Chapter 9
Australopithecus sediba from Malapa, South Africa

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Abstract First discovered in August of 2008, the site of Malapa, South Africa revealed two relatively complete partial skeletons that we assigned to a new species, *Australopithecus sediba*. Additional individuals have since been detected, and await excavation at the site. It appears that these hominins were washed into the cave through a deep vertical shaft, likely in a single depositional event resulting from a large storm inflow. Burial and cementation were rapid, occasioning the exceptional preservation of these skeletons. Uranium-lead and paleomagnetic dating combine to precisely constrain the age of the site to 1.977 ± 0.0015 Ma. Cranial and postcranial remains of *A. sediba* demonstrate numerous australopith-like features that denote a hominin at an australopith adaptive grade, prompting its inclusion in the genus *Australopithecus*. However, *A. sediba* also displays a series of characters that align it more closely with *Homo* than any other australopith species. We consider the evidence supporting the appearance of *Homo* prior to 1.977 Ma to be inconclusive, therefore we hypothesize that *A. sediba* from Malapa could be ancestral to *Homo*. Alternatively, if the existence of *Homo* prior to 1.977 Ma can be confirmed, this would not preclude a population of *A. sediba* that predated Malapa from occupying this role. Therefore we hypothesize that *A. sediba* indeed represents the ancestor of the genus *Homo*.

> "Every fossil that might potentially be intermediate is always classified as either *Homo* or *Australopithecus*. None is ever classified as an intermediate…. The most perfect intermediate you could possibly imagine would *still* find itself shoehorned into either *Homo* or *Australopithecus*. In fact, it would probably be called *Homo* by half the palaeontologists and *Australopithecus* by the other half. And unfortunately, instead of getting together to agree that ambiguously intermediate fossils are exactly what we should *expect* on the evolution theory, the palaeontologists could probably be relied upon to give an entirely false impression by seeming almost to come to blows over their terminological disagreement."
>
> Richard Dawkins 2009, *The Greatest Show on Earth*

Keywords *Homo* • Skeletal morphology • Taxonomy

Introduction

The recently discovered site of Malapa (site U.W. 88; Zipfel and Berger 2010) represents an especially rich early hominin locality in Africa. It contains the partially articulated and associated skeletal remains of several individuals of the newly recognized species *Australopithecus sediba*, alongside an abundant, well-preserved fauna (Berger et al. 2010; Dirks et al. 2010). It appears that all of these skeletons were accumulated during a seemingly rapid, homogenous depositional event that occurred approximately 1.977 Ma (Dirks et al. 2010; Pickering et al. 2011a). The site of Malapa was first discovered by one of us (LRB) on August 8, 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 Area to the northwest of Johannesburg, South Africa (Fig. 9.1). The locality was recognized as a deroofed cave of at least 15 × 10 meters in an area where limited limestone mining had taken place, probably during the late nineteenth or early twentieth century. No scientific or official record of the site was found to exist at the time of discovery, and subsequent research has demonstrated that the site was unknown to science.

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K. E. Reed, J. G. Fleagle, R. E. Leakey (eds.), *The Paleobiology of* Australopithecus,
Vertebrate Paleobiology and Paleoanthropology, DOI: 10.1007/978-94-007-5919-0_9,

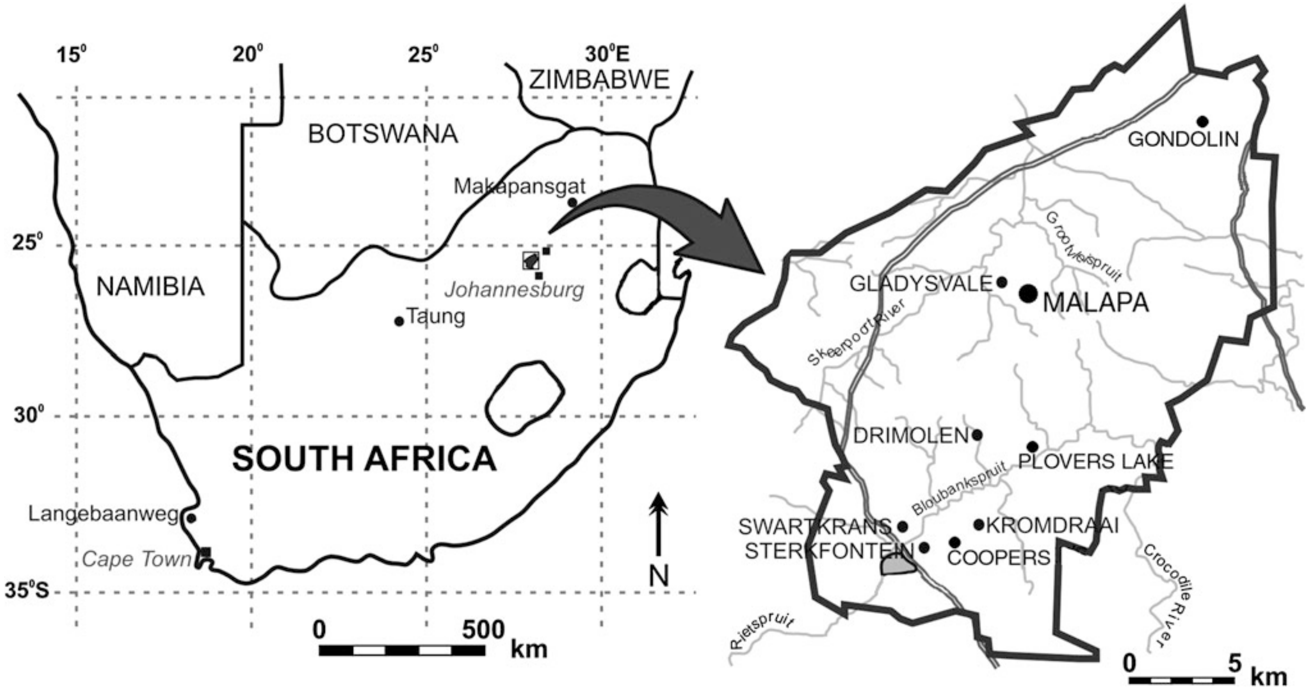

Fig. 9.1 Map of hominin-bearing fossil localities in the Cradle of Humankind World Heritage Area of South Africa. *Solid line* surrounding fossil sites on the right denotes the boundaries of the Cradle of Humankind. Modified from de Ruiter et al. (2009)

On the 15th of August 2008, upon our initial return to the site to investigate its fossil-bearing potential, the first hominin specimens were discovered by Matthew Berger. This discovery prompted considerable interest in the site, as the first specimen recognized, a hominin clavicle, was directly associated with a fragment of a mandible in a single block of ex situ calcified clastic sediment presumably displaced from the in situ locality by limestone miners. In the following weeks we came to recognize the rich potential of the site as more and more skeletal elements were encountered during the course of preparation of this single block, including both cranial and postcranial remains of a relatively complete juvenile individual (MH1, Fig. 9.2). Then, on September 4, 2008, on only the third visit to the site, a second, well-preserved adult partial skeleton and two associated maxillary teeth (MH2) were discovered by LRB in situ in the calcified clastic sediments of the mining pit. Removal of the slightly dislodged, but otherwise in situ block containing the adult hominin 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 right scapula and clavicle were found in a block that also contained the adult's mandible. Thus by early 2009 it had become clear that we were dealing with at least two relatively complete partial skeletons. These skeletons showed little damage other than a moderate amount of breakage that was due primarily to a series of three or four mining blasts, a small amount of taphonomic damage likely incurred in a massive debris flow as the skeletons were transported to their final resting place, and perhaps some perimortem trauma to a small number of elements of the upper body of MH1. In February of 2009, a block containing the diaphysis of the humerus of MH1 was found by LRB, and during the course of preparation of this specimen, we uncovered a well-preserved partial cranium and several other postcranial elements. This discovery allowed us to reassemble a significant part of the head and body of the juvenile MH1, and continued preparation of the adult MH2 skeleton revealed it to be significantly 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 provenience of both specimens within the site.

In this paper we discuss the geological setting from which the hominins were recovered that demonstrates their homogeneity in time and space, outline the characteristics that define *A. sediba*, and discuss the potential taxonomic and phylogenetic implications of this new hominin taxon.

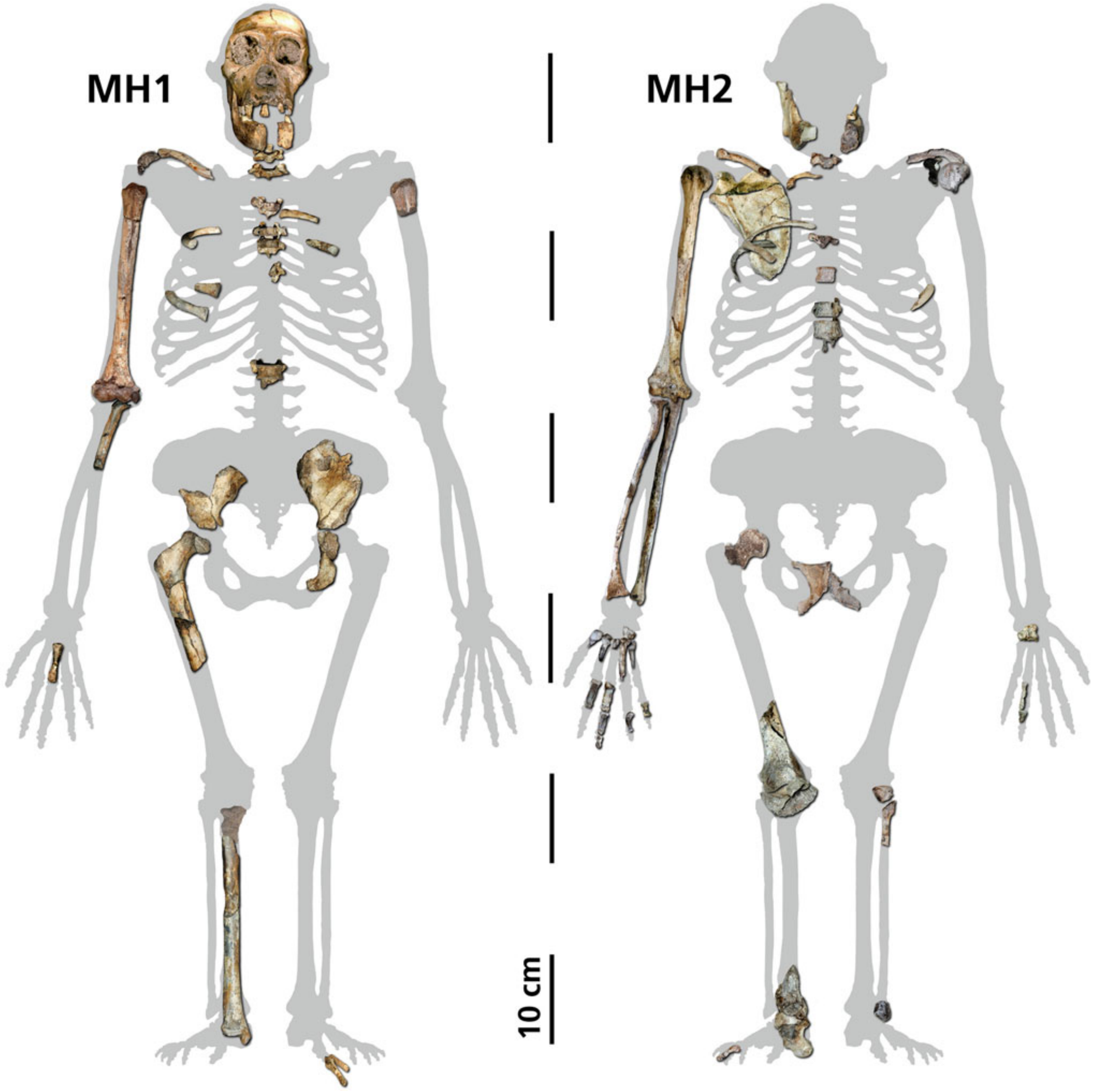

Fig. 9.2 Associated skeletal elements of MH1 (*left*) and MH2 (*right*) in approximate anatomical position. Note that since this image was produced, we have recognized that the right tibia pictured here is from a separate individual, MH4. Picture reprinted with permission of Peter Schmid

Geology and Dating of the Site

Work at Malapa has benefited greatly from geologists and geochronologists having been involved at the site from the very beginning. Dirks et al. (2010) and Pickering et al. (2011a) describe the geology of the area and the site, and provide a more detailed chronological context that we summarize here. The site of Malapa resides at the north end of a series of north–south trending caves housed in a late Archaean dolomite of the Lyttleton Formation of the Malmani Subgroup of the Chuniespoort Group. This is the same formation that houses a number of other fossil-bearing caves, including the site of Gladysvale, which is located only 2 km to the west of Malapa (Berger et al. 1993). The calcified clastic sediments that make up the majority of the Malapa deposit are comprised of five distinct sedimentary facies interspersed with sheets of flowstone. All of the sedimentary facies were deposited by water action or mass flow, and show little evidence of post-depositional compaction. Intrusions in the calcified clastic sediment housing the hominins (Facies D) indicate that the event that transported the only partially decomposed and still partially articulated hominin carcasses to their final resting place occurred as a single depositional episode, perhaps during a single large storm inflow, and that transport was over a very short distance. Cementation of these debris flow sediments was rapid, and as of yet there is no definitive indication of mammalian carnivore damage to any of the specimens. These factors contribute to the high quality of preservation of the Malapa fossils. At present, we interpret these geological data to mean that the hominins and other fauna associated with them somehow entered a natural death trap, likely through the opening of a vertical shaft some several meters above the cave floor. Cosmogenic dating of the surrounding land surface, which allows us to calculate erosion rates, indicates that the cave floor resided approximately 30–50 m below the land surface at the time of deposition. The hominins and other animals were most likely killed by a fall, and their rotting carcasses might have been a factor in attracting the several large carnivores that have also been found in the same sediments. We can only speculate as to why the hominins and other fauna approached the cave in the first place, though at least two possible explanations present themselves. Either they were unaware of its existence, and fell in by accident, or more likely they were attracted to the cave by water or some other resource that was to be had in the vicinity of the cave opening, or within the cave itself, and fell in while attempting to access this resource.

Dating the South African fossil-bearing cave deposits has in the past been notoriously difficult, though recent breakthroughs in the application of a variety of dating techniques have shown tremendous promise. In particular, advances in the use of U–Pb dating have allowed very precisely constrained dates to be recorded for speleothems and flowstones associated with the fossils from sites such as Sterkfontein, Coopers, Swartkrans, and Malapa (Walker et al. 2006; de Ruiter et al. 2009; Dirks et al. 2010; Pickering and Kramers 2010; Pickering et al. 2011b). Examining the fauna associated with the Malapa hominins, taxa such as *Equus* and *Tragelaphus* cf. *strepsiceros* first appear ca. 2.33 Ma in Africa (Brown et al. 1985; Bernor and Armour-Chelu 1999; Berger et al. 2002) providing a maximum age bracket for Malapa, while the presence of *Megantereon whitei*, with its last appearance datum at 1.5 Ma (Lewis and Werdelin 2007), provides a minimum age bracket. Immediately below the adult hominin skeleton is a flowstone seam that provided samples suitable for U–Pb dating. Samples were sent to two separate labs for analysis, which returned independent dates of 2.024 ± 0.062 Ma (Bern) and 2.026 ± 0.021 Ma (Melbourne). These dates are effectively identical within error, and further refine the maximum age estimate for the hominins, whose remains in some places actually contact this flowstone. A normal polarity event is recorded near the base of this flowstone that correlates with the Huckleberry Ridge Subchron [2.05–2.03 Ma (Lanphere et al. 2002)]. Higher up in the same flowstone we detected a reversed polarity event that correlates with the Matuyama Chron (2.03–1.95 Ma). We initially used the transition from the reversed polarity Matuyama Chron to the normal polarity Olduvai Chron at 1.95 Ma (Ogg and Smith 2004) to constrain the age of the Malapa fossils to 1.95–1.78 Ma, since the hominin-bearing sediment (Facies D) records a normal polarity (Dirks et al. 2010). However, subsequent stratigraphic research revealed an additional datable flowstone above the hominin skeletons, with a U–Pb date of ca. 2.048 ± 0.140 Ma (Pickering et al. 2011a); this date appears anomalously older than the U–Pb dates for the flowstone underlying the hominins, though taking the error margins into account results in a not-incompatible range of 2.188–1.908 Ma. Combining the minimum potential U–Pb age of 1.908 Ma with the reversed polarity detected in this new flowstone demonstrates that the flowstone must have formed before the onset of the Olduvai Normal event at 1.95 Ma (i.e. within the Matuyama reversal). Given that the hominin-bearing sediments underlying this reversed polarity flowstone record a normal polarity, these sediments must have been deposited during the short-lived pre-Olduvai normal polarity excursion that is dated to 1.977 ± 0.0015 Ma (Channell et al. 2002). The 3000 year time span reflected in this pre-Olduvai event provides us with an especially precise age estimate for the Malapa fossils, resulting in an age estimate undreamed of in a South African fossil cave.

The Fossil Hominin Sample from Malapa

To date, we have recovered in excess of 200 numbered hominin specimens from Malapa, largely originating from the holotype and paratype skeletons MH1 and MH2. And, while our initial report included only these specimens, we have since recognized an infant (MH3) and another adult individual (MH4) in ex situ blocks of calcified clastic sediment. Continued exploration of in situ cave sediments has revealed traces of possibly more individuals, though this remains to be confirmed. This remarkable hominin assemblage is rendered all the more striking when we note that we have not yet begun excavations, as infrastructure development is still currently underway. The singular exception to this is the removal of the in situ block containing the right upper limb skeleton of MH2, which had been detached from the adjacent matrix by miner's blasting, otherwise we have not disturbed the in situ deposits. Apart from limited blasting by limestone miners at the turn of the last century, the site is in almost pristine condition.

At present, while the MH1 type specimen is the only individual that preserves a cranium, the skeleton of MH2 is more complete, though recovery of additional remains of both individuals from blocks of calcified clastic sediment continues at a substantial pace. As noted in our original descriptions, MH1 preserves much of the cranium, minus the cranial base and much of the right side of the cranial vault (Fig. 9.3). The right half of the mandible is preserved from close to the mandibular symphysis to the complete ascending ramus with condyle, and we have recently recovered portions of the left half of the mandible. All of the maxillary premolars and molars are present, with the third molars still forming in the crypt. The maxillary left lateral incisor is in place, while the isolated right central incisor and canine have been recovered. The right mandibular molars are preserved, including the 3rd molar in the crypt, along with the left canine in a small fragment of the anterior mandible. Postcranially, MH1 preserves portions of the axial skeleton, pectoral girdle, upper limb, pelvic girdle, and lower limb. Some, but not all, secondary growth centers in the humerus, ulna, radius, os coxa, and femur were unfused at the time of death. Combined with the state of eruption and attrition of the dental remains, we estimate that MH1 was at a developmental stage equivalent to a human child of 12–13 years, making it roughly comparable in ontogenetic age to the type specimen of *Homo habilis* (OH7) and the Nariokotome *Homo erectus* skeleton (KNM-WT 15000). The development of the supraorbital torus and glabellar prominence, pronouncement of the canine juga, eversion of the gonial angle of the mandible, relatively large and rugose muscle scars of the postcranial skeleton, and relatively narrow sciatic notch of the pelvis all support the contention that MH1 was a male individual, even in the absence of comparisons with MH2.

MH2 is represented by a relatively complete but fragmented mandible, the damage being more extensive on the left side. Three isolated maxillary teeth and significant portions of the axial skeleton, pectoral girdle, upper limb, pelvic girdle, and lower limb are preserved. All of the teeth of MH2 are relatively worn, while the epiphyseal lines of all observable long bones are completely fused and obliterated, indicating this individual was fully adult at the time of death. Compared to MH1, the mandibular ramus is smaller in height, and the gonial angle less everted (the gonial region in MH2 is damaged and displaced, and reconstruction of this area would minimize the artificial eversion that is presently evident in the specimen). The ramus of MH1 is slightly narrower than MH2, though it is likely that continued growth of this juvenile individual would alter this. Since our initial description of this skeleton, an undistorted partial pelvis of MH2 has been recovered, but unfortunately the specimen lacks the ischium, precluding metric evaluation of sciatic notch morphology as an aid to sex diagnosis. Notwithstanding, features of the cranial remains, as well as

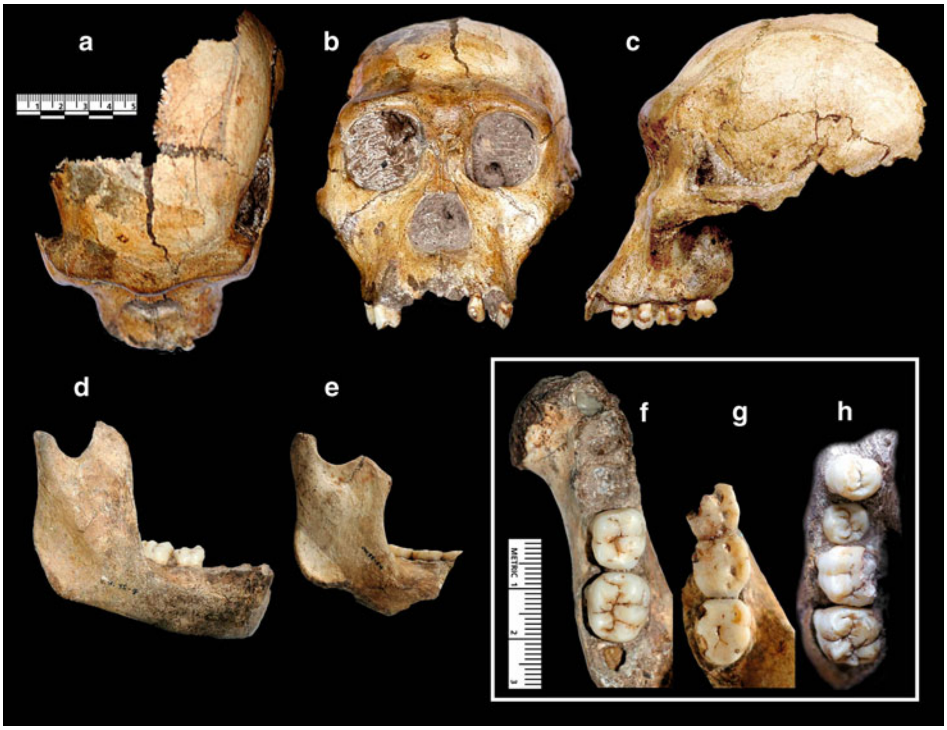

Fig. 9.3 Craniodental elements of *A. sediba*: **a** UW 88-50 superior aspect; **b** UW 88-50 frontal aspect; **c** UW 88-50 left lateral aspect; **d** UW 88-8 right lateral aspect; **e** UW 88-54 right lateral aspect; **f** UW 88-8 occlusal aspect; **g** UW 88-54 occlusal aspect; **h** UW 88-50 occlusal aspect. Picture reprinted with permission of Peter Schmid

Table 9.1 Dental metrics of *A. sediba* from Malapa

	MH1								MH2			
	Maxillary				Mandibular				Maxillary		Mandibular	
	Left		Right		Left		Right		Right		Right	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
I1			10.1	6.9							4.4	5.6
I2	7.7	5.1									5.1	6.6
C			9.0	8.8	8.0	8.5					7.1	7.4
P3	9.0	11.2	7.7[a]	10.8							7.8	9.3
P4	9.2	11.4	10.6[a]	13.3							8.4	9.7
M1	12.9	12.0	11.3[a]	11.0			12.5	11.6			11.8	11.1
M2	12.9	13.7	12.5	13.3			14.4	12.9			13.1	12.2
M3	13.3	14.1	13.1	13.6			14.9	13.8	11.3	12.9	14.2	12.7

[a] The right P3 is not erupted, while the left is; this possibly pathological condition is likely influencing the dental metrics of the right premolars and probably the right first molar

the fact that the pubic body of the os coxa is mediolaterally broad and square shaped, and the muscle markings of the other postcranial remains are typically weakly to moderately rugose in comparison to MH1, lead us to suggest that MH2 was a female.

Data on dental dimensions of *A. sediba* are presented in Berger et al. (2010), and we summarize these here (Table 9.1). Apart from the maxillary incisors, the teeth of *A. sediba* are relatively small, generally plotting at the lower end or outside the range of tooth sizes for *Australopithecus africanus*, and within the ranges of specimens assigned to early *Homo*, including African *H. erectus*. The canine teeth of both individuals in particular are small. Only a single specimen of *A. africanus*, TM 1512, has a maxillary canine that is smaller than MH1, while the mandibular canine of MH1 is smaller than any *A. africanus* specimen. The molars of MH2 are smaller than those of MH1, falling below the size range of *A. africanus*. In fact, the molars of MH1 are 9.0 % (M_1), 8.6 % (M_2) and 8.8 % (M_3) larger than those of MH2, indicating minimal size dimorphism between the two in the postcanine dentition. Conversely, the femoral head of MH1 is approximately 9.1 % smaller than that of MH2, though it is likely that additional appositional growth in MH1 would have decreased this size difference. On the other hand, the distal humerus of MH1, which has a fused epiphysis, is slightly larger than MH2's distal humerus. These small levels of dimorphism appear similar to that seen in modern humans. But, unlike definitive representatives of the genus *Homo*, the molars of *A. sediba* increase in size from M1 to M3, as is seen in *A. africanus* and other australopiths. Also, the cusps of the premolars and molars of *A. sediba* are centrally arranged, unlike the marginal arrangement of specimens attributed to early *Homo*. The overall pattern that emerges is that the teeth of *A. sediba* are similar in absolute size to specimens attributed to early *Homo*, while the post-canine dentition shows a cuspal arrangement and posterior molar size increase that is more similar to *A. africanus*.

Australopithecus sediba

In the early days of our investigation, prior to the cranium of MH1 being fully exposed, our craniodental studies were restricted to the mandibular remains of both individuals and the attendant maxillary teeth of MH2 when attempting to determine the taxonomic affinity of these finds. We were initially struck by the similarities between these mandibles and other specimens attributed to early *Homo*. Thus, our initial working hypothesis was that the skeletons we had recovered from Malapa likely represented some form of early *Homo*. This perception was strengthened by several derived characters we noted in the pelvis of MH1, three pieces of which had been recovered during late 2008. However, as our analysis proceeded over the following months, it became apparent that although there were derived features in both the cranial and pelvic remains, the overall body plan appeared to be that of a hominin at an australopith adaptive grade (or occupying an australopith adaptive plateau, sensu White et al. 2009). Once the cranium had been sufficiently prepared from the matrix, detailed comparisons between it and other hominin crania from both East and South Africa reinforced our appraisal of the predominantly australopith nature of these individuals.

The cranial capacity of MH1 was established through a variety of actual and virtual methods at a surprisingly small 420 cc, even though our assessment of its ontogenetic development indicated this juvenile would have completed some 97 % of its brain growth by the time of death. More recently, virtual reconstruction of the endocast of MH1 revealed a brain with an australopith-like convolutional pattern (Carlson et al. 2011). In contrast, the posterior positioning of the olfactory lobes and the breadth of the orbitofrontal region of the brain appears more derived than that seen in other relatively complete specimens of *A. africanus*, foreshadowing the condition found in later *Homo*. This suggests that brain reorganization was decoupled from the brain expansion that marks later specimens of *Homo*.

On present evidence, the species *A. sediba* is not marked by any autapomorphies, though it can be distinguished from other hominin taxa by a unique constellation of characters outlined in Berger et al. (2010) (Table 9.2). It is worth highlighting the more notable differences. *A. sediba* can be differentiated from *Australopithecus afarensis* in the relatively weak development of the cranial crests in the former, and the relatively pronounced postorbital constriction in the latter. In *A. afarensis* a prominent supraorbital bar appears, though a supratoral sulcus is absent, while in *A. sediba* a weak supraorbital torus and supratoral sulcus are evident. *A. afarensis* shows considerable subnasal prognathism and procumbent incisors, while *A. sediba* shows limited prognathism and more vertically oriented incisors. The large, high, flaring zygomatics of *A. afarensis* result in a facial profile that is tapered superiorly and inferiorly, while in *A. sediba* the zygomatics are smaller, lower, and less flaring, resulting in a facial profile that is tapered inferiorly, but squared superiorly. In addition, the mandibular symphysis in *A. afarensis* is weakly inclined and receding, with a well-developed post-incisive planum, while in *A. sediba* the mandibular symphysis is nearly vertical, as is the weakly developed and steeply inclined post-incisive planum. Although fewer remains of *A. anamensis* have been recovered, what is preserved is distinctly more similar to *A. afarensis* than to *A. sediba*, in particular in mandibular morphology. *Australopithecus garhi*, *Australopithecus aethiopicus*, *Australopithecus boisei*, and *Australopithecus robustus* all reveal pronounced cranial cresting patterns and megadont post-canine teeth not witnessed in *A. sediba*. In addition, the derived facial morphologies of the three "robust" taxa are incompatible with *A. sediba*, thus *A. sediba* is readily distinguishable (see Rak 1983). In particular, the highly derived facial morphology of *A. robustus* is not seen in *A. sediba*, therefore we can certainly rule out *A. robustus* as a possible conspecific South African form.

The closest morphological comparison to *A. sediba* within the australopiths is *A. africanus*, as the two share numerous similarities in the cranium, face, palate, mandible, and teeth (Table 9.2; see also Table 9.1 of Berger et al. 2010). Nonetheless, they can be differentiated in that *A. africanus* is marked by a relatively tapered cranial vault, which in *A. sediba* is more squared with distinctly vertically oriented parietals. The temporal lines in *A. africanus* tend to be relatively closely spaced, even meeting as a small sagittal crest in Stw 505, while in *A. sediba* they are notably widely spaced. *A. africanus* lacks a true supraorbital torus, while *A. sediba* displays a weak torus and shallow but distinct supratoral sulcus. The lateral orbital margins of *A. africanus* are rather unique in that they face predominately anteriorly and show a distinct angular indentation that is unknown in any other australopith (Rak 1983), including *A. sediba* with its laterally facing, gently concave lateral orbital margins. In addition, the frontal process of the zygomatic is expanded both medially and laterally in its contribution to the lateral orbital margin in *A. africanus*, while in *A. sediba* it is only medially expanded, and only the medial aspect of the process contributes to the lateral orbital margin. *A. africanus* shares with *A. afarensis* the large, flaring zygomatics and tapered upper facial profile, as opposed to the smaller, less flared zygomatics of *A. sediba* that results in its squared upper facial profile. *A. sediba* is marked by canine juga and fossae that do not conform to the pattern of canine pillars and maxillary furrows described by Rak (1983) for most specimens of *A. africanus*. The mandibular symphysis of *A. sediba* is slightly more vertical than that of *A. africanus*, and with a weakly developed and steeply inclined post-incisive planum that differs from the stout, weakly inclined post-incisive shelf seen in the latter. The mandibular corpus of *A. sediba* is also considerably more gracile than *A. africanus*, with a distinct subalveolar fossa that is weakly apparent to absent in *A. africanus*.

Given the derived appearance of *A. sediba* relative to *A. africanus*, which makes it appear quite *Homo*-like in morphology, some have questioned its position within the genus *Australopithecus*, preferring instead to place it within the genus *Homo* (Balter 2010; Cherry 2010). However, there are several characters that we contend precludes placing *sediba* in *Homo*. The cranial capacity of MH1 has been estimated at 420 cc, and to include this cranium in the genus *Homo* would require another revision of the definition of *Homo* in order to accommodate such a small brain (e.g., Leakey et al. 1964). Additional morphological features link select specimens of the *A. africanus* hypodigm with *A. sediba*. For instance, although *A. sediba* possesses a weak supraorbital torus that is not seen in *A. africanus*, the glabellar region of the former is especially pronounced, appearing most similar to Sts 71. The premaxillary suture is still evident at the superior extent of the nasal aperture in *A. sediba*, a feature Clarke (2008) considers indicative of australopiths. Although *A. sediba* lacks the anterior pillars of *A. africanus*, it nonetheless displays a well-developed canine jugum with an associated canine fossa that appears most similar to that of Sts 52 (a specimen that does not display anterior pillars), and

Table 9.2 List of craniodental characters distinguishing species of *Australopithecus* and *Homo*. This list is extracted from the larger table in Berger et al. (2010)

	A. aethiopicus	*A. boisei*	*A. robustus*	*A. garhi*	*A. afarensis*	*A. africanus*	*A. sediba*	*H. habilis*	*H. rudolfensis*	*H. erectus*
Cranial capacity	Small	Small	Small	Small	Small	Small	Small	Intermediate	Large	Large
Orientation of parietals	Tapered	Tapered	Tapered	Tapered	Tapered	Tapered	Vertical	Variable	Vertical	Vertical
Position of temporal lines on parietals	Crest	Crest	Crest	Crest	Crest	Variable	Wide	Variable	Wide	Wide
Postorbital constriction	Marked	Marked	Marked	Moderate	Marked	Moderate	Slight	Moderate	Moderate	Slight
Supraorbital expression	Bar	Bar	Bar	Intermediate	Bar	Intermediate	Torus	Torus	Intermediate	Torus
Glabellar region forms as prominent block	No	Yes	Yes	No	No	Variable	Yes	No	Variable	No
Canine juga prominence/ anterior pillars	Weak	Weak	Pillars	Prominent	Prominent	Variable	Prominent	Variable	Weak	Weak
Patency of premaxillary suture	Obliterated	Obliterated	Occasional	?	Obliterated	Occasional	Trace	Obliterated	Obliterated	Obliterated
Eversion of superior nasal aperture margin	Slight	Variable	None	?	?	None	Slight	Slight	Slight	Slight
Subnasal projection	Marked	Moderate	Moderate	Marked	Marked	Variable	Weak	Variable	Weak	Weak
Canine fossa	Absent	Absent	Absent	Present	Present	Present	Present	Present	Absent	Absent
Incisor procumbency	Vertical	Vertical	Vertical	Procumbent	Procumbent	Variable	Vertical	Variable	Vertical	Vertical
Anterior nasal spine relative to nasal aperture	Posterior	Posterior	Posterior	?	Absent	Anterior	Anterior	Anterior	?	Anterior
Expansion of frontal process of zygomatic bone	Medial and lateral	Medial and lateral	Medial and lateral	?	Medial and lateral	Medial and lateral	Medial	Medial	Medial	Medial
Angular indentation of lateral orbital margin	?	Curved	Curved	?	?	Indented	Curved	Curved	Curved	Curved
Lateral flaring of zygomatic arches	Marked	Marked	Marked	?	Marked	Marked	Slight	Slight	Slight	Slight
Outline of superior facial mask	Tapered	Tapered	Tapered	?	Tapered	Tapered	Squared	Squared	Squared	Squared
Zygomaticoalveolar crest/malar notch	Straight	Straight	Straight	?	Straight	Straight	Straight	Notch	Notch	Notch
Height of masseter origin	High	High	High	Low	Low	High	High	Low	Low	Low
Derived facial morphology of robust australopiths	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent

(continued)

Table 9.2 (continued)

	A. aethiopicus	*A. boisei*	*A. robustus*	*A. garhi*	*A. afarensis*	*A. africanus*	*A. sediba*	*H. habilis*	*H. rudolfensis*	*H. erectus*
Orientation of mandibular symphysis	Vertical	Vertical	Vertical	?	Receding	Receding	Vertical	Vertical	Vertical	Vertical
Post-incisive planum of mandible	Prominent	Prominent	Prominent	?	Prominent	Prominent	Weak	Prominent	Weak	Weak
Mandibular corpus cross-sectional area at M1	Large	Large	Large	?	Small	Small	Small	Small	Variable	Small
Maxillary I1 - MMR development, lingual face	?	Moderate	Moderate	?	Moderate	Moderate	Moderate	Weak	Weak	Weak
Median lingual ridge of mandibular canine	?	Weak	Weak	?	Prominent	Prominent	Weak	Weak	Weak	Weak
Post-canine megadonty	Present	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent
Arrangement of molar cusp apices	Central	Central	Central	Marginal	Marginal	Central	Central	Marginal	Marginal	Marginal

unlike specimens generally assigned to early *Homo*. Although there is a small anterior attachment of the nasal septum (or anterior nasal spine, see McCollum et al. 1993) in *A. sediba*, it is neither as pronounced nor as projecting as that of most fossil specimens attributed to early *Homo*. Likewise the morphology of the margins of the nasal aperture and the orientation of the nasal bones indicates that *A. sediba* was not possessed of a *Homo*-like projecting nose, and accordingly does not appear to evince the derived thermoregulatory features found in the faces of most members of the genus *Homo* (Dean 1988; Franciscus and Trinkaus 1988). Despite the fact that the zygomatics of *A. sediba* are not as flaring as in other australopith specimens, the zygomaticoalveolar crest is long, straight, and steeply inclined as in *A. africanus*, resulting in a relatively high origin for masseter that differs from the malar notch typically seen in early *Homo*. And dentally, the upper central incisors of *A. sediba* show a moderately developed mesial marginal ridge on the lingual face, and the cuspal apices are centrally positioned, both features aligning *A. sediba* with the australopiths and not *Homo* (Grine 1989; Strait et al. 1997).

As in the craniodental remains, the postcranium of *A. sediba* evinces a mosaic of features that appear transitional between australopiths and later *Homo* in its unique combination of primitive and derived traits. The inference that *A. sediba* was at an australopith adaptive grade was based on such features as small body size, a relatively long forelimb with a high brachial index, upper limb joint dimensions that are large relative to those of the lower limb, a relatively primitive calcaneous, and what appeared at the time to be a fairly conical-shaped thorax (this latter inference was based on the relative dimensions of a complete first rib and mid-thoracic rib from MH2; subsequent discoveries and analysis are, however, causing us to revisit this interpretation). Thus the overall postcranial *bauplan* is australopith-like. MH1 and MH2 are comparable in size to the smaller, presumably female, individuals known from *A. afarensis* and *A. africanus*: estimated body masses (based on femoral head superoinferior diameter, and using the mean of the all hominoid and *H. sapiens* prediction equations from McHenry 1992) are about 30.5 and 37.4 kg for MH1 and MH2, respectively (cf. female mass estimates for other australopiths in McHenry 1992). In most aspects of the postcranial skeleton, *A. sediba* is similar to the smaller-bodied representatives of *A. afarensis*, and to *A. africanus* generally, in having features that might be interpreted as reflecting a significant arboreal component to its locomotor repertoire (Stern and Susman 1983; McHenry and Berger 1998; Stern 2000). These include arms that are long relative to body size, a high brachial index, large upper limb joint surfaces relative to those of the lower limb, relative pronouncement of some upper limb entheses, and a highly mobile knee.

The hand of *A. sediba* reveals a suite of australopith-like characters, including a strong flexor apparatus that indicates a probable arboreal component (Kivell et al. 2011). At the same time, the relatively long thumb and short fingers of *A. sediba* are notably *Homo*-like, and possibly indicate a precision grip capable of stone tool production. Similarly, the ankle and foot of *A. sediba* reveal a mosaic of australopith-like and *Homo*-like features, suggesting these hominins practiced a unique form of bipedalism that still included arboreal locomotion (Zipfel et al. 2011). In particular, the gracile calcaneal body and robust medial malleolus find their closest comparison with australopiths, while the talocrural joint appears mostly *Homo*-like in both form and function. And, the partial pelves of both MH1 and MH2 share features with australopiths such as a large bi-acetabular diameter, small sacral and coxal joints, and long pubic rami (Kibii et al. 2011). Conversely, the vertically oriented and sigmoid-shaped iliac blades, greater robusticity of the iliac body, sinusoidal anterior iliac borders, shortened ischia, and more superiorly oriented pubic rami are all characters shared with *Homo*. This mosaic of pelvic features combines with the small cranial capacity of *A. sediba* to suggest that the birthing of large-brained babies was not the principal force driving the evolution of the pelvis ca. 1.977 Ma.

The preliminary picture appears to be one of a postcranial skeleton that is symplesiomorphic with other australopiths in most characters of the upper and lower limbs. This contrasts with the relatively derived features seen in the pelvis of *A. sediba* (Berger et al. 2010; Kibii et al. 2011), which when combined with the observation of a *Homo*-like pattern of humeral/femoral load sharing (based on the structural properties of the diaphyses of these elements), suggests that the Malapa hominins may have differed in important ways from other australopiths in their locomotor kinematics. Elucidation of these differences must await further detailed analysis of the fossil material.

We were thus confronted with a hominin that retained a significant number of primitive characters in the cranium, face, arms, thorax, and feet, with perhaps the most notable among these being the low estimated adult cranial capacity of MH1. In conjunction with these, the spate of derived features in the cranial, dentognathic, and pelvic remains make these skeletons appear more derived toward *Homo* than any other australopith taxon on record. While we are fully cognizant that by the guidelines of phylogenetic systematics, the synapomorphies shared between the Malapa hominins and later *Homo* suggest placement of the new species into the genus *Homo*, we find ourselves in philosophical agreement with the arguments of Wood and Collard (1999) that an exclusively cladistic approach is insufficient (see also Trinkaus 1990, for a critical discussion of the use of cladistics in paleoanthropology). Rather, in line with Wood and Collard (1999), we consider a genus to be a monophylum whose members occupy a common adaptive grade. Detailed analysis of both craniodental and postcranial remains demonstrates that the Malapa fossils are not yet at a *Homo* adaptive grade (see below). We also agree with Wood and Collard (1999) that *habilis* and *rudolfensis* are not yet at the adaptive grade of *Homo*, and therefore suspect that they might indeed belong in the genus *Australopithecus*. However, such a systematic revision of the hominins is beyond the scope of this paper, therefore in this paper we refer to these latter two species as being in *Homo*, while noting that a more comprehensive systematic and phylogenetic analysis is presently underway.

Considering the conditions that Wood and Collard (1999, p. 70) cite as necessary for attribution of a fossil taxon to *Homo*, the Malapa fossils clearly fail two of their six criteria (both body mass and body proportions should be more similar to humans than australopiths) and quite probably fail on a third (should show obligate bipedalism *with limited climbing ability*). The status of the Malapa hominins on a fourth criterion (should show extended ontogenetic development) is currently unknown, though craniodental indicators currently appear inconsistent with a human pattern. The fifth criterion (teeth and jaws similar in relative size to humans) appears to position the Malapa hominins within *Homo*, though we would note that the small teeth from Malapa retain an australopith-like cuspal arrangement. The remaining criterion (should be more closely related to humans than to australopiths) is the essence of our argument, and here too we think that the Malapa fossils do not belong in the genus *Homo*, since they appear more closely related to *A. africanus* than to *H. sapiens*.

The Status of Stw 53

Another hominin specimen from South Africa, Stw 53, has a bearing on this discussion. Derived from the "Stw 53 Infill" (renamed Member 5A) and dating to either 2.6–2.0 Ma (Kuman and Clarke 2000) or perhaps less than 2.0 Ma (Herries et al. 2009, 2013; Pickering and Kramers 2010), the specimen was initially described as probably belonging to early *Homo* (Hughes and Tobias 1977), and soon came to be widely accepted as such (Cronin et al. 1981; Wood 1987, 1992). Eventually it was firmly attributed to *H. habilis* (Curnoe and Tobias 2006), though one of these authors shortly thereafter designated Stw 53 as the type specimen of a new species, "*H. gautengensis*" (Curnoe 2010). However, the attribution of Stw 53 to *Homo* has been challenged (Kuman and Clarke 2000; Clarke 2008, 2013; Berger et al. 2010). In particular, Stw 53 possesses a number of characters in the cranium and face that most closely align it with

A. africanus. These include closely spaced temporal lines, marked post-orbital constriction, a weakly developed supraorbital torus, narrow and non-projecting nasal bones, anterior pillars, marked nasoalveolar prognathism, medial and lateral expansion of the frontal process of the zygomatic bone, and laterally flared zygomatics (Clarke 2008; Berger et al. 2010). The derived craniodental morphology of *A. sediba* raises further doubt regarding the attribution of Stw 53 to early *Homo*, as Stw 53 looks more *A. africanus*-like relative to MH1, while MH1 looks more *Homo*-like relative to Stw 53. If Stw 53 really is an advanced representative of *A. africanus*, as it indeed appears to be, then there is little reason to consider it to represent a discrete species of early *Homo*. Without Stw 53, the diagnosis of the taxon "*H. gautengensis*" does not discriminate the remaining hypodigm from other previously named taxa, and there is little reason to consider it a valid species.

The assignment of Stw 53 to *A. africanus* has important ramifications for other specimens that were assigned to *Homo* based on their similarity to Stw 53. Most notably, OH 62 was referred to *H. habilis* based in large part on its resemblance to Stw 53 (Johanson et al. 1987). Following on this, KNM-ER 3735 was also tentatively referred to *H. habilis*, in part because of its likeness to OH 62 (Leakey et al. 1989). As a result, we must be cautious regarding our current perceptions of the postcranium of *H. habilis*, since the only skeletal remains that can be directly associated with *H. habilis* are the manual remains attributed to the type specimen OH 7 (Leakey et al. 1964). The foot skeleton OH 8 and the leg bones OH 35 have also been put forth as representing *H. habilis* (Susman and Stern 1982), and have even been argued to belong to the type specimen OH 7 (Susman 2008), although sufficient doubts exist (DeSilva et al. 2010) as to warrant caution in accepting this attribution (though see Susman et al. 2011). The postcranium of *A. sediba* appears more *Homo*-like than that of either OH 62 or KNM-ER 3735 (Berger et al. 2010), which supports the inference that these latter specimens might sample a late-surviving, non-robust australopith. In addition to these specimens, the assignment of A.L. 666-1 to *H. habilis* was likewise based, in part, on a favorable comparison with Stw 53 and OH 62 (Kimbel et al. 1997), thus those characters that aligned A.L. 666-1, Stw 53, and OH 62 might not be as diagnostic of early *Homo* as was initially thought.

The Taxonomic and Phylogenetic Status of *Australopithecus sediba*

Recent efforts with U–Pb dating at Sterkfontein have resulted in revised age estimates for *A. africanus* material from this site, the largest sample available for this taxon. Pickering and Kramers (2010) have produced a minimum age estimate of ca. 2.0 Ma for the top of Member 4 of Sterkfontein, possibly representing the latest appearance of this taxon in the fossil record. However, if Stw 53 is better placed in *A. africanus* (Clarke 2008; Berger et al. 2010), and if the Stw 53 Infill is actually dated to younger than 2.0 Ma (Herries et al. 2009, 2013; Pickering et al. 2011a, b), then the last appearance of this taxon could overlap with *A. sediba* at 1.977 Ma. If so, then *A. africanus* and *A. sediba* would not represent a simple anagenetic lineage. Although the samples of *A. africanus* from Taung and Makapansgat are imprecisely dated, they are generally considered to fall within the broad time span of 2.4–2.8 Ma (Delson 1984; Kimbel 1995; Vrba 1995; White 1995). Consequently, the age of *A. africanus* can be broadly constrained to somewhere between 2.8 and 2.0 (or less) Ma, though as White (1995) has noted, these first and last appearance datums are of relatively low fidelity, and we cannot be certain of the actual dates for the origin or extinction of *A. africanus*. As a result, the exact relative time-frames for both *A. africanus* and *A. sediba* are currently poorly understood.

Based on current literature, a probable age of 1.977 ± 0.0015 Ma might be considered inconsistent with the contention that *A. sediba* represents a candidate ancestor for the genus *Homo*. We note that a small number of fossils dated in excess of 1.977 Ma have been referred to the genus *Homo* (Howell et al. 1987; Hill et al. 1992; Schrenk et al. 1993; Kimbel et al. 1996, 1997; Suwa et al. 1996; Prat et al. 2005), while fossils of a broadly equivalent age to *A. sediba* have been assigned to *H. erectus* (Wood 1991; Gabunia and Vekua 1995). We contend, however, that the evidence for early *Homo* prior to 1.977 Ma is not unequivocal. Beyond a few isolated teeth, which can be difficult to diagnose taxonomically (Howell et al. 1987; Suwa et al. 1996; Pickering et al. 2011a), only three relatively poorly preserved and isolated craniodental specimens older than 1.977 Ma have been attributed to early *Homo*: A.L. 666-1 (Kimbel et al. 1997), KNM-BC 1 (Hill et al. 1992), and UR 501 (Schrenk et al. 1993). Questions regarding the taxonomic assignment of these fossils, as well as the provenience and dates of each of these specimens can and have been raised, thus a definitive presence of *Homo* prior to1.977 Ma has not been established (see also Kimbel 1995, 2009; White 1995; Pickering et al. 2011a). Along these lines, it also bears noting that an isolated *os coxa*, KNM-ER 3228, which is undeniably *Homo*-like in its overall morphology, was recovered from 1.95 Ma deposits at Koobi Fora (Rose 1984). While the KNM-ER 3228 and Malapa *ossa coxae* both share many derived *Homo*-like features, the Koobi Fora specimen appears to signal the establishment of larger-bodied, *H. erectus*-like (at least in terms of their postcranial morphology) hominins in East Africa that are roughly contemporaneous with the hominins from Malapa.

Notwithstanding, even if both the dates and the taxonomic assignment of the few fragmentary craniofacial surface finds stand, and even if the fossil hip bone from Koobi Fora signals the contemporaneous presence of hominins with more *Homo*-like body plans, it does not preclude *A. sediba* from being ancestral to the genus *Homo*. In this latter situation it is clear that the Malapa hominins themselves would be too young to be ancestral to the earliest fossils attributed to the genus *Homo*, but it is probable that the species *A. sediba* is not too young. We hypothesize that the fossils recovered from Malapa sample a population that in turn samples a species that almost certainly existed for some period both earlier and later in time (see Wood 2010, for an informative discussion of first and last appearance datums of hominin species). Although at present we have no fossil evidence to support such a notion, the reality is that Malapa represents a single point in a biological continuum, and the species *A. sediba* should not be considered exclusively endemic to Malapa, nor to a single moment in time that occurred approximately 1.977 Ma. We therefore propose that even if the dates and attributions of these three purported early *Homo* specimens stand (A.L. 666-1, KNM-BC 1, UR 501), the possibility remains that an ancestral population of *A. sediba* existed prior to the appearance of the earliest *Homo*. Given the mosaic of features seen in *A. sediba* that are shared by both *Australopithecus* and early *Homo*, and which are found in specimens in a sound temporal setting and of exceptional quality of preservation and completeness from Malapa, we contend that *A. sediba* presently represents the best candidate for the immediate ancestor of the genus *Homo*.

Conclusions

In our initial publication we suggested that *A. sediba* was derived from *A. africanus* via a cladogenetic event (Berger et al. 2010). It is possible that the two represent an anagenetic lineage, though as we point out above, a younger age estimate for Stw 53, and its recognition as a probable *A. africanus*, would argue against such a notion. Additional support for a cladogenetic interpretation comes from the constellation of *Homo*-like characters in *A. sediba*, alongside its *Australopithecus*-like traits, which push it outside the range of variability seen in the entirety of the *A. africanus* sample from the geographically disparate sites of Taung, Sterkfontein, and Makapansgat. Even though *A. sediba* is morphologically closest to *A. africanus*, the derived appearance of aspects of the cranium and postcranium outlined above prevent inclusion of MH1 and MH2 within the *A. africanus* hypodigm. It is important to note that the *A. africanus* sample is already recognized for its extremely high levels of morphological diversity, possibly even sampling more than one species (Lockwood and Tobias 2002; Clarke 2008). Given that *A. sediba* exceeds the total known morphological diversity of the *A. africanus* sample, yet is both temporally and geographically closest to the site of Sterkfontein, from which the largest and most diverse sample of *A. africanus* comes, we see this as strong evidence for its unique specific status. As a result, our present interpretation is that although there are features shared between *A. africanus* and *A. sediba*, there are nonetheless sufficient differences to warrant a specific separation between them.

Clearly more research into the tempo and mode of later Pliocene australopith evolution is needed. However, present fossil samples from across Africa allow us to hypothesize as to the phylogenetic position of *A. sediba*. On present evidence, *A. sediba* appears derived from *A. africanus*, probably via cladogenesis. In turn, *A. sediba* shares more derived characters with specimens assigned to early *Homo* than any other candidate ancestor, including *A. afarensis*, *A. garhi*, or *A. africanus*. In the initial announcement of *A. sediba* (Berger et al. 2010), we proposed four possible hypotheses regarding the phylogenetic position of *A. sediba*: (1) *A. sediba* is ancestral to *H. habilis*; (2) *A. sediba* is ancestral to *Homo rudolfensis*; (3) *A. sediba* is ancestral to *H. erectus*; and (4) *A. sediba* is a sister group to the ancestor of *Homo*. In an accompanying cladistic analysis, the most parsimonious cladogram placed *A. 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). Although caution must be employed when performing a cladistic analysis on possibly interdependent characters of uncertain taxonomic valence, our cladogram was consistent with our interpretations based on gross morphology and cranial and dental metrics. We are presently continuing our analysis of the phylogenetic status of *A. sediba* along numerous avenues of research, and although it is unlikely that our interpretations will meet with universal acceptance, we do look forward to continuing to expand our understanding of the genus *Australopithecus* and the debate regarding the origin of the genus *Homo*.

Acknowledgments We would like to thank our exceptional fossil preparation team, including C. Dube, B. Eloff, C. Kemp, M. Kgasi, M. Languza, J. Malaza, G. Mokoma, P. Mukanela, T. Nemvhundi, M. Ngcamphalala, S. Jirah, S. Tshabalala, and C. Yates, our chief preparator. Other individuals who have given significant support to this project include B. de Klerk, C. Steininger, B. Kuhn, L. Pollarolo, B. Zipfel, J. Kretzen, D. Conforti, J. McCaffery, C. Dlamini, H. Visser, R. McCrae-Samuel, B. Nkosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. We also thank E. Mbua, P. Kiura, V. Iminjili, and the National Museums of Kenya for access to comparative specimens in their care. S. Potze and T. Perregil facilitated access to the fossil hominins of the Ditsong Museum (formerly Transvaal Museum). T. Stidham assisted with the cladistic analysis of the Malapa hominins. J. Smilg facilitated CT scanning of the specimens. R. Clarke and F. Kirera provided valuable discussions on these and other hominin fossils in Africa. We would like to thank the South African Heritage

Resource agency for the permits to work on the Malapa site and the Nash family for granting access to the Malapa site and continued support of research on their reserve. The University of the Witwatersrand's Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeontological Science provided institutional support and facilities, as did the Gauteng Government, Gauteng Department of Agriculture, Conservation and Environment, and the Cradle of Humankind Management Authority. The South African Department of Science and Technology, the South African National Research Foundation, the Institute for Human Evolution (IHE), the Palaeontological Scientific Trust (PAST), the Andrew W. Mellon Foundation, the Africa Array Program, the United States Diplomatic Mission to South Africa, Duke University, the Ray A. Rothrock Fellowship of Texas A&M University, the Texas A&M Program to Enhance Scholarly and Creative Activities, the University of Zurich 2009 Field School, and Sir Richard Branson all provided substantial funding for the excavations and research conducted at Malapa.

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