

FIVE YEARS AFTER
AUSTRALOPITHECUS SEDIBA

NEW DISCOVERIES
CHANGING OUR UNDERSTANDING
OF HUMAN EVOLUTION

ZEVENENDERTIGSTE KROON-VOORDRACHT

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(1868-1945)

Palaeoanthropology is not generally known for its well preserved record. With the entirety of the fossil hominin record from Africa numbering in just the few thousand, and with the vast majority of these remains comprising just isolated teeth and small fragments of bone, often from poor context, reconstructing an accurate picture of human evolution over the last several million years has proven difficult, often resulting in fierce debate over what amount to differences in what are quite literally scraps of fossilized bone. But recent discoveries are dramatically improving the hominin fossil record and allowing us greater insight into the mode and tempo of human evolution. With the discovery of these more complete remains, including partial skeletons, and our ability to more accurately date these same remains, the potential for a clearer understanding of the evolution of the homininae has never been greater. But increasingly, these better preserved, better contextualized remains are not, in their morphology nor in their timing, synching with the story of human evolution as derived from the more fragmentary record we had recovered over the past more than eight decades. In fact, some fossils differ so dramatically from our pre-conceived image of how human evolution occurred, that they appear to tell another story entirely, different from that based upon the previous record. Could there be, as some commentators suggest, a vast complexity in human evolution, with many species existing at one time, and multiple examples of homoplasy occurring over and over, where similar looking features evolve at different time for similar purposes in the hominin lineage? Or must we ask, were the hypotheses derived from that fragmentary, poorly contextualized record simply wrong, and that the story derived from this more complete, better contextualized record that is now emerging should simply replace the hypotheses generated over the last several decades of research? For scientists outside of palaeoanthropology the answer might seem simple – the better record should, until proven otherwise, replace the more fragmentary one.

But the study of human origins is after all, conducted by humans, and sacred cows – even in science, are often hard to slaughter. In order to highlight the difficulties we face in the study of human origins, in comparing the “new” record with the “old” one, I am going to briefly examine here the case for the fossils from the site of Malapa, representing the species *Australopithecus sediba* as a potential candidate ancestor for the genus *Homo*, contrast this against the existing record, and attempt to explore where this species might fit in the story of human evolution. At the same time I will elaborate upon arguments for, and against it being the best candidate for the ancestry of our genus and attempt to explain why these fossils are so important to human evolutionary studies at this moment in time.

The site of Malapa represents an unusually rich early hominin locality in Africa and may represent one of the single richest assemblages of pre-Holocene hominins yet discovered. Dating to just under 2 million years in age, it contains a number of associated skeletal remains of several individuals. These remains are found alongside an abundant, well preserved fauna and flora that is probably unmatched in its quality among known South African cave sites. The hominin skeletons of Malapa additionally preserve critical areas of anatomy that have, in many cases, not been seen in such completeness, or lacking distortion, in the entirety of the early hominin fossil record.

I first discovered the site of Malapa on August 1, 2008, during the course of a geospatial survey for new fossil-bearing cave deposits in the dolomitic region of the Cradle of Humankind World Heritage Site, Northwest of Johannesburg. I recognized Malapa as a de-roofed cave of at least 25 x 20 meters, in an area where limited lime mining had taken place, probably during the late 19th or early 20th century, almost certainly before Robert Broom began exploring the area in the mid-1930's.



The site of Malapa viewed from the North in 2012. The discovery site of the first hominins is within the cluster of trees. Photo by Lee R. Berger.



The fossil bearing pit at Malapa where the first discoveries were made. This photo was taken on one of the first visits to the site in 2008. Photo by Lee R. Berger.

On the 15th of August, 2008, on the first trip back to the site to investigate its fossil-bearing potential, the first hominin specimens were discovered by my then 9 year old son Matthew – this specimen would become known by its accession number of MH-1 or Malapa Hominin 1. In the following weeks and months we quickly recognized that the site had significant potential, as additional hominin fossils were encountered, including my discovery on September 4, 2008, of a second, well-preserved adult partial skeleton. This skeleton was importantly found *in situ*, thus giving us the precise location of the hominin remains and leading to the discovery of the *in-situ* location of MH1 just a few centimeters above her.



Moments after the discovery. Matthew Berger, then 9 years of age, holding the rock containing the first hominin remains discovered at Malapa on August 15th, 2008. Photo by Lee R. Berger.



Moments after the discovery of MH-2 – with Dr. Job Kibii (right). The author is pointing to a proximal femur belonging to MH-1, while Dr. Kibii holds a modern human humerus next to the proximal humerus and scapula found in-situ moments before by the author. Photo by Brian Kuhn September 4th 2008.

Over the course of the last five years, my team and I have conducted a number of analyses of this material and in 2009 and early 2010 came to the conclusion that the fossil hominin remains from Malapa represented a new species of early hominin, previously unrecognized in the fossil record. It was clear that the species possessed a number of both primitive and derived characters that were unexpected given the fossil hominin record that had been recovered to date. This led us in 2010 to describe a new species of early hominin – *Australopithecus sediba*. We would eventually put a very precise date of 1.977 to 1.98 million years ago on the deposit using uranium-lead dating, a method of dating in part pioneered at Wits.



The skeletons of MH-1 and MH-2 as described in the 2010 publications in Science of the new species Australopithecus sediba. Photo by Brent Stirton and National Geographic.

We have clearly demonstrated in more than thirty academic publications over the past years that *Australopithecus sediba* is an unexpected addition to the early hominin record. With its small but in some ways derived brain, reduced dental size and incipient nose among other characters, the cranial morphology of this species appears to share features with both more primitive australopiths and later *Homo*. Post-cranially, we have equally found *Australopithecus sediba* to show an unexpected mosaicism in its anatomy including longer, more ape-like arms, hands that exhibit an elongated thumb and shortening of the fingers, a more derived pelvic structure and aspects of the foot and ankle that are both surprisingly primitive, as well as surprisingly derived. With the significant amount of research published about *Australopithecus*

sediba and the site of Malapa, the species and site, even in this short period of time, is perhaps now as well known as any other early hominin species.



Science cover.

Reconstruction of a ~2-million-year-old Australopithecus sediba skeleton (height: ~1.3 meters) based on fossils from the Malapa Hominin 1 (MH1), MH2, and MH4 specimens from Malapa, Gauteng, South Africa. Brown indicates discovered fossils. Au. Sediba exhibits a mosaic morphology distinct from that of other australopiths and early Homo. Reconstruction: Peter Schmid and casting technicians at the University of the Witwatersrand's Evolutionary Studies Institute; Photo: Brett Eloff, courtesy of Lee R. Berger and the University of the Witwatersrand.

Though some colleagues were critical of the novel species designation, as is to be expected, the veracity of our assignment of these remains to a new species now has practically universal acceptance. What does not have universal acceptance is one part of our hypotheses put forward that suggests that *Australopithecus sediba*, while different than other hominins found, may be the best candidate direct ancestor of the genus *Homo*.

In the first publications of this material my colleagues and I suggested that *Australopithecus sediba* was most probably derived from *Australopithecus africanus* via a cladogenetic event, or that it might represent some form of anagenetic lineage from a species not dissimilar to *africanus*, although one probably less megadont.



The skull of Australopithecus sediba MH-1 perched upon a rock above the Malapa site in the Cradle of Humankind. Photo credit Brent Stirton and National Geographic. First published in National Geographic Magazine, August 2011.

In our analysis *Australopithecus sediba* forms a stem group of *Homo* based upon craniodental characters. As we have discussed, anatomical support for a cladogenetic interpretation comes from the constellation of *Homo*-like characters in *sediba*, that appear directly alongside its australopith-like traits. This mosaicism places *sediba* outside the range of variability seen in the whole of the *Australopithecus africanus* samples, even though the *africanus* samples derive from the four different sites of Taung, Sterkfontein, Gladysvale and Makapansgat. Even though *Australopithecus sediba* is morphologically closest to *africanus*, the derived appearance of aspects of the cranium and postcranium prevent inclusion within the *africanus* hypodigm.

At least one commentator has, however, suggested that *Australopithecus sediba* is simply a chronospecies of *africanus*. This however, seems unlikely, given both the extremely short time period between the last known occurrence of *africanus* at around 2.1 million years, and the date of Malapa at just under 2 million years, and the many apparent retained primitive characters of the younger *Australopithecus sediba* species.

Another valid point raised by commentators is that given the many characters that *sediba* shares with early *Homo* across its body, and the many variances in morphology between *sediba* and other australopiths, why do we not simply place it in the genus *Homo*?

My colleagues and I have, however, have argued that despite the numerous differences between *sediba* and *Australopithecus africanus*, and indeed between *sediba* and all other australopiths, we have maintained the opinion that *Australopithecus sediba* is better placed with the genus *Australopithecus*, rather than in the genus *Homo* for the simple reason that if the definition of a genus is accepted as being a Grade level one, *sediba* is certainly adaptively closer to the australopiths than it is to definitive members of the genus *Homo* such as *Homo erectus*. *Australopithecus sediba* differs from *H. erectus* in a significant number of postcranial

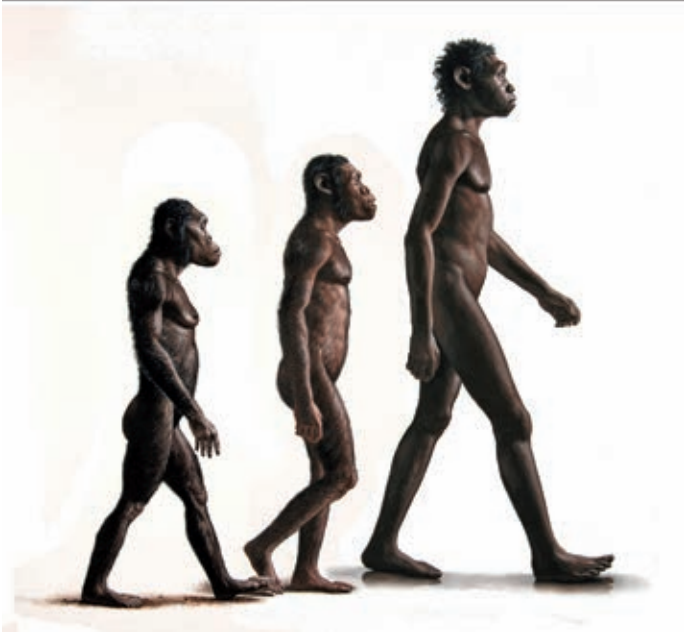
characters, many of which are in critical functional areas of anatomy that almost certainly indicate fundamental differences in the adaptive niche of *sediba* compared to that of *Homo erectus* for example, widely considered certainly within the genus *Homo*. We therefore have concluded that the conservative approach is to maintain *sediba* within the genus *Australopithecus* until such time as a definition of the genus *Homo* would be shown to encompass such rather critical adaptive differences.



The hand as an example of mosaicism in Australopithecus sediba demonstrating the unusual mix of primitive and derived characters that characterizes many parts of the skeleton of this species. From Kivell et al. 2011 in Science.

Of course we have also considered the possibility that given all of these differences between both australopiths and early *Homo* that *sediba* should be placed within in its own genus, and my colleagues and I have corresponded numerous times over such matters with as yet no conclusion to the debate, though I have gone so far as to suggest, only half-jokingly, that if it were found that our arguments justified naming a separate genus, we should use a generic name such as *Humanapithecus* loosely translating to “human ape”, or some similar name that both recognizes the

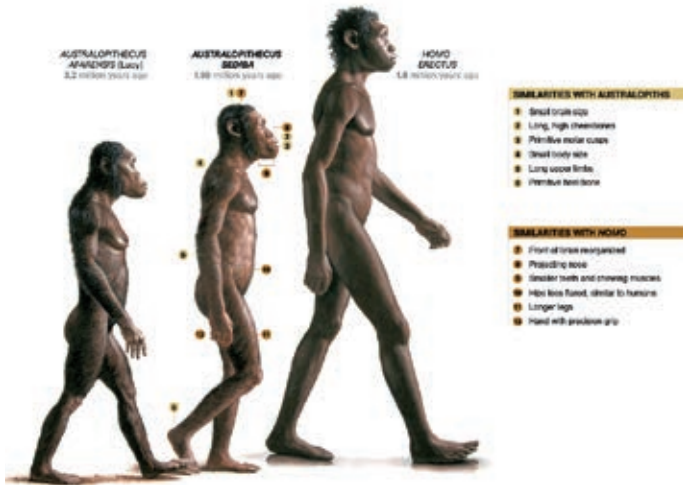
close affiliation with both the genus *Australopithecus* and the genus *Homo*, but also pays tribute to the mosaic nature of *sediba*'s anatomy.



Australopithecus sediba juvenile specimen MH-1 (Karabo) (centre), compared to a female *Australopithecus afarensis* (A.L. 288-1 or Lucy) (left) and a male juvenile *Homo erectus* (KNMER-15000) (right).

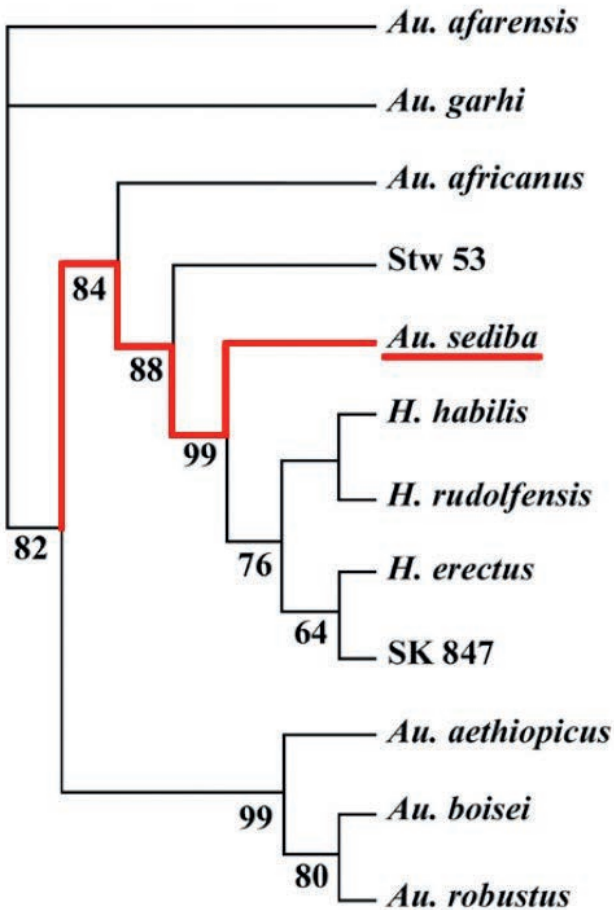
So where does *sediba* fit within the family tree of hominins? Despite the shortcomings of the fossil record around 2 million years, something I will address in more detail in a moment, there are enough fossil hominin remains from East- and southern Africa; if we take that record at face value, we can hypothesize as to the phylogenetic position of *Australopithecus sediba*. As mentioned previously, based on presently available

evidence, *sediba* appears derived from an early form of *Australopithecus africanus*, or something closely resembling at least the more gracile specimens attributed to this species. In turn, *Australopithecus sediba* appears to share more derived characters with specimens assigned to specific fossils presently associated with early *Homo*, but more particularly with early *Homo erectus* more so than any other candidate ancestor, including *Australopithecus afarensis*, *Australopithecus garhi*, or *Australopithecus africanus*. In the initial announcement of *Australopithecus sediba*, my colleagues and I proposed four possible hypotheses regarding the phylogenetic position of *sediba*: 1) *Australopithecus sediba* is ancestral to *Homo habilis*; 2) *Australopithecus sediba* is ancestral to *Homo rudolfensis*; 3) *Australopithecus sediba* is ancestral to *Homo erectus*; or 4) *Australopithecus sediba* is a sister group to the ancestor of the genus *Homo*.



Primitive and derived features of Australopithecus sediba compared to Australopithecus and Homo. Image from National Geographic and John Gurche.

In an accompanying cladistic analysis in that paper, and several that have followed, the most parsimonious cladogram always places *Australopithecus sediba*, perhaps not surprisingly, as a stem taxon for the *Homo* clade comprised of *Homo habilis*, *Homo rudolfensis* and *Homo erectus*.

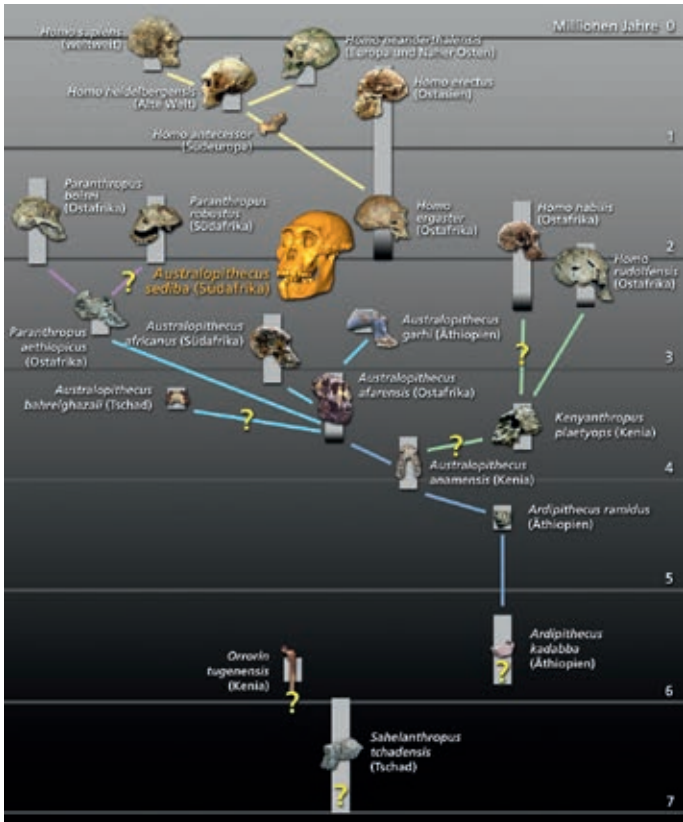


The place of Australopithecus sediba in human evolution as initially described by Berger et al. (2010) in the journal Science.

But is *sediba* at 2 million years in age simply too young to have given rise to the genus *Homo*?

While we have continued our analysis of the phylogenetic status of *Australopithecus sediba* along numerous avenues of research that are focusing particularly on the comparative anatomy of this species, there has been some discussion generated over the approximate two million year old age of *Australopithecus sediba* as seeming to exclude it, through chronological arguments alone, from being considered a potential ancestor of the earliest members of the genus *Homo*. It has been argued, time and again, that *sediba* is simply too young at two million years in age, and this is based on the widespread perception that there are substantially earlier, better candidate fossils that actually represent the earliest members of the genus *Homo*. If this were so, then at least from a relatively simplistic view of anagenetic evolution, the *Australopithecus sediba* fossils from Malapa could not of course, give rise to the genus *Homo*.

So let us examine the question of whether *Australopithecus sediba* is simply too late in time to be considered a candidate ancestor of the genus *Homo*? Before addressing this question in detail, it has to be said that such a view of the potential phylogenetic position of *Australopithecus sediba*, somewhat disingenuously ignores the possibility that the Malapa fossils represent a late surviving population of the species that gave rise to these other forms. In addition, given the extraordinary importance that these supposedly early candidate fossils – purportedly representing members of the genus *Homo* – now have in laying claim to the earliest origins of the genus, their morphology and context deserve critical scrutiny if they are going to weigh themselves against the new, well-preserved, well-provenanced evidence from Malapa. Hypothesizing that any given species gave rise to our genus is an extraordinary claim, and extraordinary claims require extraordinary evidence. So let us, for a moment examine the evidence that is put forward for fossils that are better candidates for the ancestry of the genus *Homo* than *Australopithecus sediba*.

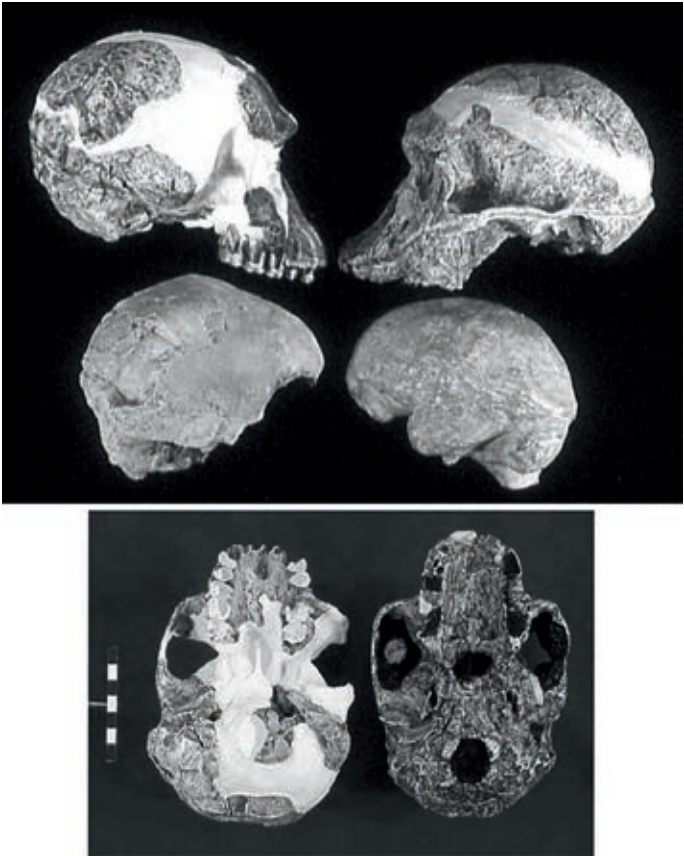


Australopithecus sediba in time on a phylogeny of commonly accepted relationships. Image by Peter Schmid.

Three main candidate fossils are typically put forward as exceeding the Malapa assemblage substantially in age and therefore being contenders for the first members of the genus *Homo*. These are the Stw 53 skull from Sterkfontein, the A.L. 666 maxilla from Ethiopia, and the U.R. 501 mandible from Malawi. Each of these fossils have, at one time or another, been said to exceed 2.1 million years in age, with the latter two specimens purported

to be between 2.3 and 2.4 million years in age. More recently, re-dating of the Koobi-Fora sequence in Kenya has suggested an age for the 1470 cranium within error placing it as a contemporary of *Australopithecus sediba*, and thus this specimen becomes critical to the discussion as well. So let us briefly examine each of these important specimens.

Let us first look close to home at Stw 53 from Sterkfontein. This fragmentary skull has been referred to early *Homo* ever since its discovery in the 1970's. Derived from the "Stw 53 Infill" or Member 5 at Sterkfontein, it has traditionally been thought to be over 2 Ma, but more recent work in fact suggests an age as young as 1.78-1.43 million years ago, making it actually two hundred to nearly six hundred thousand years younger in time than *sediba*. Alun Hughes and Philip Tobias initially described Stw-53 as most probably belonging to a species of early *Homo* closely related to *Homo habilis*, a hypothesis that soon came to be widely accepted due to the small face and its dentition as well as interpretations of the shape of its cranium among other traits. But given finds over subsequent years, Stw 53 now looks less *Homo*-like and more like a late australopith. In fact *sediba* itself shows that in these features, Stw 53 is in fact more *Australopithecus africanus*-like in those features than *sediba* is. The derived craniodental morphology of *Australopithecus sediba* alone, therefore raises further doubt regarding the attribution of Stw 53 to early *Homo*, as Stw 53 quite simply overall looks more *africanus*-like relative to MH1, while MH1 looks more *Homo*-like relative to Stw 53. I must acknowledge though that the morphology of Stw 53 is equivocal and depending on one's definition of the genus *Homo* (for which there is no clear consensus), its attribution into the either genus *Homo* or *Australopithecus* shall probably remain a point of contention among scientists. Thus, to summarize, there is little evidence at present as to why Stw 53 should be considered at all as a candidate for the first evidence of the genus *Homo*, as it neither appears to exceed *Australopithecus sediba* in chronological age, nor is it morphologically compatible (or at least convincing in its morphology) with such a hypothesis.



Stw 53 (left in both images) compared to Sts 5 “Mrs Ples” attributed to Australopithecus africanus. The endocranial cast of each specimen is pictured below the specimens in the upper images. From Clarke (2008) Latest information on Sterkfontein’s Australopithecus skeleton and a new look at Australopithecus. South African Journal of Science 104, November/December 2008.

If there is a “sacred cow” of early *Homo* older than two million years then it would be the A.L. 666 palate from Ethiopia dated to 2.3 million years. Most scientists and even most commentators view this fossil as the best single candidate for the earliest occurrence of the genus in Africa. The specimen in question is a single, fragmentary maxilla.

As I mentioned earlier the claim to the first definitive fossil evidence of the genus *Homo* is an extraordinary one and of great importance. And to be rather blunt, in my own opinion, the A.L. 666 maxilla quite simply does not meet the criteria of extraordinary evidence for a number of reasons.

Firstly, it is an isolated surface find. Like many of the fossils from lacustrine environments, the fossil was found fragmented across the surface of a slope. The maxilla was then reconstructed from these fragments, a task that in and of itself leaves aspects of its reconstructed morphology open to interpretation. When excavations were conducted, no further evidence of this specimen was found *in-situ* leaving its provenience also in question. Thus, although it has been placed within the context of the horizon it lay *on*, there is no absolute certainty that it is from this 2.3 million year old horizon though one must admit that there is also no evidence of younger deposits at the exact spot of discovery. The very fragmentary nature of A.L. 666 clearly indicates that it underwent some taphonomic and erosional process that displaced it from its original situation. Given the importance of its bearing on the question at hand, it is not an understatement to say that A.L. 666’s exact stratigraphic position is of some considerable importance.

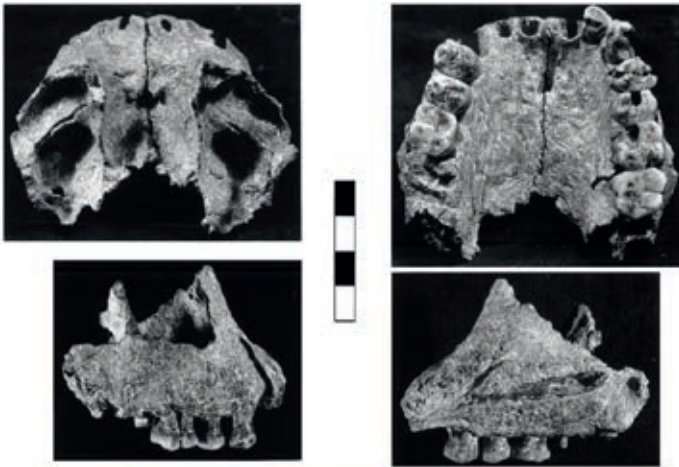


Figure 2. The maxilla A.L. 656-1. Clockwise from top left: superior, palatal, left medial, right lateral.

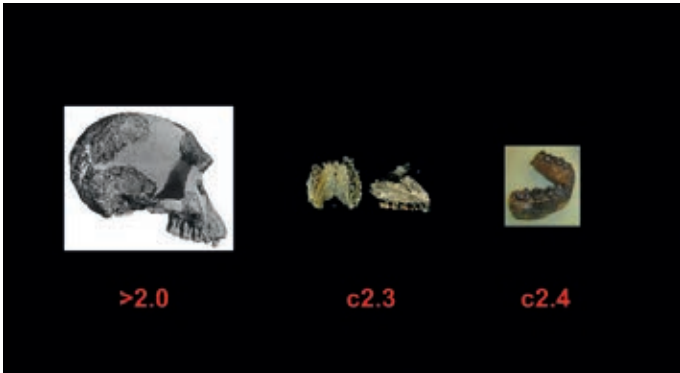
The maxilla of A.L. 666. Figure from Kimbel et al 1996 Late Pliocene Homo and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. Journal of Human Evolution 31: 549–561.

Secondly, and perhaps more important than the provenance of the specimen which perhaps we must take at face value, the completeness of the *Australopithecus sediba* material illustrates to us some very important lessons about what questions we may address using isolated, and often fragmented areas of anatomy in fossils, and those which we should not.

To illustrate this important point, if, in almost any area of critical anatomy, my colleagues and I had tried to use an individual element or complex to determine the genus of *Australopithecus sediba*, we might very well have come up with very different conclusions than we did at the time. This is true of even the maxillary-dental complex. As I mentioned earlier, many colleagues have put forward differing interpretations to those of our original studies, with a significant number of scientists arguing that *sediba*

should in fact rather be placed within the genus *Homo*. Without belaboring the details of these arguments, the fact now stands that the Malapa hominins demonstrate that *we cannot use at least some isolated areas of anatomy – such as the maxilla – in isolation, specifically to answer questions about the generic attribution of a particular specimen*. Put simply, if the generic position of *sediba* is in question based upon a myriad of anatomical areas that are well preserved, how can we begin to ask such a complex question of a single maxilla like A.L. 666?

It is now clear to me, that we as a field must move towards a more holistic anatomical approach to answer such taxonomic questions, in conjunction with contextual approaches that clearly acknowledge both the strength and weaknesses of the geological context of any given specimen. *Sediba* has clearly demonstrated to us that dentitions, other parts of the structures associated with mastication and many areas of the postcranial skeleton are quite simply not suitable for asking questions of this nature, no matter how many shared derived features they contain. It is thus in my opinion not unreasonable to apply such a conservative approach as my colleagues and I have to the study of *sediba*, to any early hominin species until fossils of a certain completeness prove otherwise. This does not in any way mean that there are not meaningful questions to be answered by these isolated and often fragmentary finds, it is simply that we now recognize certain questions that cannot be answered by these finds outside of extraordinary context.



Three candidate fossils for the earliest member of the genus Homo. Left to right Stw-53 suggested to be around 2 million years old; A.L. 666 suggested to be around 2.3 million years old (image is the palate in two views); and UR 501 from Malawi, suggested to be around 2.4 million years in age. Composite image created by the author from internet sources.

Additionally, I would like to make the point that the simple fact that a fossil – such as AL 666 – has been accepted as being assigned to a certain taxon for many years, does not mean that new evidence should not be taken into account regarding existing interpretations. To repeat my earlier comments, extraordinary claims require extraordinary evidence and even more to this point – nostalgia is not evidence. A.L. 666 at the time of its discovery was extraordinary. In the light of a myriad of new, more complete, better provenanced finds – such as those of *Australopithecus sediba* from Malapa – it is no longer so extraordinary in its completeness nor context, and thus is insufficient in and of itself to be used with definitive reference to the question of the origins of the genus *Homo*.

The isolated mandible UR 501 from Malawi has also been put forward as a good candidate ancestor for the genus *Homo*. Found on the surface next to Lake Malawi and dated using fauna also

found on the surface in nearby deposits, it too suffers many of the same problems as presented by A.L. 666 when applied to the question of the origins of the genus *Homo*. In fact, its context and anatomy might be considered more in question. It is after all a surface find, from a lacustrine deposit, and it is dated only by faunal comparisons to a purported 2.4 million years ago. The use of an isolated mandible to assign generic association has been clearly drawn into question by the constellation of morphologies found in *Australopithecus sediba* and other finds, and the derived nature of *sediba*'s mandibular and dental morphology. In fact, as a point of illustration, the *sediba* mandible, at least that of the female specimen, is practically indistinguishable from derived members of the genus *Homo* such as *Homo erectus*. Thus, again demonstrating that this area of anatomy, in isolation, should not be used to ask questions of higher order taxonomy. Thus the U.R. 501 mandible also, therefore quite simply does not meet the criteria of extraordinary evidence with reference to the question of whether it represents the earliest member of the genus *Homo*.



The UR 501 mandible from Malawi. Photo by Gerbil licensed under Creative Commons http://commons.wikimedia.org/wiki/File:HPCR-UR_501-01.jpg

Finally there are the series of fossils presently lumped into the taxon *Homo rudolfensis*. Chief among these is the fragmentary skull KNMER 1470. This specimen has been taxonomically controversial since its discovery. It may be hard to imagine, but the KNM-ER 1470 skull has varyingly been assigned to *Homo* species indeterminate, the genus *Paranthropus* aff, *Australopithecus africanus*, *Homo habilis* and finally *Homo rudolfensis*, its presently most popular taxonomic affiliation. It should be clear from this list, that the fragmentary nature of the fossil itself and the resultant varying reconstructions of its actual form, are in part responsible for such a diversity of opinions on its taxonomy. Additionally, as Bernard Wood has noted, the presence and degree of sexual dimorphism in early *Homo* can and will greatly influence with what taxon KNM-ER 1470 is associated with. That is, we don't know whether early *Homo* is highly sexually dimorphic or not, and thus we don't know whether 1470 is a big female or a small male of whatever taxon it actually belongs to. Unfortunately, KNM-ER 1470 also lacks dentition, preserving only the roots, thus we get no real glimpse of even this critical area of anatomy. I am not, however, doubting the present consensus that 1470 is in fact representative of the genus *Homo*, I am simply pointing out the difficulty of using specimens even of this nature for solving vexing taxonomic questions.



KNM-ER 1470 and the KNM-ER 60000 mandible purportedly representing Homo rudolfensis. Image by Fred Spoor.

More recently some colleagues have attempted to associate other specimens found in both Kenya, and in Tanzania with 1470 (such as the KNM-ER 60000 mandible) to make arguments about the variability in *Homo rudolfensis* (Leakey et al. 2012). While I acknowledge it is tempting to impose the morphology of such similar sized specimens found around similar temporal periods to the same morphology as 1470, and thus the same taxon, I would caution that such an exercise could result in false associations, and such an exercise is thus, in my opinion, simply not worth the risk in light of the ever growing fossil record. We should perhaps, as a field, exercise greater caution in attributing isolated remains with species until better, or more complete skeletons of certain taxa come to light – something that exploration will I have no doubt solve over the course of time.

Given the proposed near temporal contemporaneity of *Australopithecus sediba* and KNM-ER 1470, it is fascinating to note the many differences in the crania of *Australopithecus sediba* and the KNM-ER 1470 cranium, even given their great disparity in preservation. Such areas of anatomy such as endocranial volume, facial shape and dental root form and size, as well as simply overall size, show these two species to be very different from each other. That both hominin species – whatever species KNMER-1470 represents – exhibit a number of derived traits of the genus *Homo*, yet barely share any of the *same* derived traits is in my opinion remarkable. Whether these intriguing differences are demonstrating the reality of homoplasy in hominins in this critical time period, or they are in fact questioning the temporal context proposed for KNMER-1470 and the other surface finds associated with this genus, will only be answered by better preserved finds found *in-situ* and preferably in association with partial skeletons.

To some observers, I realize that it will surely appear that the KNM-ER 1470 cranium has significantly more derived features than *Australopithecus sediba*, or at least more “important” derived features, as we have spent more than 80 years of our science concentrating on largely the cranium and dentitions as our chief diagnostic tools for assessing taxonomy in early hominins. Using only the heads, one might reasonably question whether the morphology seen in *sediba* represents a suitable ancestral form that could give rise to a morphology like KNM-ER 1470. The answer to this, unfortunately, probably awaits both the discovery of earlier specimens of *Australopithecus sediba* and/or better preserved cranial and post-cranial remains associated with the KNM-ER 1470 morphs from East Africa.

In summary, at first glance *Australopithecus sediba* appears to add despairing complexity to our present understanding of the emergence of early *Homo* by adding yet another species, this time with an unexpected mosaic of primitive and derived characters, to what we thought we knew of the experiments occurring between the last australopiths and the first definitive members

of the genus *Homo* somewhere around 2 million years ago. *Homo habilis* and *Homo rudolfensis* both appear to show a trend in encephalization without the frontal complexity seen in *Australopithecus sediba*, as well as a retention of the general megadentia seen in many late australopiths, as well as, at least in the case of *Homo habilis*, retention of more primitive australopith aspects in its post-cranial anatomy, surprisingly *more* primitive in some areas than that observed in *sediba*.

If however, we have been misled in the past five decades since the description of *Homo habilis* by a fragmentary and poorly contextualized fossil record into developing a hypothesized evolutionary scenario that was simply incorrect, then the picture may not be as complex as it first seems. If *Australopithecus sediba*, or a species very much like it, arose out of an *Australopithecus africanus*-like species, or even if *sediba* stems from an even earlier branching from an at present unrecognized australopithecine and gives rise directly to early *Homo*, then *Australopithecus sediba* is not morphologically far from a plausible candidate ancestor of the genus *Homo*, having already acquired a great many of the most complex functional areas and adaptations usually considered critical to our genus. Furthermore, if one removes from this debate fossils representing isolated areas of anatomy that are now shown to be of low taxonomic value, as well as removing from the debate fossils from poorly contextualized situations – such as surface finds – there is very little left but the fossils from Malapa to consider prior to 1.9 million years ago.

It would be in this situation that *sediba* might be seen as simply an ancestor of the later encephalized forms presently attributed to two separate but poorly known species within the genus *Homo* – *Homo habilis* and *Homo rudolfensis*. Alternatively, it may be that we have simply mixed both australopiths and early *Homo* specimens – due to their fragmentary nature – together into *Homo habilis* and/or *Homo rudolfensis*, and some, or all of the fossils presently assigned to these species might be better placed within the genus *Australopithecus*. This seemingly surprising idea

has in fact been suggested or endorsed by a wide range of colleagues over many years.

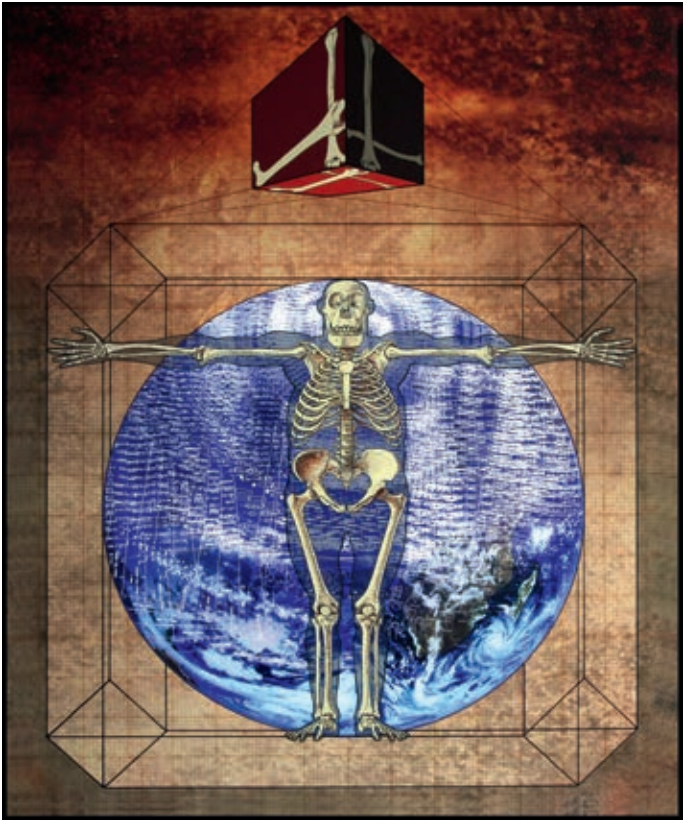
It may also be that *Australopithecus sediba* is simply the direct ancestor of *Homo erectus*, bypassing the need for including these other forms in the phylogeny leading to the origins of the genus *Homo*. In this latter case, invoking the near unsolvable argument that all shared-derived characters we see in these near contemporaneous forms of early hominin are simply homoplasy is unnecessary. Regardless of its actual phylogenetic position, it is probable that certain species once considered as potential candidate ancestors of the genus *Homo* are simply too derived in their morphology to be now considered ancestral to our lineage.



The face of Karabo, a juvenile male and the Holotype of Australopithecus sediba. From National Geographic, reconstruction by John Gurche.

Given what I have presented here, I hope you have understood why my colleagues and I suggest that at the very least, *Australopithecus sediba*, should be considered as likely a candidate ancestor for the earliest members of the genus *Homo* as any other presently available fossil species, or individual fossil specimen – and perhaps the best candidate. This is regardless of whether *Australopithecus sediba* fits our pre-conceived ideas of what that ancestor should look like, these pre-conceptions largely being based upon what I hope you now see is an extremely fragmentary fossil record that I have shown you some examples of, as well as a large number of fossils from poor geological and chronological context.

Despite the now recognized limitations that *Australopithecus sediba* places upon the use of certain fragmentary areas of the anatomy of fossil hominins when dealing with questions of generic and possibly specific associations, we face, in my opinion, an exciting period in palaeoanthropology. Practically never before have we seen more associated remains being discovered, in good context, so rapidly from across the continent. Improved absolute dating methods and excavation techniques are allowing us to now contextualize these finds, particularly in the South African context, in a way not possible even just a few years ago.



Vitruvian sediba – art by John Gurche.

With the largesse of these recent, more complete finds however, must come the recognition that we now understand the greater complexity in the anatomy of early hominins and that we must be cautious in what questions we ask of certain aspects of the often fragmentary hominin fossil record. The remarkable skeletons of *Australopithecus sediba* from Malapa clearly demonstrate that we may still find surprising and often unpredicted mosaicism in early hominin anatomy, and this should breed caution and con-

servatism in our interpretations and analyses, particularly when it comes to the interpretation of more fragmentary remains. This situation will of course improve as more, and more complete fossils are discovered for each species of early hominin, in different temporal ranges, and in varying geographical areas of the World. I hope that you realize that the situation we find ourselves in at present in palaeoanthropology is not one of despair in the face of an unsortable mess of fossil fragments, but one with an expanding record of better and better preserved specimens. I believe these most recent discoveries, of which Malapa is just a single example, should be viewed as a clarion call for more exploration and more excavations, and the discovery of more and better fossils in good context.

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