

Special Issue: *Australopithecus sediba*

Malapa at 10: Introduction to the Special Issue on *Australopithecus sediba*

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ABSTRACT

This is a special issue on full descriptions of the *Australopithecus sediba* fossils. There are nine contributions:

- Williams, S.A., DeSilva, J.M., and de Ruiter, D.J.: Malapa at 10: Introduction to the Special Issue on *Australopithecus sediba*
- De Ruiter, D.J., Carlson, K.B., Brophy, J.K., Churchill, S.E., Carlson, K.J., and Berger, L.R.: The Skull of *Australopithecus sediba*
- Williams, S.A., Meyer, M.R., Nalla, S., García-Martínez, D., Nalley, T.K., Eyre, J., Prang, T.C., Bastir, M., Schmid, P., Churchill, S.E., and Berger, L.R.: The Vertebrae, Ribs, and Sternum of *Australopithecus sediba*
- Churchill, S.E., Green, D.J., Feuerriegel, E.M., Macias, M.E., Mathews, S., Carlson, K.J., Schmid, P., and Berger, L.R. The Shoulder, Arm, and Forearm of *Australopithecus sediba*
- Kivell, T.L., Churchill, S.E., Kibii, J.M., Schmid, P., and Berger, L.R.: The Hand of *Australopithecus sediba*
- Churchill, S.E., Kibii, J.M., Schmid, P., Reed, N.D., and Berger, L.R.: The Pelvis of *Australopithecus sediba*
- DeSilva, J.M., Carlson, K.J., Claxton, A.G., Harcourt-Smith, W.H., McNutt, E.J., Sylvester, A.D., Walker, C.S., Zipfel, B., Churchill, S.E., and Berger, L.R.: The Anatomy of the Lower Limb Skeleton of *Australopithecus sediba*
- Holliday, T.W., Churchill, S.E., Carlson, K.J., DeSilva, J.M., Schmid, P., Walker, C.S., and Berger, L.R.: Body Size and Proportions of *Australopithecus sediba*
- Zhang, A.Y. and DeSilva, J.M.: Computer Animation of the Walking Mechanics of *Australopithecus sediba*

This special issue is guest-edited by Scott A. Williams (Department of Anthropology, New York University) and Jeremy M. DeSilva (Department of Anthropology, Dartmouth College). This is article #1 of 9.

Malapa, the sole site from which the species *Australopithecus sediba* is currently known, was discovered on 8 August, 2008 (Berger 2012; Berger et al. 2010; de Ruiter et al. 2013a) (Figure 1). The first hominin fossil, belonging to Malapa Hominin 1 (MH1), was discovered a week later, on 15 August, followed by Malapa Hominin 2 (MH2) on 4 September. Limited material belonging to additional hominin individuals (Berger 2012, 2013; Berger et al. 2010; de Ruiter et al. 2013a; DeSilva et al. 2013) and associated fauna (Brophy et al. 2016; Dirks et al. 2010; Gilbert et al. 2015; Hartstone-Rose et al. 2013; Kuhn et al. 2011, 2016; Lazagabaster et al. 2018; Val et al. 2011, 2015) have also been recovered.

Australopithecus sediba represents the first widely accepted South African australopith species named since 1938. With an age estimate of 1.977 ± 0.0015 Ma, Malapa is one of the most tightly chronologically constrained hominin fossil sites in Africa (Pickering et al. 2011).

Ten years of research on *Au. sediba* have resulted in numerous publications, including the announcement (Berger et al. 2010), initial descriptions of the fossils (Carlson et al. 2011; Churchill et al. 2013; de Ruiter et al. 2013b; DeSilva et al. 2013; Kibii et al. 2011; Kivell et al. 2011; Schmid et al. 2013; Williams et al. 2013; Zipfel et al. 2011), and dating and context of the site of Malapa (Dirks and Berger 2013; Dirks

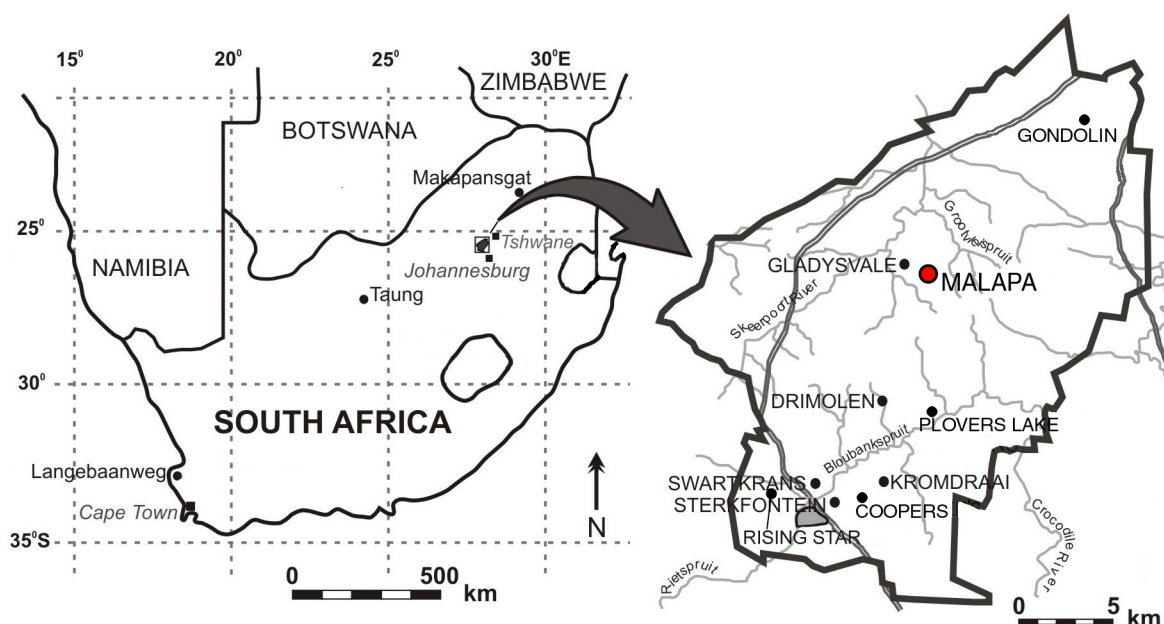


Figure 1. Map of the Cradle of Humankind World Heritage Area, Gauteng Province, South Africa. Malapa (red circle) and other hominin-bearing localities (black circles) are shown (modified from de Ruiter et al. [2009, 2013] with permission).

et al. 2010; Herries et al. 2013; Holt et al. 2016; Pickering et al. 2011). Subsequent publications have provided analyses of the diet surmised from dental calculus (Henry et al. 2012) and biomechanics (Ledogar et al. 2016); pathology, trauma, and taphonomy (L'Abbé et al. 2015; Randolph-Quinney et al. 2016; Val et al. 2018); growth and development (Cameron et al. 2017; Carlson et al. 2016; Lacruz et al. 2015); phylogenetic position of the species (Berger 2012; Carter et al. 2014; Dembo et al. 2015; de Ruiter et al. 2013b; Irish et al. 2014; Kimbel and Rak 2017; Ritzman et al. 2016; Robinson et al. 2018); and functional and evolutionary interpretations of other aspects of morphology (Daegling et al. 2016; de Ruiter et al. 2017; Irish et al. 2016; Meyer et al. 2017; Prang 2015a,b, 2016a,b; Rein et al. 2017; Williams 2011, 2012).

To date, two partial skeletons, MH1 and MH2, have been analyzed, while additional individuals await excavation/preparation (Berger 2012; de Ruiter et al. 2013a) (Figure 2). In the initial announcement of *Au. sediba* it was recognized that this species shares features across the skull and postcranial skeleton with both australopiths and representatives of early *Homo* (Berger et al. 2010). The authors of that announcement favored a grade-based attribution to *Australopithecus*, centered in part on the small brain size and relatively primitive nature of several aspects of the postcranial skeleton. At the same time, they hypothesized that *Au. sediba* represents the ancestor of the genus *Homo*, or a close sister group to that ancestor. Although *Au. sediba* has been widely accepted as a valid species, critics have challenged the hypodigm of the species (Been and Rak 2014; Rak and Been 2014) and the taxonomic choice to include it in the genus *Australopithecus* (as opposed to *Homo*) (see Balter 2010; Gibbons 2011). Further, the hypothesis that *Au. sediba* might be closely related to the ancestry of *Homo* (Berger et al. 2010; Pickering et al. 2011) has been chal-

lenged (Kimbel 2013; Kimbel and Rak 2017; Lordkipanidze et al. 2013; Spoor 2011; Wood and Harrison 2011; see also Balter 2010; Cherry 2010). However, recent Bayesian phylogenetic analyses (Dembo et al. 2015, 2016) provide support for a proposed link between *Au. sediba* and *Homo*. We look forward to continued scholarship addressing the phylogenetic position of *Au. sediba*, and we anticipate that the papers presented in this volume will contribute materially to this discussion.

Here, full descriptions of the available fossils recovered between 2008–2016 from Malapa are provided, along with comparative analyses of the material. Updates are given (e.g., on identification of elements or seriation of vertebrae and ribs), when relevant. The minimum number of fossil elements represented in this material is 135 (MNE=135), representing a minimum of three individuals (MNI=3). The skull is known from 16 specimens, ten from MH1 and 6 from MH2. The postcranial axial skeleton is known from 47 specimens, 18 from MH1 and 29 from MH2 (30 if the sacrum is counted here; it is included in the tally of pelvis elements). The upper limb (including the hand) is also known from 47 specimens, six from MH1 and 41 from MH2. The pelvis (ossa coxae and sacrum) consists of seven specimens, four from MH1 and three from MH2. The lower limb is known from 18 specimens, six from MH1, ten from MH2, one from MH4, and one specimen unassigned to an individual.

In this issue, de Ruiter and colleagues (2018) present the skull—the cranial, mandibular, and dental material. They highlight the mosaic of australopith-like and *Homo*-like characters that comprise *Au. sediba*. They conclude that although *Au. africanus* and *Au. sediba* likely shared a common ancestor, the precise nature of this shared ancestry remains unresolved. In contrast, the numerous features that



Figure 2. Malapa Hominins 1 and 2 associated fossils in approximate anatomical position. Adult female MH2 is shown on the left, juvenile male MH1 on the right. Note that the tibia positioned with MH1 is thought to belong to another proposed individual, MH4 (photo credit: Brent Stirton/Courtesy of Getty Images).

Au. sediba shares with members of the genus *Homo*, encompassing a variety of distinct functional systems, suggests to these authors that *Au. sediba* represents a candidate ancestor to the genus *Homo*, or a close sister-group to that ancestor. Williams and colleagues describe the postcranial axial skeleton—sternum, vertebrae, and ribs. They find that the *Au. sediba* vertebrae are among the most diminutive in the hominin fossil record. Additionally, Williams et al. challenge the notion that the Malapa assemblage represents more than one species, showing that there is no convincing evidence for this contention; rather, the postcranial axial material at Malapa is best understood of as the remains of two individuals, one adult (MH2), one juvenile (MH1) of the same species, *Au. sediba*.

The appendicular skeleton is described in four papers (Churchill et al. 2018b—upper limb; Kivell et al. 2018—hand and wrist; Churchill et al. 2018a—pelvis; DeSilva et al. 2018—lower limb) and two additional analyses focused on body size and proportions (Holliday et al. 2018) and

gait (Zhang and DeSilva 2018). Churchill and colleagues describe the upper limb (excluding the hand and wrist)—scapulae, clavicles, humeri, radii, and ulnae. They find the shoulder and forelimb of *Au. sediba* to be quite primitive, and fully consistent with arboreal locomotion in this hominin. Kivell and colleagues describe the wrist and hand. They find the *Au. sediba* hand to have a unique combination of anatomies, unlike that found in any other hominin, one functionally consistent with a hand capable of both powerful gripping (during climbing) and precision manipulation. Churchill and colleagues describe the ossa coxae and sacrum. They find that, while australopith-like in many respects, the *Au. sediba* pelvis possesses anatomies once thought to be unique to *Homo*. DeSilva and colleagues describe the lower limb—femora, tibiae, fibulae, ankle, and foot bones. They find a curious combination of anatomies unlike any other australopith, likely related to adaptations for both bipedal walking and frequent climbing. Holliday et al. estimate body mass and limb proportions in *Au. sed-*

iba, predicting that both MH1 and MH2 weighed approximately 35 kg. Additionally, limb proportions would have been similar to other australopiths and to *Homo floresiensis*, intermediate between African apes and modern humans. Zhang and DeSilva create a digital animation of the proposed walking mechanics of *Au. sediba*, including a hyper-pronatory gait.

These combined papers, encompassing virtually the entire skeleton, highlight the mosaic nature of the anatomies across the skull and skeleton of *Au. sediba* and solidify its status as a unique taxon, distinct from all other hominins, including *Au. africanus*. While some features are shared with *Au. africanus* and seem likely to represent symplesiomorphies, others are shared with *Homo* and are therefore either synapomorphies of an *Au. sediba*-*Homo* clade to the exclusion of *Au. africanus*, or are convergent characters in *Au. sediba* and members of the genus *Homo*. Still other features are autapomorphic for *Au. sediba*, highlighting its unique functional morphology and behavior along with its status as a late australopith-grade hominin that is potentially positioned in, or as the outgroup to, what is classically considered the *Homo* clade. The recovery and analysis of new Plio-Pleistocene fossil material both at Malapa and elsewhere will allow researchers to test these phylogenetic hypotheses.

Beyond what we have learned about the paleobiology of *Au. sediba* from the Malapa remains, the treatment of these fossils has led to new methodological insights and contributed to a paradigm shift in our field regarding both scientific and public access to fossils. Malapa faunal fossils have been subject to experimental laser preparation techniques (du Plessis et al. 2013; Roberts et al. 2012). Malapa remains have further stimulated innovative approaches for using medical and micro-CT scans to locate and preliminarily identify hominin fossils (Smilg 2017; Smilg and Berger 2015), and to digitally extract and reconstruct them (Churchill et al. 2013; DeSilva et al. 2013; Val et al. 2011; Williams et al. 2018). Manual preparation of breccia blocks from Malapa is occurring in view of the public at Maropeng (the visitor center for the Cradle of Humankind) and can be observed in real time online. Additionally, visitors to the Cradle of Humankind World Heritage Site can watch ongoing excavations at Malapa thanks to a viewing platform designed by award-winning architect Krynauw Nel.

From the beginning, Lee Berger and the fossil access committee at the Institute for Human Evolution (now the Evolutionary Studies Institute) at the University of the Witwatersrand have made the Malapa fossils openly available for scientific study by any serious scholar. Our science only works if published statements about fossils can be independently validated. While the authors of the manuscripts presented in this description of the Malapa remains have spent the last decade studying these fossils, and deliver an honest assessment and interpretation of this material, ours is not the last word. Nor do we expect our colleagues to simply believe what we have written, as science is rooted in evidence, not belief. We therefore invite our colleagues to study the material for themselves and to test the many hy-



Figure 3. Life reconstruction of *Australopithecus sediba* commissioned by the University of Michigan Museum of Natural History (© Sculpture Elisabeth Daynes / Photograph S. Entressangle).

potheses we have presented in these pages. To that end, the fossils discussed in these pages have been scanned and 3D surface renderings can be downloaded for free at <https://www.morphosource.org/>. The more eyes on these fossils, the better. Who knows what wonderful new insights will emerge as new generations of paleoanthropologists inevitably spot things about the Malapa fossils that we unwittingly missed? The availability of digital renderings of the fossils on MorphoSource, physical casts of the fossils made by the Marapo Stones and Bones Casting Project, and paleoartists' reconstructions like those by Elisabeth Daynes (Figure 3) do not just benefit scholarly pursuits; they are the kinds of K-12 and college educational resources that will inspire future generations of paleoanthropologists.

The first fossil of *Au. sediba* (U.W. 88-1) was discovered by Matthew Berger, then a nine-year-old, who happened to stop and examine the rock he tripped over while following his dog Tau away from the Malapa pit. His curiosity, and his father's identification of the fossil as a hominin clavicle,

set off a chain of events that has led us to this effort—31 international collaborators from 25 institutions describing the anatomy of two partial skeletons of *Au. sediba*—a decade later. Imagine for a moment that Matthew stumbled over the rock and continued following his dog without noticing the fossil. Perhaps Lee would have continued up the hill, away from Malapa, to search for more caves. If those events had occurred instead, our science would not know about *Au. sediba*, but *those fossils would still be there*, still encased in calcified clastic sediments, still waiting to be discovered. The fortuitous discovery of the Malapa fossils and other similarly fortuitous recent finds (e.g., Berger et al. 2015) should be reminders to us all that there is still so much to discover about our evolutionary past.

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