Australopithecus sediba: A New Species of Homo-Like Australopithecus from South Africa

Despite a rich African Plio-Pleistocene hominin fossil record, the ancestry of Homo and its relation to earlier australopithecines remain unresolved. Here we report on two partial skeletons with an age of 1.95 to 1.78 million years. The fossils were encased in cave deposits at the Malapa site in South Africa. The skeletons were found close together and are directly associated with craniodental remains. Together they represent a new species of Australopithecus that is probably descended from Australopithecus africanus. Combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early Homo than any other australopithecus species and thus might help reveal the ancestor of that genus.

The origin of the genus Homo is widely debated, with several candidate ancestors being proposed in the genus Australopithecus (1–3) or perhaps Kenyanthropus (4). The earliest occurrence of fossils attributed to Homo (H. aff. H. habilis) at 2.33 million years ago (Ma) in Ethiopia (5) makes it temporally antecedent to all other known species of the genus Homo. Within early Homo, the hypodigms and phylogenetic relationships between H. habilis and another early species, H. rudolfensis, remain unresolved (6–8), and the placement of these species within Homo has been challenged (9). H. habilis is generally thought to be the ancestor of H. erectus (10–13), although this might be questioned on the basis of the considerable temporal overlap that existed between them (14). The identity of the direct ancestor of the genus Homo, and thus its link to earlier Australopithecus, remains controversial. Here we describe two recently discovered, directly associated, partially articulated Australopithecus skeletons from the Malapa site in South Africa, which allow us to investigate several competing hypotheses regarding the ancestry of Homo. These skeletons cannot be accommodated within any existing fossil taxon; thus, we establish a new species, Australopithecus sediba, on the basis of a combination of primitive and derived characters of the cranium and postcranium.

The following is a description of Au. sediba: Order Primates Linnaeus 1758; suborder Anthropoidea Mivart 1864; superfamily Hominoidea Gray 1825; family Hominidae Gray 1825; genus Australopithecus Gray 1825; species Australopithecus sediba sp. nov.

Etymology. The word sediba means “fountain” or “wellspring” in the seSotho language.

Holotype and paratype. Malapa Hominin 1 (MH1) is a juvenile individual represented by a partial cranium, fragmentated mandible, and partial postcranial skeleton that we designate as the species holotype [Figs. 1 and 2, supporting online material (SOM) text S1, figs. S1 and S2, and table S1]. The first hominin specimen recovered from Malapa was the right clavicle of MH1 (UW88-1), discovered by Matthew Berger on 15 August 2008. MH2 is an adult individual represented by isolated maxillary teeth, a partial mandible, and partial postcranial skeleton that we designate as the species paratype. Although MH1 is a juvenile, the second molars are already erupted and in occlusion. Using either a human or an ape model, this indicates that MH1 had probably attained at least 95% of adult brain size (15). Although additional growth would have occurred in the skull and skeleton of this individual, we judge that it would not have appreciably altered the morphology on which this diagnosis is based.

Locality. The two Au. sediba type skeletons were recovered from the Malapa site (meaning “homestead” in seSotho), situated roughly 15 km NNE of the well-known sites of Sterkfontein, Swartkrans, and Kromdraai in Gauteng Province, South Africa. Detailed information regarding geology and dating of the site is in (16).

Fig. 1. Craniodental elements of Au. sediba. UW88-50 (MH1) juvenile cranium in (A) superior, (B) frontal, and (C) left lateral views. (D) UW88-8 (MH1) juvenile mandible in right lateral view. (E) UW88-54 (MH2) adult mandible in right lateral view. (F) UW88-8 mandible in occlusal view. (G) UW 88-54 mandible in occlusal view, and (H) UW 88-50 right maxilla in occlusal view (scale bars are in centimeters).
Diagnosis. *Au. sediba* can be distinguished from other species of *Australopithecus* by a combination of characters presented in Table 1; comparative cranial measures are presented in Table 2. A number of derived characters separate *Au. sediba* from the older chronospecies *Au. anamensis* and *Au. afarensis*. *Au. sediba* exhibits neither the extreme megadontia, extensive cranial cresting, nor facial prognathism of *Au. garhi*. The suite of derived features characterizing *Au. aethiopicus*, *Au. boisei*, and *Au. robustus*, in particular the pronounced cranial muscle markings, derived facial morphology, mandibular corpus robusticity, and postcanine megadontia, are absent in *Au. sediba*. The closest morphological comparison for *Au. sediba* is *Au. africanus*, as these taxa share numerous similarities in the cranial vault, facial skeleton, mandible, and teeth (Table 1). Nevertheless, *Au. sediba* can be readily differentiated from *Au. africanus* on both craniodental and postcranial evidence. Among the more notable differences, we observe that although the cranium is small, the vault is relatively transversely expanded with vertically oriented parietal walls and widely spaced temporal lines; the face lacks the pronounced, flaring zygomatics of *Au. africanus*; the arrangement of the supraorbital torus, nasoalveolar region, infraorbital region, and zygomatics result in a derived facial mask; the mandibular symphysis is vertically oriented with a slight bony chin and a weak post-incisive prominence; and the teeth are differentiated by the weakly defined buccal grooves of the maxillary premolars, the weakly developed median lingual ridge of the mandibular canine, and the small absolute size of the postcanine dentition. These exact differences also align *Au. sediba* with the genus *Homo* (see SOM text S2 for hypodigm used in this study). However, we consider *Au. sediba* to be more appropriately positioned within *Australopithecus*, based on the following craniodental features: small cranial capacity, pronounced glabelar region, patent premaxillary suture, moderate canine jugum with canine fossa, small anterior nasal spine, steeply inclined zygomaticoalveolar crest, high masseter origin, moderate development of the mesial marginal ridge of the maxillary central incisor, and relatively closely spaced premolar and molar cusps.

Postcranially, *Au. sediba* is similar to other australopiths in its small body size, its relatively long upper limbs with large joint surfaces, and the retention of apparently primitive characteristics in the upper and lower limbs (table S2). *Au. sediba* differs from other australopiths, but shares with *Homo* a number of derived features of the os coxa, including increased buttressing of the ilium and expansion of its posterior portion, relative reduction in the distance between the sacroiliac and hip joints, and reduction of distance from the acetabulum to the ischial tuberosity. These synapomorphies with *Homo* anticipate the reorganization of the pelvis and lower limb in *H. erectus* and possibly the emergence of more energetically efficient walking and running in that taxon (17). As with the associated cranial remains, the postcranium of *Au. sediba* is defined not by the presence of autapomorphic features but by a unique combination of primitive and derived traits.

Cranium. The cranium is fragmented and slightly distorted. The minimum cranial capacity of MH1 is estimated at 420 cm$^3$ (SOM text S4). The vault is ovoid, with transversely expanded, vertically oriented parietal walls. The widely spaced temporal lines do not approach the midline. Postorbital constriction is slight. The weakly arched supraorbital torus is moderately developed and laterally extended, with sharply angled lateral corners and a weakly defined supratoral sulcus. A robust glabelar region is evident, with only a faint depression of the supraorbital torus at the midline. The frontal process of the zygomatic faces primarily laterally and is expanded medially but not laterally. The zygomatic prominence does not show anterolateral expansion. The zygomatics are weakly flared laterally, resulting in an uninterrupted frontal profile of the facial mask that is squared superiorly and tapered inferiorly. The zygomaticoalveolar crests are long, straight, and steeply inclined, resulting in a high masseter origin. The root of the zygomatic begins at the anterior margin of M$^1$. The nasal bones are widened superiorly, become narrowest about one-third of the way down, and flare to their widest extent at their inferior margin. The nasal bones are elevated as a prominent ridge at the internasal suture, with an increasingly anterior projection inferiorly. The bone surface of the maxilla retreats gently away from the nasal aperture laterally, resulting in an everted margin of the superolateral portion of the aperture relative to the infraorbital region. The infraorbital portion of the nasal aperture becomes bluntly rounded. The infraorbital region is slightly convex (18) and is oriented at an approximately right angle to the alveolar plane. There is a trace of a premarginal suture near the superolateral margin of the nasal aperture. Prominent canine juga delineate moderately developed canine fossae. Anterior pillars are absent. The inferior margin of the nasal aperture is marked by a stepped nasal sill and a small but distinct anterior nasal spine. The subnasal region is straight in the coronal plane and only weakly projecting relative

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**Table 2.** A number of derived characters separate several *Australopithecus* species from each other. The combination of characters presented in Table 1; comparative cranial measures are presented in Table 2. A number of derived characters separate *Au. sediba* from the older chronospecies *Au. anamensis* and *Au. afarensis*. *Au. sediba* exhibits neither the extreme megadontia, extensive cranial cresting, nor facial prognathism of *Au. garhi*. The suite of derived features characterizing *Au. aethiopicus*, *Au. boisei*, and *Au. robustus*, in particular the pronounced cranial muscle markings, derived facial morphology, mandibular corpus robusticity, and postcanine megadontia, are absent in *Au. sediba*. The closest morphological comparison for *Au. sediba* is *Au. africanus*, as these taxa share numerous similarities in the cranial vault, facial skeleton, mandible, and teeth (Table 1). Nevertheless, *Au. sediba* can be readily differentiated from *Au. africanus* on both craniodental and postcranial evidence. Among the more notable differences, we observe that although the cranium is small, the vault is relatively transversely expanded with vertically oriented parietal walls and widely spaced temporal lines; the face lacks the pronounced, flaring zygomatics of *Au. africanus*; the arrangement of the supraorbital torus, nasoalveolar region, infraorbital region, and zygomatics result in a derived facial mask; the mandibular symphysis is vertically oriented with a slight bony chin and a weak post-incisive prominence; and the teeth are differentiated by the weakly defined buccal grooves of the maxillary premolars, the weakly developed median lingual ridge of the mandibular canine, and the small absolute size of the postcanine dentition. These exact differences also align *Au. sediba* with the genus *Homo* (see SOM text S2 for hypodigm used in this study). However, we consider *Au. sediba* to be more appropriately positioned within *Australopithecus*, based on the following craniodental features: small cranial capacity, pronounced glabelar region, patent premaxillary suture, moderate canine jugum with canine fossa, small anterior nasal spine, steeply inclined zygomaticoalveolar crest, high masseter origin, moderate development of the mesial marginal ridge of the maxillary central incisor, and relatively closely spaced premolar and molar cusps.

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Table 1. List of characters used to diagnose *Au. sediba*. These characters are commonly used in hominin phylogenetic studies (11, 38–40) or have been recorded as diagnostic for various hominin taxa in the past (3, 10, 36). Recognizing the potential pitfalls of performing a cladistic analysis on possibly interdependent characters of uncertain valence, we produced a cladogram from the data in this table as a test of the phylogenetic position of *Au. sediba* (fig. S3). Our most parsimonious cladogram places *Au. sediba* at the stem of the *Homo* clade.

<table>
<thead>
<tr>
<th>Characters</th>
<th><em>Au. afarensis</em></th>
<th><em>Au. garhi</em></th>
<th><em>Au. africanus</em></th>
<th><em>Au. sediba</em></th>
<th><em>H. habilis</em></th>
<th><em>H. rudolfensis</em></th>
<th><em>H. erectus</em></th>
<th><em>Au. aethiopicus</em></th>
<th><em>Au. boisei</em></th>
<th><em>Au. robustus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vault</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cranial capacity (1)</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td>Intermed.</td>
<td>Large</td>
<td>Large</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td>A-M incursion of temporal lines on frontal bone (9)</td>
<td>Strong</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
<td>Strong</td>
<td>Strong</td>
<td>Strong</td>
</tr>
<tr>
<td>Position of temporal lines on parietal bones</td>
<td>Crest</td>
<td>Crest</td>
<td>Variable</td>
<td>Wide</td>
<td>Variable</td>
<td>Wide</td>
<td>Wide</td>
<td>Crest</td>
<td>Crest</td>
<td>Crest</td>
</tr>
<tr>
<td>Compound temporal nuchal crest (males)</td>
<td>Extensive</td>
<td>?</td>
<td>Absent</td>
<td>Variable</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Extensive</td>
<td>Variable</td>
<td>Absent</td>
</tr>
<tr>
<td>Postorbital constriction (5)</td>
<td>Marked</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Slight</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Slight</td>
<td>Marked</td>
<td>Marked</td>
</tr>
<tr>
<td>Pneumatization of temporal squama</td>
<td>Extensive</td>
<td>?</td>
<td>Extensive</td>
<td>Reduced</td>
<td>Reduced</td>
<td>Reduced</td>
<td>Reduced</td>
<td>Extensive</td>
<td>Variable</td>
<td>Reduced</td>
</tr>
<tr>
<td>Facial hafting</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
<td>High</td>
<td>High</td>
</tr>
<tr>
<td>Frontal trigon</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Supraglenoid gutter width</td>
<td>Narrow</td>
<td>?</td>
<td>Narrow</td>
<td>Narrow</td>
<td>Narrow</td>
<td>Narrow</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
<td>Wide</td>
</tr>
<tr>
<td>Parietal transverse expansion/tuber</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td><strong>Facial skeleton</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glabellar region forms as prominent block</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Lat. half of infraorbital margin blunt and protruding</td>
<td>No</td>
<td>?</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Zygomatic arch relative to inferior orbital margin</td>
<td>Above</td>
<td>?</td>
<td>Level</td>
<td>Level</td>
<td>Level</td>
<td>?</td>
<td>Level</td>
<td>Above</td>
<td>Above</td>
<td>Above</td>
</tr>
<tr>
<td>Nasal bone projection above frontomaxillary suture</td>
<td>Expanded</td>
<td>?</td>
<td>Variable</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Tapered</td>
<td>Expanded</td>
<td>Expanded</td>
</tr>
<tr>
<td>Infraorbital foramen height (32)</td>
<td>High</td>
<td>?</td>
<td>Variable</td>
<td>High</td>
<td>High</td>
<td>?</td>
<td>High</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
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</table>

Numbers in parentheses in the first column refer to measures presented in Table 2; descriptions of these character states are provided in SOM text S3. Abbreviations are as follows: A-M, anteromedial; costa supr., costa supraorbitalis; intermed., intermediate; lat., lateral; med., medial; mesognath., mesognathic; mod., moderately; MMR, mesial marginal ridge; orthogn., orthognathic; procumb., procumbent; proj., projecting; TMJ, temporomandibular joint.
<table>
<thead>
<tr>
<th>Characters</th>
<th><em>Au. afarensis</em></th>
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<th><em>Au. sediba</em></th>
<th><em>H. habilis</em></th>
<th><em>H. rudolfensis</em></th>
<th><em>H. erectus</em></th>
<th><em>Au. aethiopicus</em></th>
<th><em>Au. boisei</em></th>
<th><em>Au. robustus</em></th>
</tr>
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<tbody>
<tr>
<td>Canine juga prominence/anterior pillars</td>
<td>Prominent</td>
<td>Prominent</td>
<td>Variable</td>
<td>Prominent</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
<td>Pillars</td>
</tr>
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<td>Patency of premaxillary suture</td>
<td>Obliterated</td>
<td>?</td>
<td>Occasional</td>
<td>Trace</td>
<td>Obliterated</td>
<td>Obliterated</td>
<td>Obliterated</td>
<td>Obliterated</td>
<td>Obliterated</td>
<td>Occasional</td>
</tr>
<tr>
<td>Inferolateral nasal aperture margin</td>
<td>Sharp</td>
<td>Sharp</td>
<td>Variable</td>
<td>Blunt</td>
<td>Variable</td>
<td>Blunt</td>
<td>Blunt</td>
<td>Blunt</td>
<td>Variable</td>
<td>Blunt</td>
</tr>
<tr>
<td>Eversion of superior nasal aperture margin</td>
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<td>?</td>
<td>None</td>
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<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Variable</td>
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<tr>
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<td>?</td>
<td>Triangular</td>
<td>Triangular</td>
<td>Triangular</td>
<td>Triangular</td>
<td>Gutter</td>
<td>Gutter</td>
<td>Gutter</td>
<td>Gutter</td>
</tr>
<tr>
<td>Nasoalveolar clivus contour in coronal plane</td>
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<td>Stepped</td>
<td>Stepped</td>
<td>Stepped</td>
<td>Stepped</td>
<td>Stepped</td>
<td>Smooth</td>
<td>Smooth</td>
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<tr>
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<td>Variable</td>
<td>Weak</td>
<td>Weak</td>
<td>Marked</td>
<td>Moderate</td>
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<tr>
<td>Anterior nasal spine rel. to nasal aperture</td>
<td>Absent</td>
<td>?</td>
<td>Anterior</td>
<td>Anterior</td>
<td>Anterior</td>
<td>?</td>
<td>Enlarged</td>
<td>Posterior</td>
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<td>Angular indentation of lateral orbital margin</td>
<td>?</td>
<td>?</td>
<td>Indented</td>
<td>Curved</td>
<td>Curved</td>
<td>Curved</td>
<td>?</td>
<td>Curved</td>
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<tr>
<td>Zygomatic prominence development</td>
<td>Prominent</td>
<td>?</td>
<td>Prominent</td>
<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Prominent</td>
<td>Prominent</td>
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</tr>
<tr>
<td>Lateral flaring of zygomatic arches</td>
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<td>?</td>
<td>Marked</td>
<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Slight</td>
<td>Marked</td>
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<tr>
<td>Outline of superior facial mask</td>
<td>Tapered</td>
<td>?</td>
<td>Tapered</td>
<td>Squared</td>
<td>Squared</td>
<td>Squared</td>
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<td>Tapered</td>
<td>Tapered</td>
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<tr>
<td>Zygomaticoalveolar crest/malar notch relative to alveolar plane</td>
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<td>?</td>
<td>Straight</td>
<td>Notch</td>
<td>Notch</td>
<td>Notch</td>
<td>Notch</td>
<td>Straight</td>
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<td>Straight</td>
</tr>
<tr>
<td>Zygomaticomaxillary steps and fossae present</td>
<td>No</td>
<td>?</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Height of masseter origin (35)</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
<td>High</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
<td>High</td>
<td>High</td>
</tr>
<tr>
<td>Malar thickness (31)</td>
<td>Thin</td>
<td>?</td>
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<td>Thin</td>
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<td>Posterior</td>
<td>Variable</td>
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<td>Canine-to-postcanine ratio (maxillary/mandibular) (61, 62)</td>
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<td>Postcanine crown area (maxillary/mandibular) (57, 59)</td>
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<td>Small</td>
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<td>Maxillary I1: MMR development, lingual face</td>
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<td>Moderate</td>
<td>Weak</td>
<td>Weak</td>
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<td>?</td>
<td>Moderate</td>
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<td>Yes</td>
<td>No</td>
<td>No</td>
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<td>Thick</td>
<td>Hyper</td>
<td>Hyper</td>
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<tr>
<td>Positions of apices of lingual (LO) and buccal (BC) cusps of premolars and molars relative to occlusal margin</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC at margin, BC slightly lingual</td>
<td>LC mod. buccal, BC strongly lingual</td>
<td>LC mod. buccal, BC strongly lingual</td>
<td>LC mod. buccal, BC strongly lingual</td>
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</table>
Table 2. Craniodental measurements for early hominins in Africa. *Au. sediba* is represented by MH1. Unless otherwise defined, measurements are based on (6). Some measures were unavailable for specimens of *Au. afarensis* and *Au. garhi*, in which case the character states in Table 1 were estimated. Several character states in Table 1 are recorded as variable, although only species average values are presented here. Measurements are in millimeters unless otherwise indicated. Descriptions of character states presented in Table 1 that are based on measurements from this table are provided in SOM text S3. Abbreviations are as follows: br, bregma; ek, ectoconchion; ekm, ectomolare; fmt, frontomolare temporale; ft, frontotemporale; g, glabella; mf, maxillofrontale; n, nasion; ns, nasospinale; or, orbitale; po, porion; pr, prosthion; rhi, rhinion; zm, zygomaxillare; zy, zygion; zyo, zygoorbitale.

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<td>1</td>
<td>Cranial capacity (cm³)</td>
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<td>3</td>
<td>Bi-porionic breadth (po-po)</td>
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<td>4</td>
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<td>5</td>
<td>Postorbital constriction index (4/14 × 100)</td>
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<td>6</td>
<td>Horizontal distance between TMJ and M²/M³</td>
<td>83</td>
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<td>Facial prognathism (sellion-prosthion angle)</td>
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<td>8</td>
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<td>Minimum frontal breadth (ft-ft)</td>
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<td>Glabella to bregma (g-br)</td>
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<td>11</td>
<td>Frontal chord (n-br)</td>
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<td>13</td>
<td>Superior facial height (n-pr)</td>
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<td>14</td>
<td>Superior facial breadth (fmt-fmt)</td>
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<td>15</td>
<td>Bi-orbital breadth (ek-ek)</td>
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<td>16</td>
<td>Bizygomatic breadth (zy-zy)</td>
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<td>Bimaxillary breadth (zm-zm)</td>
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<td>Interorbital breadth (mf-mf)</td>
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<td>Orbital breadth (mf-ek)</td>
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<td>Nasal bridge length (n-rhi)</td>
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<td>Nasal bridge breadth superior</td>
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<td>24</td>
<td>Nasal bridge breadth at anterior lacrimal crests</td>
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<td>25</td>
<td>Nasal bridge breadth inferior</td>
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<td>26</td>
<td>Nasal bridge height (nasion subtense at anterior lacrimal crests)</td>
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<td>Nasal aperture height (rhi-ns)</td>
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<td>Maximum nasal aperture width</td>
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<td>Infraorbital foramen height (to inferior orbital margin)</td>
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<td>Prosthion to zygomaxillare (pr-zm)</td>
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<td>Prosthion to zygomatic (pr-zym)</td>
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<td>Incisor alveolar length</td>
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<td>Premolar alveolar length</td>
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continued on next page
### Table: Dental Size and Proportions

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<td>Cross-sectional area at M3</td>
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<td>Mandibular canine crown area</td>
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### Notes:

- Item Measurement 41 to 62 denote small-bodied to the facial plane. The face is mesognathic. The palate is consistently deep along its entire extent, with a parabolic dental arcade.

**Mandible.** Descriptions apply to the more complete juvenile (MH1) mandible unless otherwise stated. The nearly vertical mandibular symphysis presents a weak lateral tubercle, resulting in a slight mental trigone, and a weak mandibular incurvation results in a slight mentum osseum. The post-incisive planum is weakly developed and almost vertical. Both mandibular corpora are relatively gracile, with a low height along the alveolar margin. The extramolar sulcus is relatively narrow in both mandibles. In MH1, a moderate lateral prominence displays its greatest protrusion at the mesial extent of M2, with a marked decrease in robusticity to P4; in MH2 the moderate lateral prominence shows its greatest protrusion at M3, with a marked decrease in robusticity to M2. The alveolar prominence is moderately deep with a notable medial projection posteriorly. The anterior and posterior subalveolar fossae are continuous. The ramus of MH1 is tall and narrow, with nearly parallel, vertically oriented anterior and posterior borders; the ramus of MH2 is relatively broader, with nonparallel anterior and posterior borders (fig. S2). The mandibular notch is relatively deep and narrow in MH1 and more open in MH2. The coronoid extends farther superiorly than the condyle. The condyle is mediolaterally broader and anteroposteriorly narrow. The endocondyloid buttress is absent in MH1, whereas in MH2 a weak endocondyloid buttress approaches the condyle without reaching it.

**Dental size and proportions.** The dentition of the juvenile (MH1) is relatively small, whereas preserved molars of the adult (MH2) are even smaller (Fig. 3 and fig. S4). For MH1, the maxillary central incisor is distinguishable only from the reduced incisors of *Au. robustus*. The maxillary canine is narrower than all canines of *Au. africanus* except TM 1512, whereas the mandibular canine falls well below the range of *Au. africanus*. Premolars and molars are at the lower end of the *Au. africanus* range and within that of *H. habilis*–*H. rudolfensis* and *H. erectus*. Molar dimensions of the adult individual (MH2) are smaller than those of *Au. africanus*, are at or below the range of those of *H. habilis–H. rudolfensis*, and are within the range of those of *H. erectus*. *Au. sediba* mirrors the *Au. africanus* pattern of maxillary molars that increase slightly in size posteriorly, though it differs in that the molar tends to be considerably larger in the latter taxon. Conversely, the *Au. sediba* pattern varies slightly from that seen in specimens KNM-ER 1813, OH 13, and OH 65 and *H. erectus*, wherein the molars increase from M1 to M3 but then decrease to M4. In broad terms, the teeth of *Au. sediba* are similar in size to teeth of specimens assigned to *Homo* but share the closely spaced cusp apices seen in *Australopithecus*.

**Postcranium.** Preserved postcranial remains of *Au. sediba* (table S1) denote small-bodied...
Numerous features of the hip, knee, and ankle indicate that *Au. sediba* was a habitual biped. In terms of size and morphology, the proximal and distal articular ends of the femur and tibia fall within the range of variation of specimens attributed to *Au. africanus*. However, several derived features in the pelvis link the Malapa specimens with later *Homo*. In the os coxa (Fig. 4), *Au. sediba* shares with *Homo* a pronounced acatabulocristal buttress; a more posterior position of the cristal tubercle; a superoinferiorly extended posterior iliac blade, with an expanded retroauricular area; a sigmoid-shaped anterior inferior iliac spine; a reduced lever arm for weight transfer between the auricular surface and the acetabulum; an enlarged and rugose iliofemoral ligament attachment area; a tall and thin pubic symphseal face; and a relatively short ischium with a deep and narrow tuboacetabular sulcus. These features are present in taxonomically unassigned postcranial remains from Koobi Fora (KNM-ER 3228) and Olduvai Gorge (OH 28), which have been argued to represent early *Homo* (20), as well as in early *Homo erectus* (21). An os coxa from Swartkrans (SK 3155) has been considered by some to also represent early *Homo* (22) but can be seen to possess the australopith pattern in most of these features. In addition, *Au. sediba* shares with later *Homo* the human-like pattern of low humeral-to-femoral diaphyseal strength ratios, in contrast to the ape-like pattern seen in the *H. habilis* specimen OH 62 (table S2).

Although aspects of the pelvis are derived, the foot skeleton is more primitive overall, sharing with other australopiths a flat talar trochlea articular surface with medial and lateral margins with equal radii of curvature, and a short, stout, and medially twisted talar neck with a high horizontal angle and a low neck torsion angle.
The calcaneus is markedly primitive in its overall morphology: the bone is strongly angled along the proximodistal axis, with the point of maximum inflexion occurring at an enlarged peroneal trochlea; the lateral plantar tubercle is lacking; the calcaneal axis is set about 45° to the transverse plane; and the calcaneocuboid facet is vertically set and lacks an expanded posterior projection for the beak of the cuboid (23).

Discussion. The age and overall morphology of *Au. sediba* imply that it is most likely descended from *Au. africanaus*, and appears more derived toward *Homo* than do *Au. africanaus, Au. garhi*, and *Au. africanaus*. Elsewhere in South Africa, the Sterkfontein cranium Stw 53, dated to 2.0 to 1.5 Ma, is generally considered to represent either *H. habilis* (10, 24, 25) or perhaps an undiagnosed form of early *Homo* (26). It played an important role in the assignment of OH 62 to *H. habilis* (27). However, the derived craniodental morphology of *Au. sediba* casts doubt on the attribution of Stw 53 to early *Homo* [see also (28)]; Stw 53 appears to be more primitive than MH1 in retaining closely spaced temporal lines; marked postorbital constriction; a weakly developed supraorbital torus; narrow, nonprojecting nasal bones; anterior pillars; marked nasoalveolar prognathism; medial and lateral expansion of the frontal process of the zygomatic bone; and laterally flared zygomatics. If Stw 53 instead represents *Au. africanaus*, the assignment of OH 62 to *H. habilis* becomes tenuous. Attribution of the partial skeleton KNM-ER 3735 to *H. habilis* was tentatively based, in part, on a favorable comparison with OH 62 and on the hypothesis that there were no other contemporaneous non-robust australopith species to which it could be assigned in East Africa (29). As a result, the interpretation of KNM-ER 3735 as *H. habilis* also becomes uncertain.

The phylogenetic significance of the co-occurrence of derived postcranial features in *Au. sediba, H. erectus*, and a sample of isolated fossils generally referred to *Homo* sp. indet. (table S2) is not clear: The latter might represent early *H. erectus*, it might sample the postcranium of *H. rudolfensis* (which would then imply an evolutionary pathway from *Au. sediba* to *H. rudolfensis* to *H. erectus*), or it might represent the postcranium of *H. habilis* (which would suggest that OH 62 and KNM-ER 3735 (two specimens with ostensibly more primitive postcranial skeletons) do not belong in this taxon). If the latter possibility holds, it could suggest a phylogenetic sequence from *Au. sediba* to *H. habilis* to *H. erectus*. Conversely, although the overall postcranial morphology of *Au. sediba* is similar to that of other australopiths, a number of derived features of the os coxa align the Malapa hominins with later *Homo* (*H. erectus*) to the exclusion of other australopiths. Additionally, *Au. sediba* shares a small number of cranial traits with *H. erectus* that are also exhibited in the *H. habilis–H. rudolfensis* hypodigm, including slight postorbital constriction and convexity of the infraorbital region (18).

Following on this, MH1 compares favorably with SK 847 (*H. erectus*) in the development of the supraorbital torus, nasal bones, infrasphenoid region, frontal process of the zygomatic, and subnasal projection. However, MH1 differs from SK 847 in its relatively smaller size, the robust glabellar region, the weakly developed supratrochlear sulcus, the steeply inclined zygomaticoalveolar crests with a high masseter origin, and the moderate canine juga, all features aligning MH1 with *Australopithecus*. It is thus not possible to establish the precise phylogenetic position of *Au. sediba* in relation to the various species assigned to early *Homo*. We can conclude that combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early *Homo* than does any other known australopith species (Table 1 and table S2) and thus represents a candidate ancestor for the genus, or a sister group to a close ancestor that persisted for some time after the first appearance of *Homo*.

The discovery of a <1.95-million-year-old (16) australopith that is potentially ancestral to *Homo* is seemingly at odds with the recovery of older fossils attributed to the latter genus (5) or of approximately contemporaneous fossils attributable to *H. erectus* (6, 30). However, it is unlikely that Malapa represents either the earliest or the latest temporal appearance of *Au. sediba*, nor does it encompass the geographical expanse that the species once occupied. We hypothesize that *Au. sediba* was derived via cladogenesis from *Au. africanaus* (=3.0 to 2.4 Ma), a taxon whose first and last appearance dates are also uncertain (31). The possibility that *Au. sediba* split from *Au. africanaus* before the earliest appearance of *Homo* cannot be discounted.

Although the skull and skeleton of *Au. sediba* do evince derived features shared with early *Homo*, the overall body plan is that of a hominin at an australopith adaptive grade. This supports the argument, based on endocranial volume and craniodental morphology, that this species is most parsimoniously attributed to the genus *Australopithecus*. The Malapa specimens dem-
onstrate that the evolutionary transition from a small-bodied and perhaps more arboreal-adapted hominin (such as *Australopithecus afarensis*) to a larger-bodied, possibly full-striding terrestrial biped (such as *Homo erectus*) occurred in a mosaic fashion. Changes in functionally important aspects of pelvic morphology, including a reduction of the sacroacetabular weight-bearing load arm and enhanced acetabulocrural buttressing (reflecting enhancement of the hip extensor mechanism), enlargement of the iliofemoral ligament attachment (reflecting a shift in position of the line of transfer of weight to behind the center of rotation of the hip joint), enlargement of the acetabulocristal buttress (denoting enhancement of an alternating pelvic tilt mechanism), and reduction of the distance from the acetabulum to the ischial tuberosity (reflecting a reduction in the ischial tuberosity) were all associated with the higher degree of apparent size differences, the overall level of dimorphism, if these sex attributes are correct, appears slight in the Malapa hominins and was probably similar to that evinced by modern humans.

The pattern of dental eruption and epiphyseal fusion exhibited by MH1 indicates that its age at death was 12 to 13 years by human standards, whereas in MH2 the advanced degree of occlusal attrition and epiphyseal closure indicates that it had reached full adulthood (SOM text S1). Although juvenile, MH1 exhibits pronounced development of the supraorbital region and canine jagus, and the nasal groove of the mandible, and large rugose muscle scars in the skull, all indicating that this was a male individual. And, although fully adult, the mandible and skeleton of MH2 are smaller than in MH1, which, combined with the less rugose muscle scars and the shape of the pubic body of the os coxa, suggests that MH2 was a female. In terms of dental dimensions, MH1 has mandibular molar occlusal surface areas that are 10.7% (M1) and 8.1% (M2) larger than those of MH2. Dimorphism in the postcranial skeleton likewise is not great, though the juvenile status of MH1 tends to confound efforts to assess adult body size. The diameter of the proximal epiphysis for the femoral head of MH1 (29.8 mm) is approximately 9.1% smaller than the superoinferior diameter of MH2’s femoral head (32.7 mm). It is likely that MH1 would have experienced some appositional increase in joint size before maturity, thus this disparity would probably have decreased somewhat. The distal humeral epiphysis of MH1 is fully fused and its articular breadth (35.3 mm) is only marginally larger than that of MH2 (35.2 mm). Thus, although the dentition and postcranial skeleton are at odds in the degree of apparent size differences, the overall level of dimorphism, if these sex attributes are correct, appears slight in the Malapa hominins and was probably similar to that evinced by modern humans.

References and Notes

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Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5975/195/DC1

SOM Text 1 to 4

Figs. S1 to S5

Tables S1 and S2

References

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