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# *Australopithecus sediba* and the earliest origins of the genus *Homo**

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**Summary -** *Discovered in 2008, the site of Malapa has yielded a remarkable assemblage of early hominin remains attributed to the species* Australopithecus sediba. *The species shows unexpected and unpredicted mosaicism in its anatomy. Several commentators have questioned the specific status of* Au. sediba *arguing that it does not exceed the variation of* Au. africanus. *This opinion however, does not take into account that* Au. sediba *differs from* Au. africanus *in both craniodental and postcranial characters to a greater degree than* Au.africanus *differs from* Au. afarensis *in these same characters.* Au. sediba *has also been questioned as a potential ancestor of the genus* Homo *due to the perception that earlier specimens of the genus have been found than the c198 Ma date of the Malapa sample. This opinion however, does not take into account either the poor condition of these fossils, as well as the numerous problems with both the criteria used to associate them with the genus* Homo*, nor the questionable provenance of each of these specimens. This argument also does not acknowledge that Malapa is almost certainly not the first chronological appearance of* Au. sediba*, it is only the first known fossil occurrence.* Au. sediba *should therefore be considered a strong potential candidate ancestor of the genus* Homo *until better preserved specimens are discovered that would refute such a hypothesis.*

**Keywords -** *Hominin, Malapa,* Homo ancestor*, Human evolution,* Australopithecus sediba.

## Introduction

The site of Malapa (site U.W. 88: Zipfel & Berger, 2010) 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 1.977-1.98 million years ago (Ma) (Pickering *et al.*, 2011), it contains a number of associated skeletal remains of several individuals, all ascribed to the newly recognized species *Australopithecus sediba*. These remains are found alongside an abundant, well preserved fauna (Dirks *et al.*, 2010; Kuhn *et al.*, 2011) and flora (Bamford *et al.*, 2010) . The hominin skeletons of Malapa preserve critical areas of anatomy that have, in many cases, not been seen in such completeness, or lacking distortion, in the whole of the early hominin fossil record (Berger *et al.*, 2010; Kibii *et al.*, 2011; Carlson *et al.*, 2011; Kivell *et al.*, 2011; Zipfel *et al.*, 2011). Remarkably, it appears that the entirety of this well-preserved material was accumulated during a seemingly rapid depositional event that occurred over a few days, weeks or months (Dirks *et al.*, 2010; Pickering *et al.,* 2011).

The site of Malapa was first discovered by the author 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, South Africa (Fig. 1). The locality was recognized as a de-roofed cave of at least 25 x 20 meters, in an area where limited limestone 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.

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* Lecture presented at the International Meeting *"Many Times Homo"*, Rome 2011.

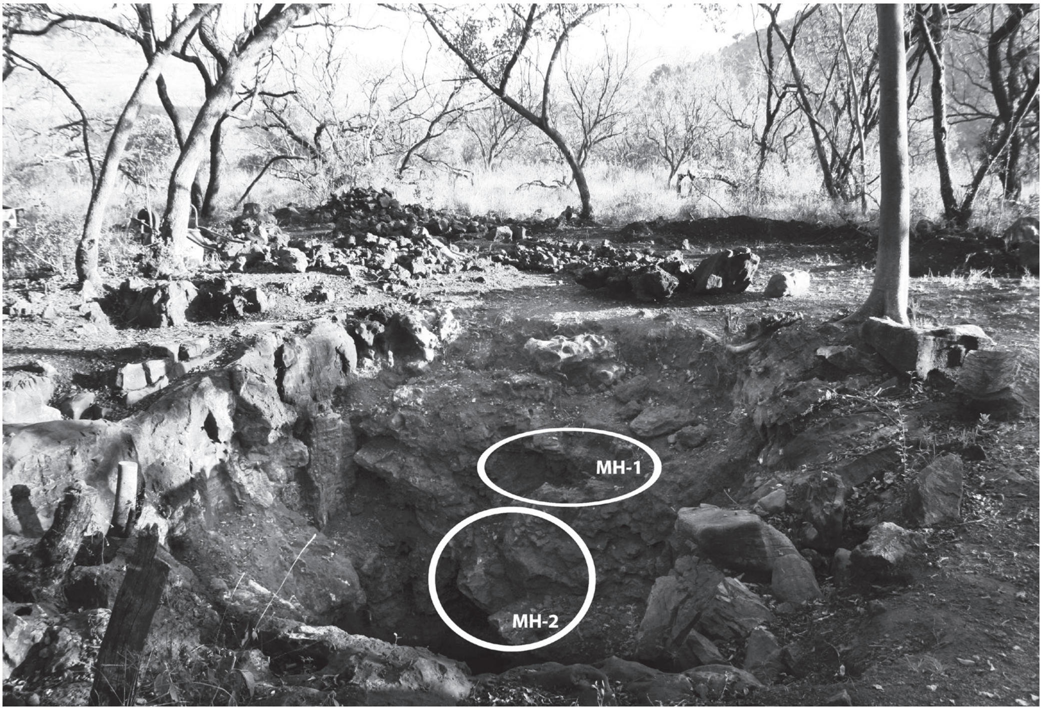

***Fig. 1 - The Malapa site in early 2009. The circled areas indicate the approximate position of discovery of MH-1 and MH-2 as labelled. By the time this photo was taken, some trees and grass have been removed from in and around the main pit. Note the loose blocks being collected for transport to the laboratory for processing. These blocks had been removed from their* in-situ *position by late 19th or early 20th Century mining activities and are not in their original positions.***

On the 15th of August 2008, upon the author's initial return to the site to investigate its fossil-bearing potential, the first hominin specimens were discovered by the author's son, Matthew. In the following weeks and months it was recognized that the site had significant potential, as additional hominin fossils were encountered, including the discovery by the author, on September 4, 2008, of a second, well-preserved adult partial skeleton and two associated maxillary teeth (MH2). These latter specimens were importantly found *in situ* in the calcified clastic sediments of the mining pit, thus giving precise location to the remains and leading to the discovery of the *in-situ* location of MH1 (Fig. 2). Removal of the block containing MH2 took place in late 2008, and preparation of the specimen revealed a partially articulated upper limb, including most of the right scapula, the lateral half of the right clavicle, parts of the thorax, and lower limb elements. During the course of recovery of *ex-situ* material from the site, the remaining parts of the adult right scapula and clavicle were found in a block that also contained the adult's mandible. The articulation between the scapula pieces, clearly allowed a direct association of these elements. Thus by early 2009 it had become clear that we were dealing with at least two partial skeletons and possibly more individuals represented by other fragmentary remains. These skeletons showed little damage other than a moderate amount of breakage, due primarily to damage from mining blasts, a small amount of taphonomic damage from insects and additional damage that likely occurred in a massive debris or mass mud flow as the skeletons were transported a short distance to their final resting place. There

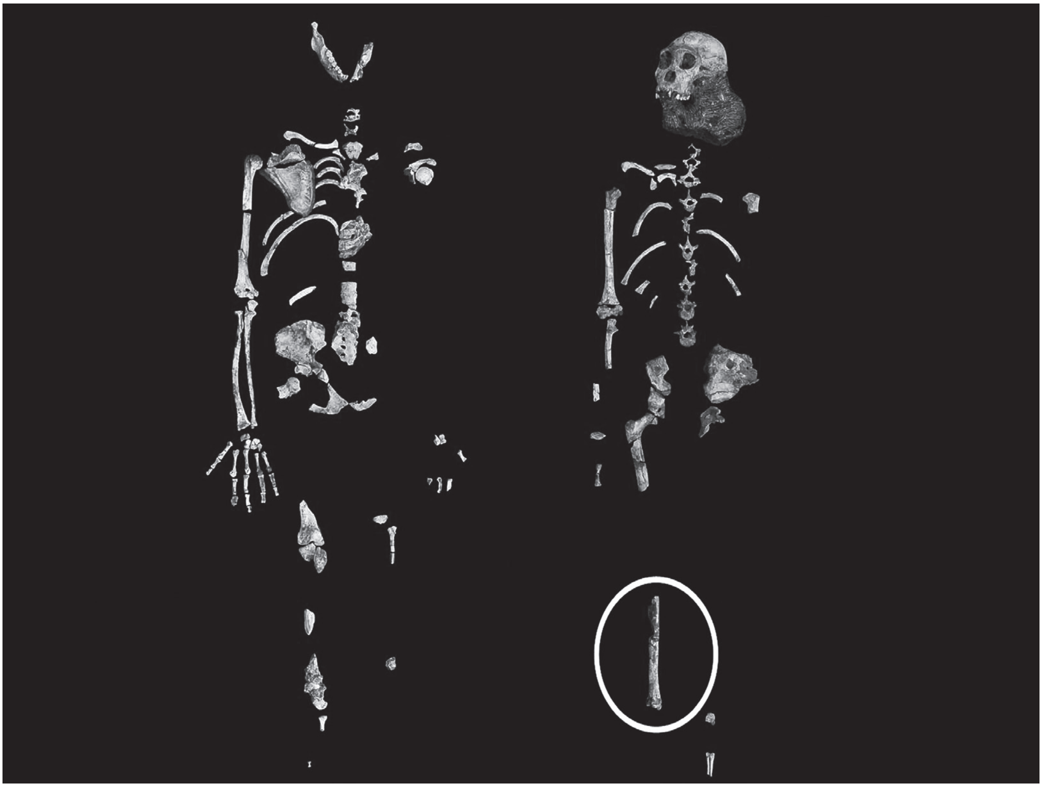

***Fig. 2 - The skeletons of MH-1 (right) and MH-2. The circled tibia is now attributed to another individual other than the Holotype skeleton. Photo courtesy of the author, adapted from an image created by Brent Stirton for National Geographic Magazine and Getty Images.***

is additionally some apparent perimortem trauma to a small number of elements, this damage being presently under study.

In February of 2009, the author discovered a block containing the diaphysis of the humerus of MH1, and during the course of preparation of this specimen, the well preserved partial cranium and several other postcranial elements were discovered in articulation or near articulation. This discovery allowed us to reassemble a significant part of the head and body of the juvenile MH1. Continued preparation of the adult MH2 skeleton revealed it to be very intact as well. Additional parts of the juvenile cranium and skeleton were discovered in the course of cleaning operations of the surface of the Malapa deposit, allowing us to confidently control the exact location from where the specimens were originally situated within the site and also associate additional elements with these, and other individuals.

Over the course of the past three and a half years, our team has conducted a number of analyses of this material and in 2009/10 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*, and we chronologically placed it within the temporal range of 1.78 – 1.95 Ma (Berger *et al.*, 2010) based upon geological and geochronological evidence available at that time. Additional material has recently been described including some of the most complete early hominin remains yet from the African fossil record, all attributed by us to this new species. Additionally, further studies of the geology of the Malapa deposit, from where the fossil hominins originate, have allowed us to refine the date of the depositional event to a slightly older 1.977-1.98 Ma (Pickering *et al.*, 2011).

With the recent publication of significantly more elements, and more detailed studies of these fossils, it is clear that *Au. 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* (Berger *et al.*, 2010; Carlson *et al.*, 2011). Post-cranially, *Au. sediba* continues 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 (Kivell *et al.*, 2011), a more derived pelvic structure (Kibii *et al.*, 2011) and aspects of the foot and ankle that are both surprisingly primitive, as well as surprisingly derived (Zipfel *et al.*, 2011).

## Is *Au. sediba* distinct species from *Au. africanus*?

In the initial publication of this material (Berger *et al.*, 2010), my colleagues and I suggested that *Au. sediba* was most probably derived from *Au. africanus* via a cladogenetic event, or that it might represent some form of anagenetic lineage from a species not dissimilar to *Au. africanus*, although one probably less megadent. Cladistically, *Au. sediba* forms a stem group of *Homo* based upon craniodental characters (Fig. 3). As we have discussed (Berger *et al.*, 2010; Pickering *et al.*, 2011), anatomical support for a cladogenetic interpretation comes from the constellation of *Homo*-like characters in *Au. sediba,* which appear directly alongside its *Australopith*-like traits. This mosaicism places *Au. sediba* outside the range of variability seen in the whole of the *Au. africanus* samples, even though the *Au. africanus* samples derive from the four geographically disparate sites of Taung, Sterkfontein, Gladysvale (Berger *et al.*, 1993) and Makapansgat. Even though *Au. sediba* is morphologically closest to *Au. africanus*, the derived appearance of aspects of the cranium and postcranium prevent inclusion of *Au. sediba* within the *Au. africanus* hypodigm (See appendix).

When 71 craniodental characters typically used for differentiating hominin fossil species are examined (see Berger *et al.*, 2010 for a list and description of 68 of these), *Au. sediba* differs from *Au. africanus* in 29 of these characters. By comparison, and as an anecdotal means of assessing the weight of these differences, *Au. africanus* can only be distinguished from *Au. afarensis* by only 16 of these 71 characters. Postcranially, *Au. sediba* differs from *Au. africanus* in at least 12 characters that are presently comparable between the Malapa and Sterkfontein/Makapansgat/Taung samples, all of which are critical morphological areas often discussed as being core to function and behavioural adaptation (see also Berger *et al.*, 2010, Kivell *et al.*, 2011; Kibii *et al.*, 2011; Zipfel *et al.*, 2011). Most critical among these are differences in hand and pelvic morphology, as well as some differences in the foot and ankle. In contrast, *Au. afarensis* and *Au. africanus* are broadly similar in these same dozen postcranial characters, the use of these postcranially characters being inadequate to separate these two species from each other.

It is additionally significant to note the importance *Au. sediba* exceeding the totality of *Au. africanus* variation in numerous craniodental and postcranial measurements (see Berger *et al.*, 2010, Kivell *et al.*, 2011; Kibii *et al.*, 2011 and Zipfel *et al.*, 2011 for detailed measurements), as the *Au. africanus* sample is already recognized for its extremely high diversity in shape and size, possibly even sampling more than one species (Clarke, 2008; Lockwood & Tobias, 2002). Given that *Au. sediba* exceeds the total known morphological diversity of the *Au. africanus* sample, yet is both temporally and geographically

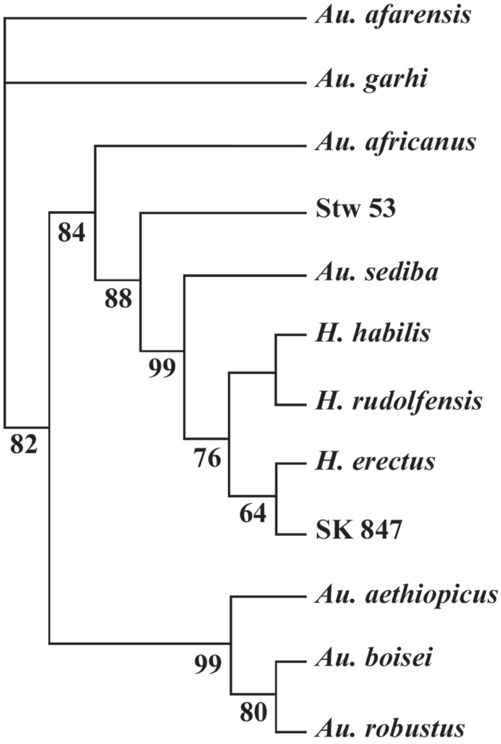

***Fig. 3 - Reproduced from Berger et al. (2010) Figure S3. The most parsimonious cladogram produced from the characters presented in Table 1, using PAUP 4.0 (beta version 10). Tree length is 128 steps if character states are unordered and multistate characters are treated as either uncertainties or as variable; tree length is 137 steps if character states are ordered and multistate characters are treated as either uncertainties or as variable; tree length is 165 if character states are unordered and multistate characters are treated as polymorphisms, and 175 steps if character states are ordered and multistate characters are treated as polymorphisms. When run with unordered character states, only one tree results; when run with ordered character states, two trees result: the one presented here, and another where KNM-ER 1470 resides with the*** **H. erectus*****/SK 847 clade. The consistency index is 0.672, the homoplasy index is 0.328, and the retention index is 0.744. Bootstrap numbers are based on 10000 replicates. As we noted in 2010, while it would be desirable to include post-cranial traits into this analysis, the inclusion of postcranial character states in the phylogenetic analysis would necessitate the exclusion of*** **H. rudolfensis** ***from the analysis. Also, the postcranial features that*** **Au. sediba** ***shares with*** **Homo** ***are found primarily in the os coxa, an element that is completely unrepresented in*** **H. habilis.** ***Taxonomic diagnoses and phylogenetic interpretations are generally based on craniodental remains, which necessitate such a focus even in taxa such as*** **Au. sediba** ***that preserve a more complete representation of the skeleton. This is not to say, however, that postcranial attributes cannot enlighten phylogenetic studies, and for these reasons the significance of the postcranial morphology of Malapa is discussed. What is important is that the postcranial remains support phylogenetic inferences derived from study of the craniodental material.***

closest to Sterkfontein, from which the largest and most diverse sample of *Au. africanus* comes, my colleagues and I have seen this as strong evidence for its unique specific status. As a result, our present interpretation is that although there are features shared between *Au. africanus* and *Au. sediba*, there are nonetheless more than enough sufficient differences to warrant separation between them, and in fact enough to confidently separate *Au. sediba* from all other known early hominin species.

At least one commentator has, however, suggested that *Au. sediba* is simply a chronospecies of *Au. africanus* (see the comments of T.D. White in Balter, 2010). This however, seems unlikely, given both the extremely short time period between the last known occurrence of *Au. africanus* (c. 2.1 Ma), and the date of Malapa at c1.98 Ma (Pickering *et al.*, 2011), and the many apparent retained primitive characters of the younger *Au. sediba*. The brief temporal separation alone between these two southern African geographically overlapping species would seem too short to accumulate the myriad of differences observed between the two species, particularly given the fewer differences observed between, for example, *Au.afarensis* and *Au. africanus*, given their presumably greater temporal and certain geographical separation.

Does however, such a high degree of variance between *Au. sediba* and the earlier australopiths indicate that it should rather be placed within the genus *Homo* as some commentators have suggested (Balter, 2010, 2011; Spoor, 2011)? My colleagues and I have, despite the numerous differences between *Au. sediba* and *Au. africanus*, and indeed between *Au. sediba* and all other australopiths, maintained the opinion that *Au. sediba* is better placed with the genus *Australopithecus*, rather than in the genus *Hom*o. One needs only to examine a comparably comprehensive list of characters that differentiate *Au. sediba* from *H. erectus* to note an equally significant number of differences craniodentally (at least 15 of the 71 characters used in the appendix differentiate the two taxa in the craniodental region (see also Table 1 in Berger *et al.*, 2010). *Au. sediba* also 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 *Au. sediba* and *H. erectus*. We therefore have concluded that the conservative approach is to maintain *Au. sediba* within the genus *Australopithecus* until such time as a definition of the genus *Homo* would be shown to encompass such rather critical (in this author's opinion) adaptive differences.

## The phylogenetic position of *Au. sediba*

Despite the shortcomings of the fossil record around 2 Ma, there are enough fossil hominin remains from East- and southern Africa to allow us to hypothesize as to the phylogenetic position of *Au. sediba*. As mentioned previously, based on presently available evidence, *Au. sediba* appears derived from *Au. africanus*, or something closely resembling at least the more gracile specimens attributed to this species. In turn, *Au. sediba* appears to share more derived characters with specimens assigned to specific fossils presently associated with early *Homo*, but more particularly with early *H. erectus* more so than any other candidate ancestor, including *Au. afarensis*, *Au. garhi*, or *Au. africanus*. In the initial announcement of *Au. sediba* (Berger *et al.*, 2010), my colleagues and I proposed four possible hypotheses regarding the phylogenetic position of *Au. sediba*: 1) *Au. sediba* is ancestral to *H. habilis*; 2) *Au. sediba* is ancestral to *H. rudolfensis*; 3) *Au. sediba* is ancestral to *H. erectus*; or 4) *Au. sediba* is a sister group to the ancestor of *Homo*. In an accompanying cladistic analysis in that paper, the most parsimonious cladogram placed *Au. sediba* as a stem taxon for the *Homo* clade comprised of *H. habilis*, *H. rudolfensis*, *H. erectus*, and SK 847 as an OTU (Berger *et al.*, 2010, supporting online material). Our cladogram was therefore consistent with our interpretations based on gross morphology and cranial and dental metrics. While we are presently continuing our analysis of the phylogenetic status of *Au. sediba* along numerous avenues of research that are focusing particularly on the comparative anatomy of the this species, there has been some discussion generated over the c1.98 Ma age of *Au. sediba* as seeming to exclude it chronologically from being considered a potential ancestor of the earliest members of the genus *Homo*. There appears to be a strong perception that there are substantially earlier, better candidate fossils that actually represent the earliest members of the genus *Homo* (Balter, 2010; Cherry, 2010) If this were so, then at least from a relatively simplistic view of anagenetic evolution, the *Au. sediba* fossils from Malapa could not give rise to the genus *Homo* as suggested by some commentators (see Balter, 2010, 2011; Spoor, 2011).

Is *Au. sediba* simply too late in time to be considered a candidate ancestor of the genus *Homo*? Firstly, such a view of the potential phylogenetic position of *Au. 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. Secondly, 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-provenienced evidence from Malapa.

## Candidates for the earliest evidence of the genus *Homo*

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*: Stw 53 from Sterkfontein (Hughes & Tobias, 1977), A.L. 666 from Ethiopia (Kimbel *et al.*, 1996; Kimbel & Rak, 1997) and U.R. 501 from Malawi (Schrenk *et al.*, 1993). Each of these fossils have, at one time or another, been said to exceed 2.1 Ma in age, with the latter two specimens purported to be between 2.3 and 2.4 Ma. More recently, re-dating of the Koobi-For a sequence has suggested an age for the 1470 cranium within error contemporary with *Au. sediba*, and thus this specimen becomes critical to the discussion as well.

*The case for Stw 53*

Stw 53 from Sterkfontein clearly has a bearing on this discussion as it has at times been referred to early *Homo* ever since its discovery in the 1970's (Hughes & Tobias, 1977). Derived from the "Stw 53 Infill" It has traditionally been thought to be over 2 Ma, but more recent work suggests an age as young as 1.78-1.43 Ma (Berger *et al.*, 2002; Herries *et al.*, 2009; Pickering & Kramers, 2010). Stw 53 was initially described as most probably belonging to early *Homo* (Hughes and Tobias, 1977), and this diagnosis soon came to be widely accepted (Cronin *et al.*, 1981; Wood, 1987, 1992; Curnoe & Tobias, 2006). Curnoe (2010) recently designated Stw 53 as the type specimen of a new species, "*H. gautengensis*"s, although as we have noted, there is little reason to consider the latter a valid taxon (Pickering *et al.*, 2011). Likewise, the attribution of Stw 53 to the genus *Homo* has been strongly challenged on both stratigraphic and anatomical grounds (Berger *et al.*, 2010; Clarke, 2008; Kuman & Clarke, 2000; Pickering *et al.*, 2011). It is important to note that both MH1 and Stw 53 are both facially small and endocranially small compared to most "early *Homo*". It is of course tempting to argue that Stw 53 is *Homo*, but diverges in some anatomical features because of its small size, but MH1 refutes such an argument, demonstrating that Stw 53 is more *africanus*-like in those features. The derived craniodental morphology of *Au. sediba* therefore raises further doubt regarding the attribution of Stw 53 to early *Homo*, as Stw 53 quite simply overall looks more *Au. africanus*-like relative to MH1, while MH1 looks more *Homo*-like relative to Stw 53. Thus, in summary, there is little evidence at present as to why Stw 53 should be considered as a candidate for the first evidence of the genus *Homo*, as it neither appears to exceed *Au. sediba* in chronological age, nor is it morphologically compatible with such an hypothesis.

*The case for A.L. 666*

Many scientists and commentators view A.L. 666, the purported 2.3 million year old fossil attributed to the genus *Homo* from Ethiopia, as the best single candidate for the earliest occurrence of the genus in Africa (Kimbel *et al.*, 1996; Kimbel & Rak, 1997; Kimbel, 2009;

Spoor, 2011). The specimen in question is a single, fragmentary maxilla. While my colleagues and I have extensively discussed this specimen (Pickering *et al.*, 2011), I would nevertheless like to reiterate the principle points of our arguments around the A.L. 666 maxilla and its validity in being considered the earliest fossil representing a member of the genus *Homo*.

As mentioned above, the claim to the first definitive fossil evidence of the genus *Homo* is an extraordinary one and of great import. In this author's opinion, the A.L. 666 maxilla quite simply does not meet the criteria of extraordinary evidence for the following reasons: Firstly, It is an isolated surface find (Kimbel *et al.*, 1996; Kimbel & Rak, 1997). Like many of the fossils from the lacustrian environments of East Africa, 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 the same 2.3 Ma horizon. 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 - and it is in question.

Secondly, the completeness of the *Au. 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. 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 *Au. sediba*, we might very well have come up with very different conclusions than we did. This is true of even the maxillary-dental complex. In fact, many colleagues have put forward differing interpretations to those of our original studies, with a significant number of scientists arguing that *Au. sediba* should in fact be placed within the genus *Homo* (e.g. Balter, 2010). 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, to answer questions about the generic association of a particular specimen. It is clear that we as a field must now turn to a more holistic anatomical approach to answer such questions, in conjunction with contextual approaches that clearly acknowledge both the strength and weaknesses of the geological context of any given specimen. *Au sediba* has clearly demonstrated to us that dentitions, other parts of the structures associated with mastication and many areas of the postcrania are quite simply not suitable for asking questions of this nature, no matter how many shared derived features they contain – at least in *Au. sediba's* lineage - and it is thus not unreasonable to apply such a conservative approach as we have 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.

Thirdly, the simple fact that a fossil has been accepted as being assigned to a certain taxa 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. A.L. 666 at the time of its discovery was extraordinary. In the light of a myriad of new, more complete, better provenienced finds – such as those of *Au. sediba* from Malapa - it is no longer so extraordinary in its completeness nor context and is insufficient in and of itself to be used with reference to the question of the origins of the genus *Homo*. *Au. sediba* now demonstrates limitations we did not previously know existed - limitations on the use of isolated area of anatomy with no associated postcranial elements to address the complex question of the presence or absence of the earliest member of the genus *Homo*.

### *The case for U.R. 501*

The isolated mandible UR 501 suffers many of the same issues as 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 a surface find, from a lacustrian deposit, and it is dated only by faunal comparisons to a purported 2.4 Ma (Schrenk *et al.*, 1993). The use of an isolated mandible to assign generic association has been clearly drawn into question by the constellation of morphologies found in *Au. sediba*, and the derived nature of *Au. sediba's* mandibular and dental morphology. It also, therefore does not meet the criteria of extraordinary evidence in the question of the earliest member of the genus *Homo*.

### *KNM_ER 1470*

Taxonomically controversial since its discovery, the KNM-ER 1470 has varying been assigned to *Homo sp*. (Leakey, 1973; Wood, 1976), *Paranthropus aff.* (Walker, 1980; Rak, 1987; Wood, 1991), *Australopithecus africanus* (Krantz, 1990), *H. habilis* (Leakey, 1976a, b; Walker & Leakey, 1978; Howell, 1978; White *et al.*, 1981; Tobias, 1991) and *Homo rudolfensis* (Alexeev, 1986; Wood, 1992) among others. It is 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 taxonomy. Additionally, as Wood (1991) 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. Grine *et al.* (1996) adequately review many of these debates around this specimen, and pay particular attention to the significant differences in size and shape between KNM-ER 1470 and all other early *Homo* crania. Unfortunately, KNM-ER 1470 also lacks dentition, preserving only the roots, thus we get no real glimpse of this critical area of anatomy, and while it is of course tempting to impose the morphology of such similar sized specimens as the OH-65 palate, with its relatively small dentition and larger roots, to the same morphology and thus taxon, such an exercise could result in false associations, particularly now that the KNM-ER 1470 cranium is dated to several hundred thousand years older than the Olduvai specimen.

Given the near temporal contemporaneity of *Au. sediba* and KNM-ER 1470, it is fascinating to note the many differences in the crania of *Au. 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. 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. This is, to say the least, surprising and a strong argument for the reality of homoplasy in hominins in this critical time period.

To some observers, it will surely appear that the KNM-ER 1470 cranium has significantly more derived features than *Au. sediba*, or at least more "important" derived features, and thus the question must be raised in the light of these, could the morphology seen in *Au. sediba* represent 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 *Au. sediba* and/or better preserved cranial and post-cranial remains associated with the KNM-ER 1470 morphs.

## Conclusions

At first glance *Au. 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 knew of the experiments occurring between the last australopiths and the first definitive members of the genus *Homo* (c2.0 Ma). *H. habilis* and *H. rudolfensis* both appear to show a trend in encephalization without the frontal complexity seen in *Au. sediba*, as well as a retention of the general megadentia seen in many late Australopiths (albeit with a few notable exceptions), as well as, at least in the case of *H. habilis*, retention of more primitive australopith aspects in its post-cranial anatomy, more primitive in some areas than that observed in *Au. sediba*. If however, we have been mislead in the past four decades by a fragmentary and poorly contextualized fossil record around 2 Ma, into developing a hypothesized evolutionary scenario that was simply incorrect, then the picture may not be as complex as it first seems. If *Au. sediba*, or a species very much like it, arose out of an *Au. africanus*-like species (or stems from an even earlier branching from a gracile australopithecine) and gives rise directly to early *Homo*, or through an intermediary species such as *H. georgicus*, then *Au. 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, there is very little left but the fossils from Malapa to consider prior to 1.9 ma. It would be in this situation that *Au. 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*. Alternatively, it may be that we have simply mixed both Australopiths and early *Homo* specimens - due to their fragmentary nature - together into *H. habilis* and/or *H. rudolfensis,* and some, or all of the fossils presently assigned to these species might be better placed within the genus *Australopithecus* (e.g Wood & Collard, 1999). It may also be that *Au. sediba* is simply the direct ancestor of *H. 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. In particular, with *Au. ghari*'s very derived hyper robust-australopithecine-like craniodental morphology, this species now appears a very unlikely candidate as an ancestor to the genus *Homo*, or *Au. sediba* itself.

Given the above, at the very least, *Au. 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 *Au. sediba* fits our pre-conceived ideas of what that ancestor should look like, these pre-conceptions largely being based upon the extremely fragmentary fossil record discussed above, as well as a large number of fossils from poor geological and chronological contexts

Despite the now recognized limitations that *Au. 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 an exciting period in palaeoanthropology. Practically never before have we seen more associated remains being discovered, in good context, so rapidly. Improved absolute dating methods and excavation techniques are allowing us to contextualize these finds, particularly in the South African context, in a way not possible even a few years ago. 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 record. The remarkable skeletons of *Au. 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 conservatism 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. The situation we find ourselves in at present is not one of despair, but is a clarion call for more exploration and excavation, and the discovery of more and better fossils in good context.

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***Appendix - A point by point comparison of anatomical/character differentiation between*** **Au. sediba** ***and*** **Au. Africanus*****, sensu lato* based on fossils published to date. 71 craniodental characters typically used to distinguish early hominin species were used. Only characters that show variance between*** **Au. africanus** ***and*** **Au. sediba** ***are listed below. In addition, 12 postcranial characters where variance between*** **Au. sediba** ***and*** **Au. africanus** ***is known are listed in this table. For a detailed description of the entirety of the craniodental character list, see Table 1 in Berger*** **et al.** ***(2010).*** **Au. sediba** ***differs from*** **Au. africanus** ***in 29 of the 71 craniodental characters examined.*** **As a comparison, Au. africanus** ***only differs from*** **Au. afarensis** ***in 16 of these same characters (see Table 1 in Berger et al., 2010).*** **Au. africanus** ***and*** **Au. afarensis** ***are similar in all 12 of the post-cranial characters listed that differentiate*** **Au. sediba** ***from the earlier australopith forms.***

| | *AU. SEDIBA* | *AU. AFRICANUS* |
|---|---|---|
| **CRANIAL CHARACTERS** | | |
| Cranial surface morphology | derived** | primitive*** |
| A-M incursion of temporal lines on frontal bone | weak | moderate |
| Temporal lines | wide | cresting/close |
| Postorbital constriction | slight | moderate |
| Pneumatization of temporal squama | reduced | extensive |
| Horizontal distance between TMJ and M2/M3 | short | long |
| Facial prognathism | reduced | moderate to pronounced |
| Parietal transverse expansion/tuber | present | absent |
| Surpraorbital expression | torus | intermediate |
| Nasal bone projection above frontomaxillary Suture | variable | no |
| Eversion of superior nasal aperture margin | slight | none |
| Expansion of frontal process of zygomatic bone | medial | medial and lateral |
| Angular indentation of lateral orbital margin | curved | indented |
| Zygomatic prominence development | slight | prominent |
| Lateral flaring of zygomatic arches | slight | marked |
| Outline of superior facial mask | squared | tapered |
| Infraorbital plate angle relative to alveolar plane | right | obtuse |
| Orientation of mandibular symphysis | vertical | receding |
| Post-incisive planum | weak | prominent |
| Post-canine crown Area | small | large |
| Overall dental size | reduced | enlarged |
| Canine size | reduced | moderate to large |
| Maxillary C development of lingual ridges | weak | marked |

***Appendix - continued.***

| | ***AU. SEDIBA*** | ***AU. AFRICANUS*** |
|---|---|---|
| Presence of accessory canine cusp | absent | present |
| Maxillary premolar molarization | weak | minor/marked |
| Maxillary premolars: buccal grooves | weak | marked |
| Median lingual ridge of mandibular canine | weak | prominent |
| Protoconid/metaconid More mesial cusp (molars) | protoconid | equal |
| **Post-Cranial Characters** | | |
| Brachial index | high | moderate/high**** |
| Phalangeal curvature | low | moderate/high |
| Phalangeal length | derived | primitive |
| Iliac flaring | derived | primitive |
| Weight transfer distance from sacroiliac to hip | derived | primitive |
| Expansion of retroarticular surface of ilium | expanded | reduced |
| Narrowing of the tuberoacetabular sulcus | narrowed | expanded |
| Expansion of the acetabulocristal sulcus | derived | primitive |
| Expansion of the acetobulosacral buttresses | derived | primitive |
| Femoral head size | moderate | moderate/small |
| Cross sectional properties of limbs | derived | primitive |
| Calcaneal morphology | ape-like***** | derived |

**Au. africnaus sensu lato* refers to all specimens presently assigned to the species *Au. africanus* from Sterkfontein (Member 4), Taung and Makapansgat (Members 3 & 4). It does not take into account the potential that more than one species exists within these assemblages. In this way, the entirety of the variability of the assemblages is taken into account without biasing the assemblage towards larger or smaller morphs and hopefully therefore expresses the variability of this taxon's morphology through time and space.

** *Derived* here refers to morphology typically associated with later members of the genus Homo.

*** Primitive here refers to morphologies typically associated with fossil specimens typically assigned to either *Au. africanus, Au. afarensis* or *Au. anamensis* and is meant to reflect the condition typically to the genus "*Australopithecus*". For the purposes of the present discussion, the term does not include specimens typically associated with so called "robust" forms (*Paranthropus (Au.) boisei, P. (Au.) robustus* etc.).

**** Based upon estimated or incomplete fossil evidence preserved for this taxon.

**** Ape-like here refers to the condition seen most commonly *in P. paniscus* and *P. troglodytes*