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The post-cranial skeletal maturation of *Australopithecus sediba*

Noel Cameron^{1, 2}

Barry Bogin^{1, 2}

Debra Bolter^{2,3}

Lee R Berger²

¹Centre for Global Health and Human Development, School of Sport, Exercise and Health Sciences, Loughborough University, Loughborough, LE11 3TU, UK

² Evolutionary Studies Institute and Centre for Excellence in PalaeoSciences, University of the Witwatersrand, Johannesburg, South Africa, Private Bag 3, Wits 2050

³Department of Anthropology, Modesto Junior College, Modesto, CA 95350

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Correspondence to:

Noel Cameron
School of Sport, Exercise and Health Sciences
Loughborough University
Ashby Road
Loughborough
Leicestershire
LE11 3TU
UK
Email: N.Cameron@lboro.ac.uk

Abstract

The ontogeny of our immediate ancestors as evidenced by maturity indicators in the post-cranial skeleton is largely undescribed because of the paucity of such material that survives taphonomic processes. In 2008 an immature hominin of the taxon *Australopithecus sediba* was discovered at the 1.9 million year old Malapa site in South Africa. The specimen includes substantial post-cranial skeletal material, and provides a unique opportunity to study its skeletal maturation in comparison with other hominins. Maturity indicators observed on the proximal and distal humerus, proximal ulna, distal radius, 3rd metacarpal, ilium and ischium, proximal femur and calcaneus were used to assess the specific and general level of skeletal maturity of each bone in comparison to standards of skeletal maturity for modern humans and for chimpanzees (*Pan troglodytes*). In comparison to modern humans the maturational ages of available indicators for *Au. sediba* correspond to between 12.0 years and 15.0 years with a mean (SD) age of 13.1 (1.1) years. The degree of normal variation in skeletal maturation in modern humans from childhood onwards is generally taken as ± 2 years (SD ± 1.0 year). In comparison to the maturational pattern of chimpanzees the *Au. sediba* indicators suggest a maturational age of 9-11 years. Based on either of these skeletal maturity estimates and the body length at death of MH1, an adult height of 150-156cm is predicted. We suggest that the skeletal remains of MH1 are consistent with an ape-like pattern of maturity. This is based on the estimates of age at death for the Nariokotome *Homo erectus* remains (KMN-WT15000), which are of similar post-cranial maturity to MH1, and by currently available estimates of age at death for *Au. sediba* based on dental maturity.

1. Introduction

The ontogeny of our immediate ancestors is primarily known from analyses of cranial and dental material (Anton and Leigh, 2003; Kuykendall, 2003). Few specimens have been found that have associated craniodental and post-cranial bones and fewer still that are clearly specimens of immature individuals (Kelley and Bolter, 2013). The discovery of two skeletons at Malapa in South Africa in 2008 is thus of significance not only for the number and quality of preservation of the bones, but also for the fact that there are, in close stratigraphic and temporal proximity, both cranial and post-cranial remains of at least two individuals, one of whom is clearly immature. The description of these skeletons, classified as *Australopithecus sediba*, concluded that they share more derived features with early *Homo* than with any other australopithecine species and that they might, therefore, help reveal the ancestor of the genus *Homo* (Berger et al., 2010). The pattern of growth and development, and whether it reflects the more ancestral pattern found in apes, or whether it is more *Homo*-like, is of significance in understanding morphological evolution, the variation found in adult morphology, and the overall pattern of life stages. In particular, the tempo of maturation as opposed to velocity of somatic growth provides a foundation for interpreting life history strategies (Bogin and Smith, 2012). Growth relates specifically to changes in size and shape, whilst maturity specifically addresses the current appearance and/or function of an indicator and its proximity to adult form.

Humans extend the time for growth and delay the pace of maturation from weaning to adulthood (Bogin and Smith, 2012). In chimpanzees, maturation is not delayed in the same way (Bogin, 1999). Attempts in the 1960s and 1970s to determine the pattern of maturity in the craniodental skeleton of previously discovered australopithecines suggested that they demonstrated a prolonged “human-like” pattern of growth and development (Kuykendall, 2003). However, that position has since been modified and it is now generally accepted that both ape-like and human-like patterns of growth are to be found amongst early hominins. Very few studies have been undertaken on the postcranial skeleton. Berge (Berge, 1998, 2002) provided a comparative analysis of the pelves of juvenile and adult African apes (N=150), modern humans (N=60), and two adult pelves and a single juvenile hip of australopithecines (Sts 14, AL 288, MLD 7). She concluded that whilst some pelvic traits of adult *Australopithecus* resemble those of neonate humans, the pelvic growth of the former was “probably” closer to the apes. Tardieu (Tardieu, 1998) argues from analysis of the femur of modern humans and australopithecines that extended time for growth and lengthening of the lower limb was an essentially *Homo* trait and that the pedomorphic features of the femur of adult *Australopithecus afarensis* is evidence of its, essentially, ape-like pattern of growth.

Previous attempts to determine the ontogeny of early hominins are largely confined to the analysis of the dentition and post-cranial skeleton of KNM-WT 15000, the Nariokotome *Homo erectus*. Ruff and Walker (1993) estimated skeletal age from

the ossification status of the distal humerus and demonstrated that the medial epicondylar epiphysis was not fused at the time of death but the lateral epicondyle, trochlea, and capitulum were fused together and also partially fused to the humeral shaft. Smith (1993) and more recently Dean and Smith (2010) analysed the skeleton and dentition of the Turkana fossil and ascertained that, indeed, it is immature and most likely a male. Smith (1993) assessed the major ossification centres of the triradiate cartilage of the innominate and the long bone epiphyses (distal and proximal humerus, proximal femur, ankle, knee, wrist, shoulder). The epiphyses of the distal humerus had begun to fuse, but most of the other epiphyses remained unfused demonstrating that KNM-WT 15000 had probably initiated but not completed the stages of physical maturation associated with puberty (i.e., sexual maturation). Smith used the appearance of maturity indicators on the teeth and post-cranial bones to construct maturity scales on which the pattern profile of maturity could be compared to that of known references for humans, chimpanzees (*Pan troglodytes*) and macaques (*Macaca mulatta*). Her conclusions were that KNM-WT 15000 had a comparable pattern profile of maturity to apes.

This assessment was reaffirmed by Dean and Smith (2010), who added an analysis of dental microanatomy and newer information on chimpanzee skeletal maturation. They found that KNM-WT 15000 had a younger dental age, an older skeletal age and a larger body mass and stature than would be expected for a modern human. Dean and Smith placed KNM-WT 15000 firmly into the pubertal stage of maturation because the process of elbow joint ossification had begun, uniting some of the four elements of the distal humerus epiphysis, and by evidence that the shoulders had broadened. Based on a human maturity calibration, Dean and Smith estimated the skeletal age of Nariokotome at >12.5 but <15 years, and likely nearer the lower limit due to the lack of fusion of the remaining major long bone epiphyses. Their estimates of dental maturation, based on enamel microstructure, range from 7.5 to 10.2 years at the time of death for the Nariokotome youth. Dean and Smith conclude that Nariokotome, and perhaps all *Homo erectus*, followed a pattern of skeletal and dental maturation distinct from both living apes and modern humans, but, "...the most parsimonious explanation for this combination of facts is that the growth curve of early *Homo erectus* was more like that of modern chimpanzees" (p. 117).

The consensus of existing dental evidence suggests that *Australopithecus africanus* and *Au. afarensis* may have had a pattern of maturation more akin to chimpanzees than to modern humans (Kuykendall, 2003; Schwartz, 2012). Analysis of postcranial evidence from DIK-1-1, the infant *Au. afarensis* from Dikika, supports this ape-like pattern (Green and Alemseged, 2012). Based on development and locomotor loading of the scapula, the morphology and orientation of the scapular spine of this infant compared with adults of *Au. afarensis* demonstrate that the growth is more ape-like than human-like. Reconstructing skeletal maturity from epiphyseal fusions in DIK-1-1 is not possible as the individual died as an infant, before growth plates begin to fuse.

The *Au. sediba* MH1 remains from the Malapa site provides the first opportunity for assessment of the skeletal maturation of multiple regions of epiphyseal fusion from post-cranial material of any immature *Australopithecus* specimen. Analysis of these may add significant new evidence to the origins of the human pattern of growth and maturation and, perhaps, the genus *Homo*.

2. Method

The post-cranial bones of MH1 currently available for maturity assessment are the proximal and distal humerus, proximal ulna, distal radial epiphysis, 3rd metacarpal, ilium and ischium, proximal femur and the right calcaneal unfused epiphysis (Figure 1). Assessments were made on the originals and high quality casts, which are in all important characteristics essentially identical to the original fossil material. Size and shape of the bones and, where relevant, the degree of epiphyseal fusion, were the primary characteristics. These were compared to reference data for modern humans from Bass (Bass, 1971), Tanner et al (2001) for the distal radial epiphysis, and Hoerr, Pyle and Francis (1962) for the calcaneal epiphysis. The modern human data were obtained from radiographs of the living bones in individuals of known ages determined during longitudinal growth studies.

FIGURE 1 ABOUT HERE

Chimpanzee skeletal maturational stages are derived from the reference data of Bolter and Zihlman (2012) and Zihlman et al (2007). Maturation can vary by sex in apes and humans, with males slightly more delayed than females of comparable ages (Schultz, 1969; Bolter and Zihlman, 2003; Cameron and Jones, 2010). Here we use wild chimpanzee males for the comparison, as MH1 has been tentatively identified as a male on overall size, morphology and localized diet patterns (Sponheimer et al., 2011; de Ruiter et al., 2013). Additionally, the skeletal maturity of MH1 is slightly delayed compared to published data on female wild chimpanzees at a similar stage of dental eruption (Bolter and Zihlman, 2012).

The chimpanzee data used here are not equivalent to the human data. The chimpanzee data come from 10 cadaveric specimens of wild chimpanzees from Tai National Forest, Gombe Reserve, and one wild specimen from the Schultz Collection in Zurich. Whilst month and year of death were known for 7 specimens, birth dates were only known for 4 specimens; for 3 specimens age is unknown (Zihlman et al., 2004, 2007; Smith et al., 2010; Smith and Boesch, 2011). For the older sub-adult males from Tai and Gombe, year of birth was estimated by primate field workers when in first contact with these individuals (Goodall, 1986; Boesch and Boesch-Achermann, 2000). The chimpanzee skeletal maturity ages were determined using maturity indicators derived by forensic methods developed on human skeletons (Krogman and Iscan, 1986).

We stress here that comparison of human and chimpanzee maturity estimates for MH1 present difficulties of interpretation. The longitudinal nature of the human data

allows for the development of maturity indicators to be described as a continuous process from first appearance of an ossification centre to its adult maturity, e.g., epiphyseal fusion. The chimpanzee data, in contrast, describe only the degree of fusion - none, partial, or complete – as a discrete set of states. The maturity characteristics prior to fusion in chimps have not been described and therefore do not contribute significantly to age estimation apart from setting an upper limit to age. We attempt to overcome these difficulties by taking a conservative approach to interpretation of the findings.

3. Results

We present in Table 1 a description of each bone element used in the analysis, and we compare each maturity indicator to human references and estimate a likely skeletal age range. In Table 2 we compare wild male chimpanzee skeletal maturity markers with MH1.

TABLES 1 AND 2 HERE

In comparison to modern humans the maturational ages of available indicators for *Au. sediba* correspond to between 12.0 years and 15.0 years with a mean (SD) age of 13.1 (1.1) years (Table 1). In comparison to the maturational pattern of chimpanzees the *Au. sediba* indicators suggest a maturational age 9-11 years (Table 2).

4. Discussion

A previous study by Berger et al (2010) estimated age at death of the *Au. sediba* MH1 individual to be 12-13 years. This analysis was based on human references for the erupted M₂ and the global state of epiphyseal fusion. A recent study (Smith et al., 2015) on the microhistology and molar emergence of 20 *Australopithecus*, *Paranthropus* and South African early *Homo* immature fossils (but not MH1) reports that all had rates of crown formation that were similar to chimpanzees or intermediate between chimpanzees and modern humans. We consider it likely that MH1 had a rapid dental development pattern similar to these other Pliocene and Pleistocene hominins (Le Cabec et al., 2014).

The age range from the maturity indicators of the skeleton suggests an age at death for the MH1 individual between 9 years, based on chimpanzee references, and 13 years, based on human references. The results presented in the current analysis suggest that the skeletal maturation of MH1 demonstrates some synchrony with both human and chimpanzee reference data. However, the estimated dental age based on microhistology allies the maturity indicators better with an ape-like model. Moreover, a more chimpanzee-like skeletal maturation is consistent with the

literature on life history evolution of the Pliocene and Early Pleistocene Hominins (Dean and Smith, 2010; Schwartz, 2012; Smith et al., 2015). Synthesising all of this research with the present skeletal findings strongly suggest that *Au. sediba* followed the early hominin pattern of biological maturation, indicating that it matured faster than modern humans and had an age at death of between 9-11 years old.

It is clear that the methods employed here provide only very broad age ranges within which the actual age of the specimen may lie.

We have used the mid-age of the range applicable to any particular human or chimpanzee skeletal maturity indicator. It is quite possible that the real age may lie anywhere within the range. Maturational symmetry within the skeleton has long been assumed to be the normal human condition (Todd, 1937) and it would be unusual, and indicative of dysmorphology, for there to be dramatic differences between the status of maturity of different skeletal indicators. It seems reasonable to assume that similar levels of maturational symmetry are common to *Pan* and *Australopithecus*. Accordingly, if the real age of any single indicator were younger or older than our estimate, then all other indicators would likely move in the same direction.

Human skeletal maturation is significantly correlated with linear growth and with some events in sexual maturation. The correlation coefficients between skeletal development, peak height velocity, and menarche, for example, are generally between $r = +0.40$ and $+0.85$ (Demirjian et al., 1985). In contrast, a considerable degree of maturational asymmetry between skeletal and dental systems is widely recognised. One review finds that the correlation between dental and skeletal maturity in samples of healthy human children and youth are not statistically significant and range from -0.02 to $+0.37$ (Demirjian et al., 1985). The same review reports that in a sample of French Canadian girls ($n=50$), assessed annually between 6 and 15 years of age, the mean chronological age for the variable '90% complete dental development' was 9.99 years. The mean age for '75% skeletal development' was 10.39 years and the mean age for menarche was 12.91 years. Dental and skeletal maturation were not significantly associated ($r = +0.17$), but skeletal development and menarche were significantly related ($r = +0.40$).

This pattern of association and variation between maturity measures means that it is, perhaps, not unexpected that previous studies found asymmetry between dental and skeletal maturation of the Nariokotome *Homo erectus* (WT-15000) or those Neanderthal individuals with associated dental and post-cranial remains (Dean and Smith, 2010; Thompson and Nelson, 2011). It may also be that the dental age of *Au. sediba* (MH1) as assessed by tooth microstructure will be significantly lower than its skeletal age, as based on human references. Relatively early dental development is essential for food processing, and functional teeth must be in place to wean infants from lactation and feed them by the provision of food by older individuals. In modern humans, the eruption and occlusion of the first four permanent teeth (molar 1 and central incisors) is usually complete by age 7 years. Human infants are weaned by

age 3 years but their dental immaturity requires that they be provisioned with specially prepared complimentary foods until the functional occlusion of molar 1 and the central incisors (Sellen, 2007). Provisioning of complimentary foods usually diminishes greatly or ends at about age 7 years and consumption of the adult diet is common (Bogin, 1999). In chimpanzees, this key dietary transition occurs about 2 years earlier. Juvenile chimpanzees at Kanyawara site in Uganda have functional occlusion of maxillary and mandibular first permanent molars by about 3.5–4.0 years of age (Smith et al., 2013). However, they continue with some food intake by nursing for up to one year or more after this occlusion (Machanda et al., 2015). They then begin adult patterns of feeding which increases with age and additional permanent tooth eruption.

Skeletal development is more delayed in humans compared with chimpanzees. This is known from a longitudinal study of hand and wrist skeletal maturation of captive chimpanzees (*Pan troglodytes*) published by Hamada et al (2003). The median chronological age at skeletal maturity of captive chimpanzees was 10.6 years while that age for healthy human boys and girls is 15-16 years.

The Hamada et al analysis of maturity states is based on the 13 ossification centres of the RUS system (radius, ulna, and short bones of the hand). The RUS system of scoring skeletal maturation was developed by Tanner and colleagues (2001). Unfortunately, the Hamada et al RUS system cannot be used for the MH1 specimen as it lacks the required hand and wrist fossil remains. No similar system of assessing skeletal maturation of sites other than the wrist and hand exists for chimpanzees.

In the wild, chimpanzees mature at a slower pace than in captivity and the 5-6 year delay in skeletal maturation between species reported by Hamada et al is reduced to a 3-4 year delay (Zihlman et al., 2004; Smith and Boesch, 2011). In either case, the slower rate of human maturation compared with chimpanzees allows for the prolonged phases of childhood, juvenile, and adolescent growth. Relative to the chimpanzee, the human advance for dental maturity allows for food processing, while the delay for skeletal maturity allows for plasticity of growth and development. The human pattern of skeletal maturation underlies a greater accommodation of human phenotypes to environmental circumstances, which may result in greater survival of individuals and greater reproductive success of humans compared with any of the apes.

5. Implications for estimates of adult height

It is possible to predict adult stature of MH1 based on the percentage of his adult stature achieved at his level of skeletal maturity at death. Skeletal maturity and percentage adult stature are highly correlated in human children and youth (Tanner

et al., 1983; Beunen et al., 1997) with correlation coefficients ranging from +0.60 at 12.5-13.5 years to +0.88 at 15.5-16.5 years. A pattern of skeletal growth and development of *Au. sediba* based on human-like maturity of 12.5 years would predict ~80% of adult stature. Given the estimated 130cm body length of MH1, a final predicted height is ~156cm.

The correlation between skeletal age and body length of chimpanzees is not known. Hamada et al (2003) studied RUS development in 7 female and 5 male captive chimpanzees. They write that they, "...found a fairly good relationship between..." anterior trunk length (measured as the distance from the cranial tip of the sternum to the cranial tip of the pubic symphysis) and RUS score, but they do not provide the statistical strength of the relationship. They do provide separate graphs for the median values for anterior trunk length and RUS score against chronological age. Using these graphs, and the chimpanzee-like skeletal age estimate of about 9 years for MH1, indicates that he had achieved a median of 85% of final body length. If this is accurate, then the estimate of his adult height is at least ~150cm.

The adult *Au. sediba* MH2, a likely female, has an estimated body length of 130cm. If MH1 would have grown to 150-156cm at adulthood then the 13-17 percent (20-26cm) difference between MH1 and MH2 is about twice the average 7-8 percent sexual dimorphism in stature of living humans (Gray and Wolfe, 1980; Gustafsson et al., 2007). Whilst the difference in estimated final height between MH1 and MH2 is larger than typical for living humans, it should be noted that in any living human population it is possible to find sexual dimorphism in height of 13-17 percent for many pairs of women and men. Moreover, the estimate of final body length for MH1 is liable to considerable error.

6. Conclusion

Despite all the caveats regarding the ape-like skeletal age estimation and adult height prediction, the immature specimen of MH1 provides a significant advance in our understanding of hominin growth and development at a time point near the origins of the genus *Homo*. Additionally compelling, the skeletal maturity of MH1 closely resembles that of WT 15000, although slightly more fusion has occurred at the elbow joint in MH1. Using dental evidence, WT 15000 is estimated to have been between 8.3 – 8.8 years at death (Dean et al., 2001; Schwartz, 2012), which is younger than the skeletal age of death of MH1 of 9-11 years we provide here. When published, the dental estimate of age at death may well be less than 9 years. The maturational similarities in *Au. sediba* and *H. erectus*, in contrast to *H. sapiens*, suggest that the evolution of modern human life history strategies is of relatively recent origin (Bogin and Smith, 2012; Schwartz, 2012; Kelley and Bolter, 2013).

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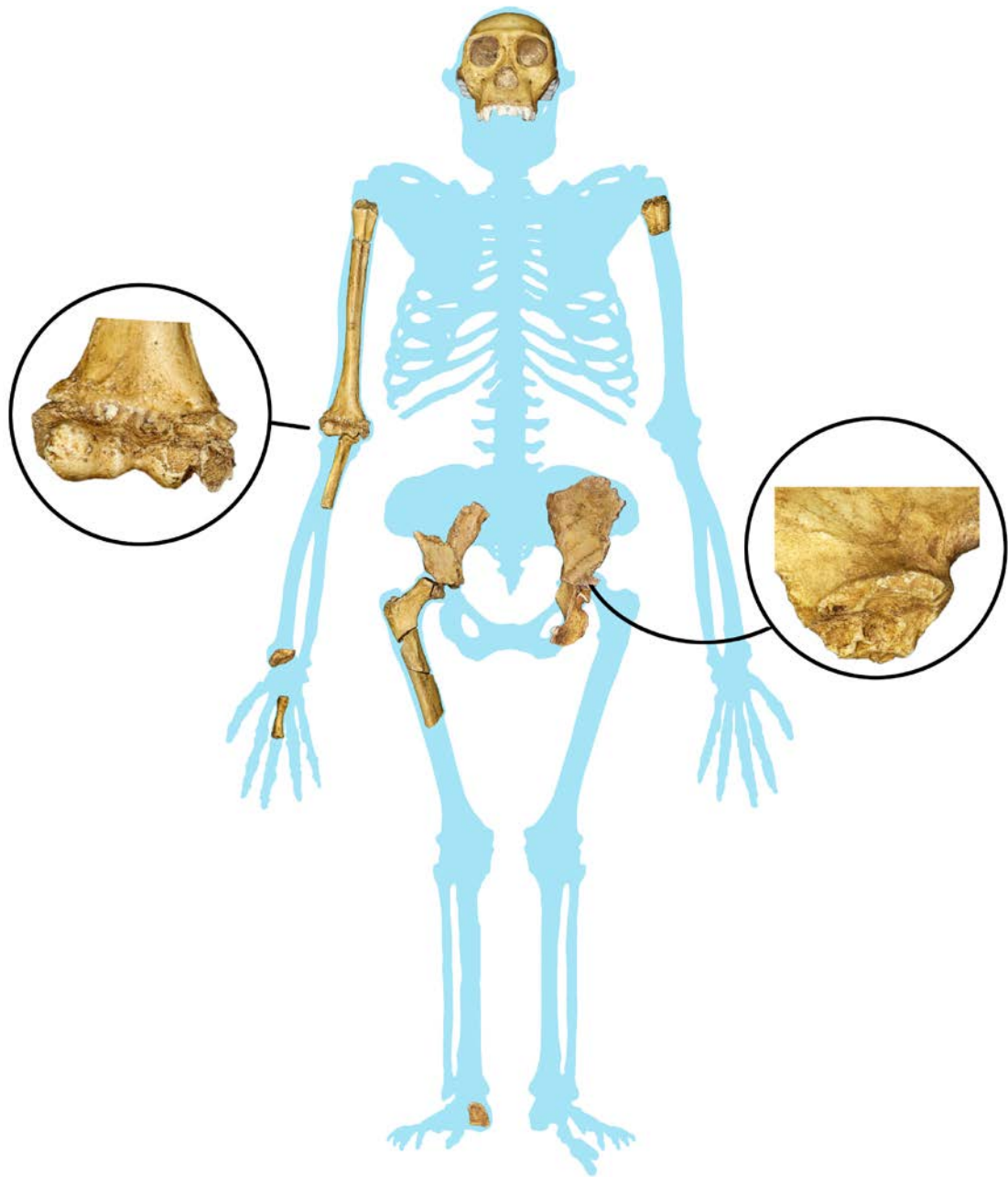


FIGURE 1. Skeletal elements used in assessment of maturity.

Left circle: Pull-out of right distal humerus showing fused three elements of composite epiphyses, and fusion to the diaphysis.

Right circle: Pull-out of left partial ilium, unfused acetabulum.

Table 1: Maturity estimations (years) of *Australopithecus sediba* (MH1) based on bone maturity indicators for *Homo sapiens*.

MH1: Bone element (by specimen catalogue numbers) with description and maturity indicator. See also Berger et al., 2010 Supplemental Information.	<i>Homo sapiens</i> age
<i>Right Distal Humerus</i> articulates with right humeral shaft (88 and 42) Description: Three elements of the composite distal epiphysis are fused with each other (42) and the humeral diaphysis (88). The distal portion of the humerus (42) is broken off right at the superior margin of the olecranon fossa. The trochlea and capitulum are fused together with a slight fusion line visible between the two elements. The lateral epicondyle is also fused as part of the composite epiphysis, with a slight superior fusion line still visible. The compound epiphysis is fused to the diaphysis with a slight fusion line visible. The medial epicondyle is unfused although present. It appears inferiorly displaced during the process of fossilization. See also Berger et al., 2010 Supplemental Materials. <i>H. sapiens</i>: Suggests an age of 12-15 years in boys. Three of the four composite elements (trochlea, capitulum and lateral epicondyle) usually fuse by 12 years in males. Fusion of these elements to the shaft suggests an age of 15 years. Medial epicondyle fuses sometime between 14-19 years.	12-15
<i>Proximal humerus</i>: (MH1 #34, 36) Descriptions: Right and left proximal humeral elements were recovered. No elements of the compound proximal epiphyses were recovered (greater tubercles, lesser tubercles, heads). Both diaphyseal surfaces are billowy and rippled, indicative of unfused metaphyseal surfaces. <i>H. sapiens</i>: fusion with the secondary epiphyseal centres of the greater and lesser tubercles occurs at circa 20 years. Based on the size and shape, suggests an age between 10-15, leaning towards the upper age band.	12.5
<i>Proximal ulna</i>: (MH1 #3) Description: Proximal end of ulna recovered with complete trochlear notch,	15

coronoid process, radial notch and prominent supinator crest. About a third of the shaft of the ulna has been preserved. The ulnar epiphysis is unfused. <i>H. sapiens</i>: the size and shape and roughened appearance of the proximal end of the ulna suggest the epiphysis was present and likely to be at the middle to upper age of the range. Epiphysis appears at 7-14 years and fusion complete by 19 years.	
<i>Distal radius epiphysis</i>: (MH1 #12) Description: The right unfused epiphysis of the distal radius is mostly complete, particularly the articular surface for the carpals. A portion of the medio-proximal area is missing although the epiphysis is thick overall, particularly the lateral side. The styloid process is well formed, as is the articular surface. <i>H. sapiens</i>: there is an absence of fusion to the metaphysis although relative size and shape suggests an age greater than 10 years. As an isolated epiphysis, comparison to Tanner-Whitehouse skeletal maturity indicators (16) would suggest an F or G rating, consistent with an age between 12 and 14 years.	13.5
<i>Ilium</i> (MH1 #102, 67, 68) and near complete <i>Ischium</i> (MH1 #14). Description: Partial left ilium and associated fragments (102, 67, 68) include unfused acetabular surface with nearly complete inferior iliac blade. Portions of the superior and lateral aspects of blade missing. Medial superior aspect of acetabular ridge is rippled, consistent with lack of fusion with the ischium and pubis at the hip joint. Near complete left ischium with some missing elements superior-medially. Articular surface for superior fusion with pubis appears roughened, consistent with lack of fusion. Ischial tuberosity surface rough, bevelled—clearly unfused. <i>H. sapiens</i>: Hip bone consists of three distinct portions that begin to fuse about the 14th year in boys. Complete ossification may take as late as 17. Epiphyses, the iliac crest, the anterior inferior iliac spine, the pubis and the ischial tuberosity appear about puberty and unite from 16-23. Suggests an age younger than 14 years.	<14

<i>Proximal Femur</i> which conjoins with shaft fragment and femoral head fragment (MH1 #4, 5, 89 and 39) Description: Right proximal femur (4) preserves the immature bone to just below the unfused lesser trochanter, with two additional shaft fragments (5 and 89) that conjoin with it. The greater and lesser trochanters and femoral head are unfused, and all unfused surfaces are billowy and rippled. The femoral head is broken medio-anteriorly, but this fragment representing about a third of the unfused femoral head was also recovered (39). <i>H. sapiens</i>: not fused, greater and lesser trochanter fuse between 14 and 19 years but the epiphysis is quite small relative to the proximal femur indicting a younger age between 10 and 14 years.	12.5
<i>Right calcaneal epiphysis</i> (MH1 #113) (originally identified as a scapular fragment). Description: This cap-like epiphysis is concave in appearance. The superior third “accessory” epiphysis has fused into place with a faint fusion line visible on the casted specimen. The central to lateral posterior edge is concave. <i>H. sapiens</i>: concave appearance but lack of fusion suggests age range of 10.5 to 13 years against Hoerr, Pyle and Francis (17) standards.	12

TABLE 2: Wild male chimpanzee skeletal maturity markers compared with MH1.

U=unfused P=partial fusion F=fused

	Distal humerus <i>composite epiphysis of trochlea, capitulum, lateral epicondyle</i>	Distal humerus <i>composite epiphysis to diaphysis</i>	Distal humerus <i>medial epicondyle to diaphysis</i>	Proximal humerus	Proximal ulna	Distal radius	Acetabulum <i>ilium, ischium, pubis</i>	Proximal femur <i>head, greater and lesser trochanter</i>	Calcaneal epiphysis	Metacarpal epiphysis
Juvenile I: First molars eruption										
5.2 yr	n/a	U	U	U	U	U	U	U	n/a	U
5.7 yr	n/a	U	U	U	U	U	U	U	n/a	n/a
age unknown	n/a	U	U	U	U	U	U	U	n/a	n/a
Juvenile II: Second molars erupted										
7.6 yr	n/a	U	U	U	U	U	U	U	n/a	n/a
8.5 yr	capitulum present; U	U	U	U	U	U	U	U	n/a	U
age unknown	capitulum present; U	capitulum P	U	U	U	U	U	U	n/a	U
MH1	F; faint line--capitulum - trochlea	F; faint line above trochlea	U	U	U	U	U	U	U	U
Sub-adult: Third molars erupted										
12-13 yrs	F	F; faint line above trochlea	F; faint line	U	P	U	F; opened at edge	Lesser & head U; Greater P	n/a	n/a

12-13 yrs	F	F	F; unfused notch superiorly	U	Left-P; Right- U	U	P	U	P	U
age unknown	F	F	F	U	F	P	F	Lesser, head P; Greater F	n/a	n/a
13-15 yrs	F	F	F	P	F	P	F	F	F	F