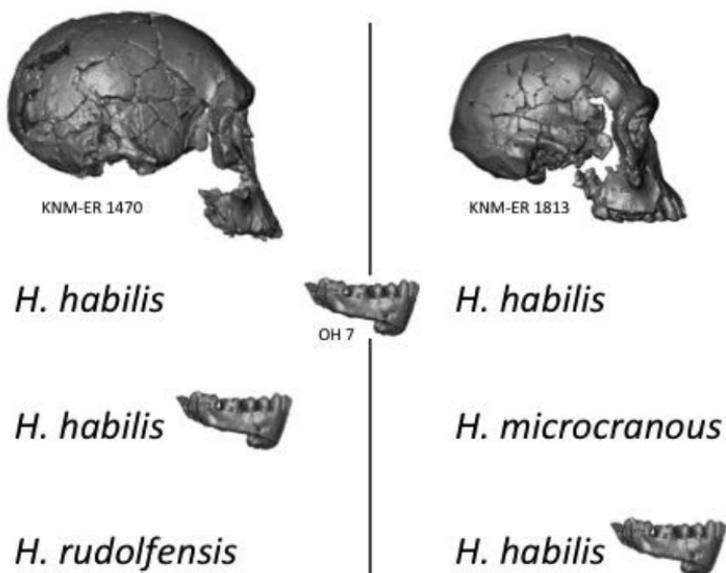


Figure 6. Naming early *Homo*, based on the type specimens of *H. habilis* (OH 7), *H. rudolfensis* (KNM-ER 1470) and *H. microcraneus* (KNM-ER 1813). If all three fossils belong to a single species it is called *H. habilis* (top). If OH 7 is associated with KNM-ER 1470 this species is called *H. habilis* and the other one *H. microcraneus* (middle). If OH 7 is associated with KNM-ER 1813 this species is called *H. habilis*, and the other one *H. rudolfensis* (bottom).

single species (e.g. Tobias, 1991; Miller, 2000); one which also includes OH 7, thus giving it the name *H. habilis* (Figure 6: top). Variants of this interpretation are that the combined *H. habilis/rudolfensis* group, including KNM-ER 1813 and KNM-ER 1470, represents a single lineage evolving through time (Suwa et al., 2007), and that all early *Homo* specimens should be included in *H. erectus* (Lordkipanitze et al., 2013). Others have concluded that early *Homo* specimens are too variable for a single species, but fossils are attributed to two species in different ways. Some researchers associate OH 7 with KNM-ER 1470 emphasizing the relatively large cranial capacity they share (Stringer, 1986; Rightmire, 1993; Blumenschine et al., 2003). The name of this species is *H. habilis* because it has priority over *H. rudolfensis*, given that it was proposed earlier (Figure 6: middle). In that case the second, small-brained species takes the name *Homo microcranous*, given to KNM-ER 1813 as the holotype (Ferguson, 1995). After a lengthy and detailed study of all the cranial hominin fossils from Koobi Fora and Ileret, Bernard Wood came to a different conclusion. He recognised two species as well, but associated OH7 not with KNM-ER 1470, but with KNM-ER 1813 and other more prognathic specimens (Wood, 1991; 1992). The latter therefore take the name *H. habilis*, whereas the species with the remarkably flat facial morphology of KNM-ER 1470 takes the name *H. rudolfensis* (Figure 6: bottom). Instead of OH 7 Wood (1991, 1992) associated the mandible KNM-ER 1802 with *H. rudolfensis*, and this specimen has virtually become a paratype of this species, although it was never designated as such.

In the 1990s fieldwork of the Koobi Fora Research Project, now led by Meave Leakey, targeted older sediments in the Turkana Basin, which resulted in the discovery of *Australopithecus anamensis* and *Kenyanthropus platyops* (Leakey et al., 1995; 2001). However, operations resumed on the eastern side in 2000, and early *Homo* became once again a focal point. Having joined the research team I became increasingly aware of the difficulty of comparing the type specimens of early *Homo* species. The most diagnostic part of the *H. habilis* type OH 7 is its lower dentition set in a distorted

mandible, whereas KNM-ER 1470 as the *H. rudolfensis* type lacks teeth altogether and is mostly diagnostic in overall facial architecture. This mismatch in preserved morphology provided a problematic comparative context for the new early *Homo* fossils we started to find. However, it was one of these new discoveries that triggered the research that would eventually resolve these problems.

THE DISCOVERY OF KNM-ER 62000

When I joined our 2008 fieldwork at Koobi Fora in June that year, slightly delayed because of administrative duties as university course tutor, I was welcomed with the news that a day or two earlier a rock had been spotted which showed the broken cross-section of two hominin-looking teeth (Figure 7). We excavated the specimen the next day, and it turned out to be a hominin face still



Figure 7. Overview of the KNM-ER 62000 site in Area 13I, Koobi Fora, June 2008.



Figure 8. Meave Leakey and Fred Spoor excavate KNM-ER 62000, June 2008. The inset shows a close-up of the fossil as it was initially spotted. Photo by Y. Kaifu.

largely encased in sandstone (Figure 8, 9a). During preparation over the following weeks and months it became increasingly clear that this was a face that bears remarkable resemblance to that of KNM-ER 1470 (Figure 9b-d). The specimen, now known as KNM-ER 62000, is substantially smaller, but shares the same straight and non-projecting midline profile in side view, with cheekbones placed forward on either side (Figure 10a,c). Finally, after 36 years the unusual face of KNM-ER 1470 was replicated, and this time that face had a well-preserved maxilla, or upper jaw bone, including several teeth.

The discovery of KNM-ER 62000 offered the opportunity to study the shape of the tooth row (dental arcade) and palate of a KNM-ER 1470-like creature. The great advantage of exploring this aspect of the cranium is that it forms the interface with the mandible. Upper and lower jaws have to fit, not only within



Figure 9. KNM-ER 62000 still encased in sandstone (a) and fully prepared (b-d), shown in right side view (a-b), from below (c), and in frontal view (d). Scale is 3 cm.

an individual, but also within a species. Regardless of natural variation we cannot expect to see species marked by long and frontally curved upper dental arcades that have mandibles with short lower arcades that are flat at the front (and *vice versa*). Importantly, this type of variation and correlation of cranial and mandibular shape can be measured and statistically tested. Why then is this particularly relevant to the study of early *Homo*? Because KNM-ER 1470, as the type specimen of *H. rudolfensis*, and KNM-ER 62000 both share a characteristic upper dental

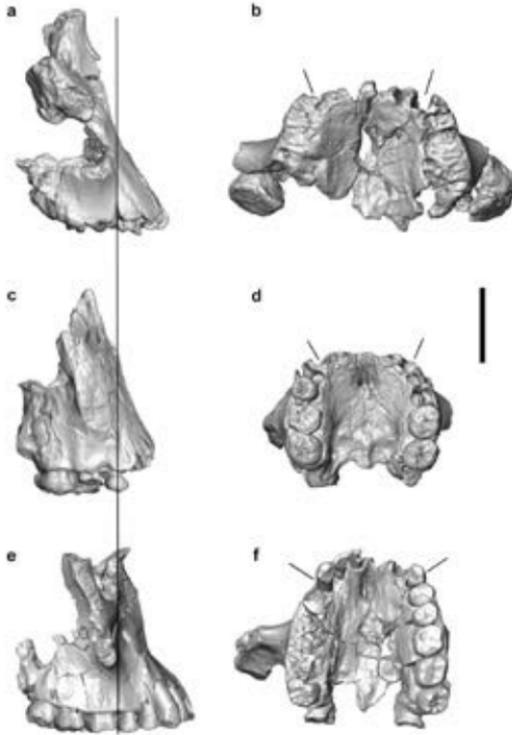


Figure 10. The faces of KNM-ER 1470 (a, b), KNM-ER 62000 (c, d) and KNM-ER 1813 (e, f) compared in right side view (a, c, e) and from below (b, d, f). Scale bar is 3 cm. The vertical line in a, c and e indicates the surface position of the cheek bones, and the short lines in b, d, and f indicate the orientation of the canine tooth sockets. KNM-ER 62000 shares with KNM-ER 1470 a straight and non-projecting midline profile, with cheekbones placed forward on either side (a, c). Seen from below their canine sockets are more part of a straight frontal tooth row and face more forward than sideways (b, d). In contrast, the more generalized face of KNM-ER 1813 is more protruding, with cheekbones set backwards (e). From below the frontal tooth row is more curved with canine sockets facing more sideways (f). See Supplementary Note 5 of Leakey et al. (2012) for more information about the CT-based surface visualizations.

arcade, and it can only be expected that their mandible will match this shape. We can thus hope to identify what type of mandible in the fossil record is likely associated with these crania.

Before we could start looking for mandibles to match with KNM-ER 62000 we had to get a better impression of what its upper dental arcade would have looked like in life. Here we had invaluable help from one of the great technical revolution in palaeontology: the use of computed tomography (CT) to visualize a fossil in 3D and be able to manipulate these digital image data in the virtual environment of a computer workstation. Not only can the inside of a fossil be studied in great detail, but adhering sandstone matrix can be removed ‘virtually’, bones and teeth can be moved and mirror-imaged, and the digital surfaces can be quantified and statistically analysed. The Netherlands was very much at the forefront of pioneering the use of CT in hominin palaeontology through the exploratory work in the 1980s by the late Jan Wind, and in particular by Frans Zonneveld (Wind, 1984; Zonneveld & Wind, 1985). Now it has become a routine tool with both medical CT and increasingly micro-CT being applied to the fossil record for a wide range of applications.

CT-scans of KNM-ER 62000 were made at a local hospital in Nairobi, as part of the ongoing CT programme of the National Museums of Kenya which I had initiated in 1995. Using the images we could evaluate the preservation of the teeth and tooth sockets, and we could digitally visualize the unerupted third molar (wisdom tooth) that is preserved in its crypt on one side. KNM-ER 62000 is a late juvenile (near adult), like the OH 7 *H. habilis* type, but careful study of growth and development shows that this does not significantly affect the specific morphology that plays a key role in the research discussed here (Leakey et al., 2012; Spoor et al., 2015).

In addition to the third molar crown KNM-ER 62000 preserves the second premolar, and the left and right first and second molars. We digitally reconstructed the well-preserved right side of the

dental arcade by adding the third molar taken from its crypt and by mirror-imaging the left first molar crown. Moreover, we also added modern human incisors, canine and first premolar, selected based on size, matching dental wear and premolar root shape. The human ‘stand-ins’ could be accurately positioned by aligning their roots with the tooth sockets and bringing their crowns in contact. In this work Christopher Dean (UCL, London) played an important role, because he is not only a highly esteemed scientist working on dental development in primates, but also a life-long practising dentist with great experience in dental implants and reconstructive dentistry. Having reconstructed the right side, the full dental arcade could now be obtained by mirror-imaging based on the cranial midplane (Figure 11).

As also indicated by the preserved parts of KNM-ER 1470 the reconstructed dental arcade and palate of KNM-ER 62000 are distinctly ‘U-shaped’, and the canines are more part of the straight frontal tooth row than the sides (Figure 10b,d). In contrast, the arcade of specimens such as KNM-ER 1813, but also modern humans and *H. erectus*, is more parabolic in shape, and the canines face more sideways (Figure 10f). Comparing this KNM-ER 62000 dental arcade with KNM-ER 1802, the mandible that is by default associated with KNM-ER 1470 and *H. rudolfensis*, gave a big surprise: no match at all (Figure 12a,c). It is too short, and is too straight in the front to provide a reasonable occlusion.

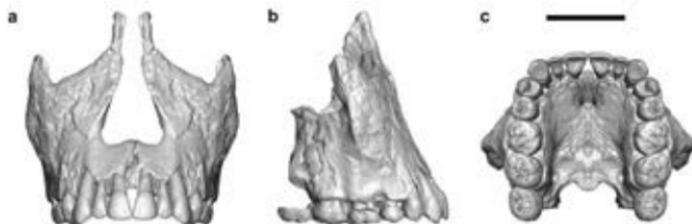


Figure 11. Dental arcade reconstruction of KNM-ER 62000 shown in frontal view (a), side view (b) and from below (c). Scale bar 3 cm.

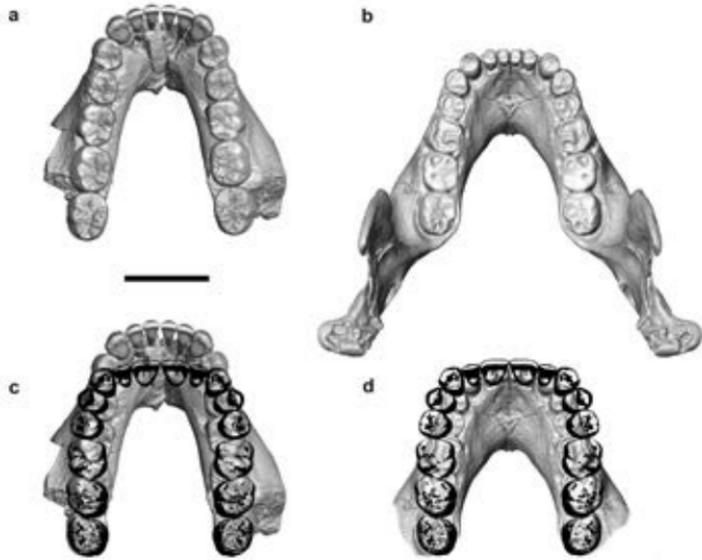


Figure 12. The mandibles KNM-ER 1802 (a) and KNM-ER 60000 (b), and their dental arcades compared with that of KNM-ER 62000 (c, d). The arcade of KNM-ER 62000 is too short, and is too straight in front to occlude well with KNM-ER 1802 (c), but it does fit well with KNM-ER 60000 (d). Scale bar is 3 cm.

In contrast, we identified three fossil mandibles that form a good match, including a newly found, and very complete mandible KNM-ER 60000 (Figure 12b,d). Not only the crania but also the mandibles appear to show two types of morphology.

The description, comparisons and interpretation of KNM-ER 62000 were published in Leakey et al. (2012). We concluded that the specimen confirmed that KNM-ER 1470, which for a long time had no equal in the fossil record, was not a ‘one-off freak’ but shows a distinct facial morphology that characterizes the species to which both fossils belong. As such, these results are most consistent with two species of early *Homo*, as documented

both by the craniofacial parts and the mandible. However, three questions remained unanswered in Leakey et al. (2012). The first one was whether statistical analyses can confirm that differences in dental arcade shape are indeed larger than normal variation seen within individual primate species. The second question was whether the apparent mismatch between the dental arcades of KNM-ER 62000 and mandibles such as KNM-ER 1802 (Figure 12c) is 'real' or just an unfortunate combination of two extremes out of the pool of a single variable species. For example, can one find a similar mismatch when selecting a particularly flat-faced cranium with a non-protruding maxilla and a mandible with a protruding chin area from the worldwide modern human population? And is it statistically likely that one would randomly get such a pair in the fossil record? The third question was a pragmatic one: assuming two separate species did exist, what should these be called? The answer completely depends on where the *H. habilis* type OH 7 fits, because that species name has priority as the one that was proposed first. Hence, does OH 7 fit with the KNM-ER 1470/62000 facial morphology, or with the one represented by KNM-ER 1813 and several other fossils (Figure 6)? As outlined above there has been a lack of consensus in the literature.

OH 7 RECONSIDERED

It will be clear from the preceding discussion that OH 7 is pivotal in any attempt to evaluate the early evolution of the genus *Homo*. However, its diagnostically most important part, the mandible, is distorted and therefore difficult to compare with other specimens. Hence, we realised that in order to make progress with our study of the early *Homo* fossils from the Turkana Basin we had to refocus our attention temporarily to see if the OH 7 mandible can be reconstructed and analysed. Given that brain size has always played a prominent role in discussions about the evolution of the genus *Homo*, it also seemed useful to re-evaluate the size and shape of the fragmented parietal bones of OH 7, in order



Figure 13. CT Scanner in Dar es Salaam, December 2010. The inset on the right is a transverse CT image of OH 7 showing the roots, cracks and sandstone fill behind the right canine root.

to obtain a new estimate of its endocranial volume based on the most up-to-date methods. Here I will briefly review the results and conclusions of this work on OH 7, but otherwise refer to Spoor et al. (2015) and its extensive supplementary information for further details.

In 2010 we visited Dar es Salaam, Tanzania, to study the Olduvai collection, and we were allowed to make CT scans of OH 7 in a local hospital. To our great relief the cross-sectional CT images showed a good contrast between bone, the teeth, the various cracks and the matrix between the broken parts (Figure 13). Back in Leipzig at the Max Planck Institute for Evolutionary Anthropology, where I was 'on loan' for five years from my normal workplace at UCL in London, I embarked on digitally dissecting every component of the fossil. It turned out that there

are only a limited number of cracks in the fossil, the individual bone pieces could be separated easily and there is no or very little plastic distortion of the bone (Figure 14a,b). The latter would have been much more difficult to correct in a reconstruction than the basic fractures which can simply be reset by matching the break surfaces on either sides. And importantly, the CT scans revealed key information about the midplane of the mandible that cannot be seen when looking at the original fossil. Covered over by the displaced right side of the mandibular body the midplane is marked on the inner side of the chin area by symmetrical features associated with the tongue muscles. Moreover, although all incisor crowns are displaced this is along a distinct horizontal crack and the incisor roots underneath maintained their original symmetrical position, marking the midplane here as well.

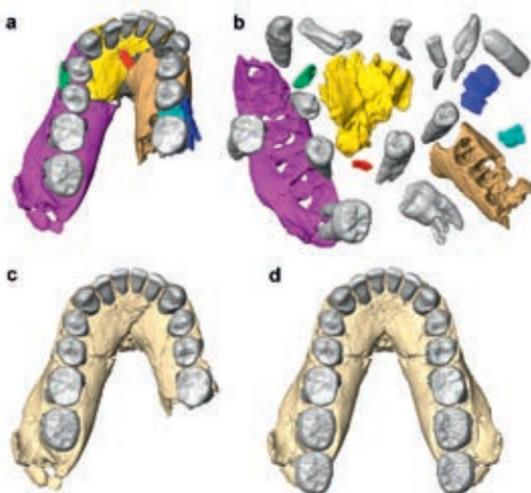


Figure 14. Computer visualization of the OH 7 mandible, (a) as preserved with colours marking broken parts, (b) all parts separated, (c) reconstruction of the original shape, and (d) reconstruction using the mirror-imagined left corpus and copies of the second molar as third molars.

The actual virtual reconstruction was done by realigning the individual parts of the mandibular body first. Subsequently the teeth were repositioned by matching wear facets between tooth crowns, which Christopher Dean and I had carefully recorded from the original specimen, by realigning the tooth roots in the sockets and by repositioning the incisor crowns on their roots along the horizontal crack. The resulting reconstruction includes all preserved parts, ranging up to the first molar on the right side (Figure 14c). As we also wanted to analyse a more complete mandible we created a second reconstruction by mirror-imaging the left side from the second molar to the canine to the right (Figure 14d). In this reconstruction we also duplicated the left second molar to represent the missing third molars to get an impression of the full dental arcade. However, this addition at the end of each tooth row was not included in any of our quantitative analyses. The two mandibular reconstructions of OH 7 we thus obtained are characterised by relatively long and parallel postcanine tooth rows, composed of the premolars and molars, and at the front the canine and incisor crowns form a gently curved arch.

Having reconstructed the OH 7 mandible we now needed to quantify the shape of the dental arcade so that fossils can be compared and variation can be assessed relative to that in extant humans and great apes. Quantifying the shape was done by placing a large series of 3D landmarks on the margins of the tooth sockets, all along the lower and upper arcades. These landmark data were subsequently analysed by Philipp Gunz at the Max Planck Institute for Evolutionary Anthropology, using sophisticated multivariate methods known as geometric morphometrics. These describe and analyse shape, and are very good at statistically demonstrating that two things are different. Proving that two things are similar is much more difficult because it can be that the landmarks that were used do not adequately describe the shape, and therefore do not express the actual differences that remain undetected. For example, using six landmarks is the only straightforward way to describe a sphere. However, those same six landmarks also fit a

cube (in two different ways), and the fundamental difference in shape is not revealed. Thus, geometric morphometrics is a good tool of exclusion, to reject a null hypothesis that two things are the same. In terms of studying hominin diversity, it is good at proving that two fossils cannot belong to the same species, but less good at proving that those two are definitively from the same species. An excellent example of this phenomenon is the recent study by Lordkipanidze et al. (2013), which used a geometric morphometric analysis of cranial shape to demonstrate that all species of early *Homo* should be attributed to the single species *H. erectus*. The landmarks they used are very general, and do not quantify the well-known features that characterize and distinguish *H. habilis*, *H. rudolfensis* and *H. erectus*, so their conclusion that everything is the same does not come as a surprise (Spoor, 2013).

The geometric morphometric study of the mandibular dental arcade includes a principal component analysis and the results are best shown plotting the first two components (Figure 15). It shows that the long and narrow shape of the OH 7 arcade is close to that of two other early *Homo* mandibles, including the KNM-ER 1802 specimen we encountered previously (Figure 12a). Remarkably, these three fossils are more similar in arcade shape to great apes and *Australopithecus* than to modern humans and *H. erectus*, which both have shorter, more parabolic arcades. The three also strongly contrasts with two mandibles which we have linked with crania KNM-ER 1470 and KNM-ER 62000, including the newly found KNM-ER 60000 (Leakey et al., 2012; Figure 12b).

In order to compare the OH 7 mandible with key maxillae, most prominently that of the newly discovered KNM-ER 62000 face, we took the novel approach of predicting the upper arcade of OH 7. We could do this reliably using advanced regression analyses, based on the strong and consistent link between the upper and lower jaw shapes in extant humans and great apes. In addition, Christopher Dean reverted to old-fashioned craftsmanship as a dentist, by manually reconstructing the upper dental arcade of

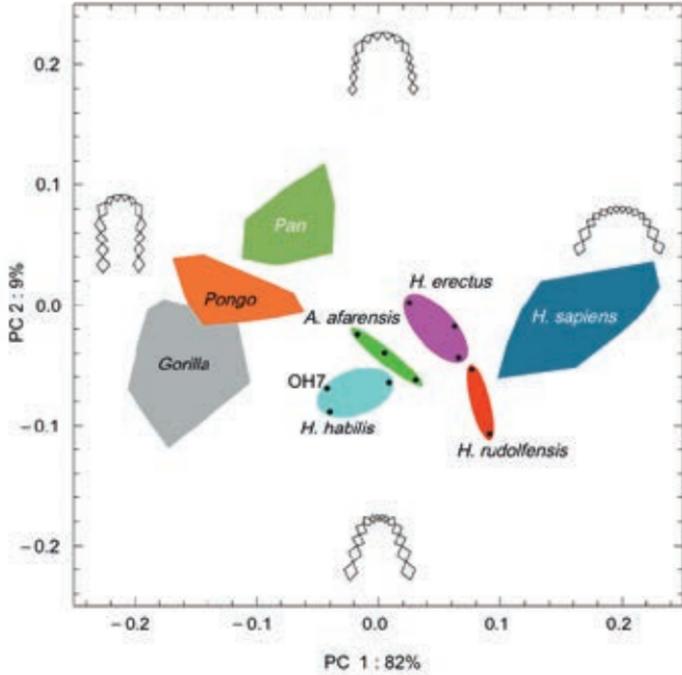


Figure 15. Principal component analysis of the mandibular dental arcade. Plot of principal components (PC) 1 and 2 with associated shape changes shown by the four wire frames. The sample ranges of the extant species is shown (convex hull). For the fossils the individual data points are shown, with surrounding ellipse for illustration only. See Spoor et al (2015, Ext. Data Fig. 4a) for full results.

OH 7, as if it was a denture to go with the mandible. Comparing these reconstructed upper arcades gives basically the same results as found for the lower arcade. OH 7 is most similar in shape to *Australopithecus*, and most distinct from KNM-ER 62000. The latter shape difference is as large as that between some extant humans and chimpanzees, and definitely rules out that OH 7 could be part of the same species as KNM-ER 62000. The same mismatch is shown when comparing OH 7 and KNM-ER 1470, even though the latter fossil cannot be analysed quantitatively, with too much of the back part of its dental arcade missing. Figure 16 shows that the dental arcade of KNM-ER 1470 will have been

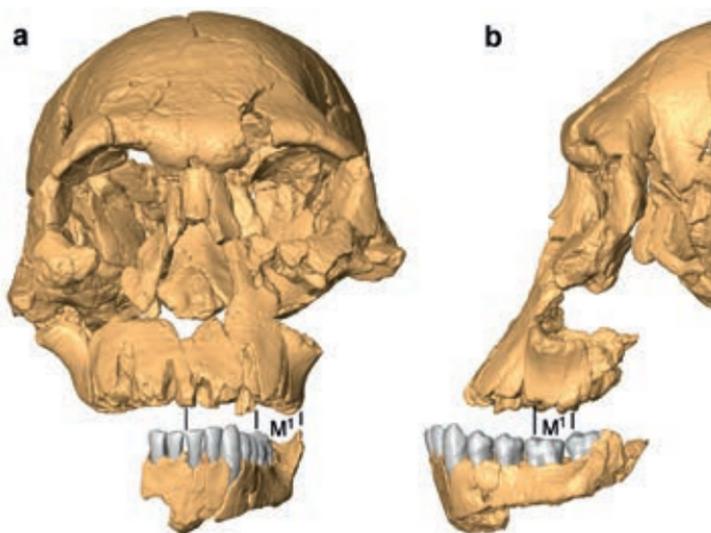


Figure 16. (a) Frontal view of KNM-ER 1470 and the reconstructed mandible of OH 7 aligned by their midplane. (b) Side view aligning these specimens on the basis of their first molar position. KNM-ER 1470 has a wider dental arcade, shown by the position of its first molar socket well to the side of the OH 7 tooth row (a), and the strong underbite shows that KNM-ER 1470 is less-protruding at the front (b).

too short and too wide to match that of OH 7. Given that OH 7 does not belong to the same species as KNM-ER 62000 and KNM-ER 1470 these latter two fossils and associated mandibles should be named *H. rudolfensis* and not *H. habilis* (Figure 6).

That more than one species is indeed present in the early *Homo* sample is clearly demonstrated by analyses of variation. When either all mandibles or all maxillae of early *Homo* are considered together their shape variation far exceeds that seen in extant species. Only when they are divided into three species groups, *H. habilis*, *H. rudolfensis* and *H. erectus*, is the respective within-group variation consistent with that of extant great apes or humans.

The new reconstruction of the OH 7 parietal bones was done by Simon Neubauer, an expert in brain evolution at the Max Planck Institute for Evolutionary Anthropology. The left and right sides are both incomplete, but as they complement each other the entire parietal part of the braincase could be reconstructed (Figure 17).



Figure 17.
A reconstructed Homo habilis skull based on the mandible and parietal bones of OH 7. The transparent parts are based on cranium KNM-ER 1813, morphed to fit OH 7. Image by Philipp Gunz, Simon Neubauer & Fred Spoor.

In extant humans and great apes the combined size and shape of this part is strongly correlated with the total endocranial volume. Using this relationship we estimated a volume between 729 and 824 ml for OH 7, which is considerably larger than previous estimates of between 647 and 687 ml calculated using less reliable methods. In fact, the new values obtained for OH 7 fall well within the range of early *H. erectus*, and are among the largest reported for other specimen attributed to early *Homo*. In all, the evidence suggests that for the period between 2.1 and 1.5 Ma the endocranial volumes of *H. habilis*, *H. rudolfensis* and *H. erectus* largely overlapped, and broadly fell between 500 and 900 ml.

THE ORIGIN AND RADIATION OF EARLY *HOMO*

So what have we learned about the early part of the *Homo* lineage, based on analyses of newly found fossils and re-analysis of OH 7, discovered over 50 years ago. Large differences in jaw shape show that in the time period between 2.1 and 1.6 Ma two different species existed, in addition to *Homo erectus*, and that these should be referred to as *Homo habilis* and *Homo rudolfensis*. Our statistical analyses reveal differences in dental arcade shape that are sometimes as large as between humans and chimpanzees. In the past differences in brain size were often considered important to characterize species of early *Homo*. However, the new analyses show that the three *Homo* species cannot be distinguished by their brain size, in contrast to their telling differences in facial appearance. *H. habilis* shows the most primitive morphology with long and parallel postcanine dental rows suggestive of a protruding lower face. Early *H. erectus* has jaws which are shorter and more diverging towards the back, foreshadowing those of *H. sapiens*. The jaws of *H. rudolfensis* are also shorter, but the postcanine rows are more parallel, and the incisor row is distinctly flat and retracted between the canines.

In addition to providing more insights into the radiation of early *Homo* between 2.1 and 1.6 Ma, our OH 7 study has also

shed unexpected light on the earlier period which is particularly important for understanding the origins of *Homo*, but notoriously lacks a good fossil record of this genus. New fossil finds over the last years have also contributed to a lively debate about the origins of *Homo*.

Until recently the A.L. 666-1 maxilla from Ethiopia, dated at 2.3 Ma, was the oldest unambiguous evidence for the genus *Homo*. We could include this specimen in our study of dental arcade shape, and found that in A.L. 666-1 it is close to the derived shape of *H. erectus* rather than to the primitive shape of *H. habilis*. This is a surprising find because A.L. 666-1 is about half a million years older than *H. habilis*. This pattern suggests that the *H. habilis* lineage originated before 2.3 Ma, preserving the primitive arcade shape also seen in *A. afarensis*. In contrast, A.L. 666-1 represents a lineage which early on evolved the more modern jaw shape subsequently seen in *H. erectus* and *H. sapiens*, and could have been ancestral to the more specialised jaw shape of *H. rudolfensis* as well (Figure 18).

Right at the time we were trying to interpret our results obtained for A.L. 666-1 we heard about the new discovery of a partial mandible in Ethiopia, which pushes back the oldest evidence for *Homo* by another 0.5 million years, to 2.8 Ma. This fossil, the LD 350-1 mandible from Ledi-Geraru, was eventually published on the same day as we published our OH 7 paper (Villmoare et al., 2015). What is important for our current story is that LD 350-1 clearly seems to belong to the *Homo* lineage, based on subtle clues (see above), but is more primitive than mandibles we attribute to *H. habilis*. Its morphology makes it a good ancestral model for this and other species of early *Homo*, but in other respects show its *A. afarensis* heritage (Figure 18).

But is this not all a bit ‘eastern African centric’? Some of our colleagues in South Africa have been very eager to point out that they have a much better ancestor for the genus *Homo*, and have perhaps even found fossils of the actual population

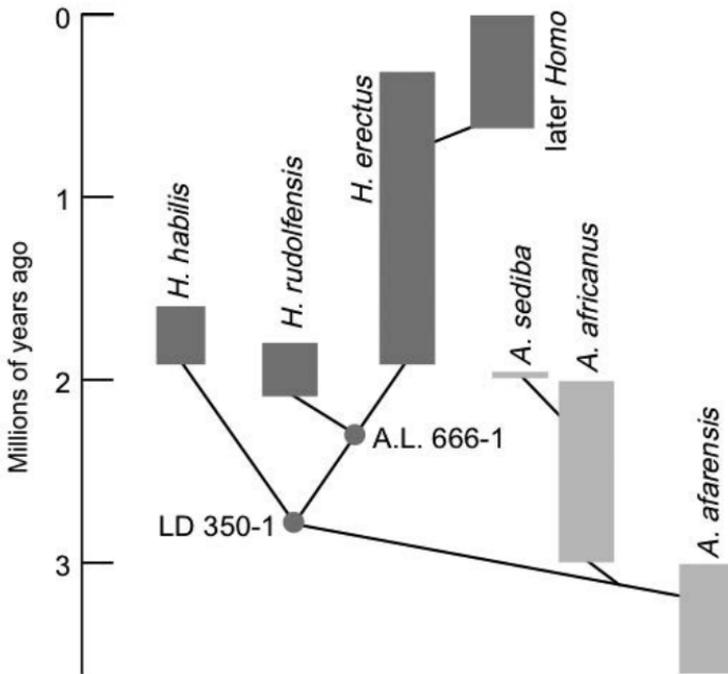


Figure 18. Origin and radiation of early Homo. Known temporal ranges are indicated, and black lines represent hypothetical phylogenetic relationships most consistent with Strait & Grine (2004), Spoor et al. (2015) and Villmoare et al (2015). Australopithecus in light grey and Homo in dark grey. *A. afarensis* is shown as the most plausible ancestral species (full temporal range from 3.8 Ma). *A. africanus* and *A. sediba* are shown to provide a temporal context to claims that the latter is ancestral to Homo.

that was ancestral. That proposed ancestor is *Australopithecus sediba*, known from the Malapa cave site and well-dated to 1.98 Ma (Berger et al., 2010; Pickering et al., 2011). Researchers worldwide have expressed their admiration for the fabulous fossil discoveries at the Malapa site, which include two partial skeletons. However, the interpretation that *A. sediba* is ancestral to *Homo* or even *H. erectus* specifically, has met with substantial scepticism (e.g. Spoor, 2011; Joordens et al., 2013; Kimbel, 2013). One problem with the link is that the only known *A. sediba* cranium (the type specimen) is a late juvenile, and several of the supposed 'gracile' features that might make the specimen look somewhat more *Homo*-like are known to change in the direction of greater robusticity in adulthood (Spoor, 2011; Kimbel, 2013; Strauss et al., 2013). And then there is the aspect of time (Figure 18). KNM-ER 1470 has been re-dated to 2.0-2.1 Ma by two independent teams (McDougall et al., 2012; Joordens et al., 2013), and A.L. 666-1 is securely dated to 2.3 Ma (Kimbel et al., 1997). This alone makes that *A. sediba* could only have been ancestral to *Homo* much earlier in time, and the Malapa fossils would have to represent a late surviving population at 1.98 Ma. Now with the discovery of the LD 350-1 early *Homo* mandible at 2.8 Ma this issue has become even more problematic. *A. sediba* is derived from *A. africanus*, but even this ancestral species is not known from deposits much older than LD 350-1 (Figure 18). An open mind is good thing, but as it stands the evidence for *A. sediba* as the ancestor of *Homo* is less than compelling.

Now that we are in South Africa, a few words about *Homo naledi* from the Rising Star cave system (Berger et al., 2015). This is a newly discovered species which in morphology appears to have most in common with early *H. erectus*. As such this is a very important find. However, until we learn more about the age of the specimens it is difficult to interpret where it fits in the evolutionary history of the genus *Homo*. If the specimens are old, *H. naledi* is likely part of an early radiation of *Homo* species, something we know little about in the context of southern Africa (Smith & Grine, 2008; Grine et al., 2009). If the specimens are

young, they likely represent a remnant population, and it would be fascinating to find out with which contemporary hominin species *H. naledi* could have interacted, including *H. sapiens*.

Having just presented what may seem like a clear-cut interpretation of the early evolution of the *Homo* lineage (Figure 18), it is good to finish by returning to the reality check of the first half. Although our knowledge of hominin evolution becomes increasingly sophisticated, we should not forget the limitations of the known and unknown unknowns. Particularly relevant for the discussion about the origin and early radiation of the genus *Homo* is the known unknown that the eastern African hominin record from between 2 and 3 Ma is poor, so that the fossils are not representative of the diversity and temporal ranges of species. Evolutionary relationships are best assessed on morphological grounds rather than specific occurrences in time, as is shown here by *H. habilis* in which primitive morphology suggests deep roots well predating its fossil record. However, occurrence dates do play an important role to formulate evolutionary scenarios (e.g. *H. naledi*), or to test the plausibility of proposed scenarios (e.g. *A. sediba*). Importantly, species and relationships between species are nothing but scientific hypotheses that constantly need to be re-examined. If the evidence convincingly points at alternative interpretations we should not be afraid to change our mind and merge or split species and revise their classification. Even if the press, the wider public and the teachers of undergraduate courses do not like it. There are no holy cows in hominin evolution, or at least there shouldn't be.

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