

# Mandibular Remains Support Taxonomic Validity of *Australopithecus sediba*

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Since the announcement of the species *Australopithecus sediba*, questions have been raised over whether the Malapa fossils represent a valid taxon or whether inadequate allowance was made for intraspecific variation, in particular with reference to the temporally and geographically proximate species *Au. africanus*. The morphology of mandibular remains of *Au. sediba*, including newly recovered material discussed here, shows that it is not merely a late-surviving morph of *Au. africanus*. Rather—as is seen elsewhere in the cranium, dentition, and postcranial skeleton—these mandibular remains share similarities with other australopithecids but can be differentiated from the hypodigm of *Au. africanus* in both size and shape as well as in their ontogenetic growth trajectory.

Mandibular remains are well represented in the hominin fossil record and have been included among the holotypes of numerous early hominin taxa, including *Australopithecus sediba* from Malapa (1, 2). The suggestion (3–5) that insufficient consideration was given to intraspecific variation when *Au. sediba* was diagnosed as a discrete taxon can be further investigated by using recently recovered mandibular remains. Most notable among these are two conjoined fragments, UW88-128 and UW88-129, that can be refit to the previously published mandibular specimen UW88-54 (1) to form a near complete right hemi-mandible with complete dentition of an adult individual, Malapa Hominin 2 (MH2) (Fig. 1). These new portions allow us to examine the premolar and M<sub>1</sub> regions of the mandibular corpus of an adult probable female of *Au. sediba* and provide a first look at the mandibular incisors and premolars of this taxon. In addition, we can now directly compare the mandibular canines of probable male and female individuals of *Au. sediba*.

As is seen in the cranium and postcranial skeleton of *Au. sediba* (1, 6–14), the reassembled mandible of MH2 exhibits a mosaic of morphological characters that align it with specimens attributed to both *Australopithecus* and early *Homo*. For instance, the mandible of MH2 shares with *Au. africanus* such features as a moderately developed lateral prominence, moderately developed lateral superior and marginal tori, weakly delineated anterior and posterior marginal tubercles,

a well-developed ectocondyloid buttress, and a well-developed lateral eminence of the ramus. However, it differs from *Au. africanus* and resembles specimens of early *Homo* by evincing relief between the alveolar prominence and the subalveolar fossa; possessing a small, steeply inclined postincisive planum; and revealing weakly developed endocoronoid and endocondyloid buttresses, which result in a triangular planum that is ill-defined along its inferior extent (15). However, gross morphology in hominin mandibles tends to be variable, as is seen in a direct comparison of MH1 and MH2; thus, we turn to size and shape analyses of mandibular corpora to assess the taxonomic validity of *Au. sediba*.

Linear dimensions of mandibular corpora have been shown to be taxonomically informative within fossil representatives of the genus *Homo* (2). In absolute measures, the mandibular corpus of MH2 is slightly taller and narrower than that of MH1 (Fig. 2 and table S1). There is considerable overlap in mandibular corpus height between *Au. afarensis*, *Au. africanus*, *Au. sediba*, *H. habilis*, *H. erectus*, and even *H. sapiens*. The corpus of MH1 is narrower than *Au. africanus* at the level of the P<sub>4</sub>; it overlaps with the lower end of the range of *Au. africanus* at the level of the M<sub>1</sub>, although only a single specimen of *Au. africanus*, the otherwise large-toothed Stw 498, is narrower. MH1 overlaps with *H. habilis* and *H. erectus* in width at the level of the P<sub>4</sub> and M<sub>1</sub>, although again plotting near the lower end of the range of both taxa. The newly reassembled mandible of MH2 is narrower still than MH1 at the level of the P<sub>4</sub> and M<sub>1</sub>, plotting below the range for *Au. africanus*, *H. habilis*, and *H. erectus*; it appears among the narrowest in the African hominin fossil record. Calculating corpus cross-sectional area by using the formula for an ellipse, MH1 and MH2 have similar values at the level of both the P<sub>4</sub> and M<sub>1</sub>. The cross-sectional areas of the mandibular corpora of *Au. sediba* are small at the level of the P<sub>4</sub> and

M<sub>1</sub>, plotting at or below the lowest end of the range of values for *Au. africanus* and within the ranges of *H. habilis* and *H. erectus*. In linear dimensions, mandibular corpus width—and to a lesser extent cross-sectional area—thus appear useful for discriminating *Au. sediba* from *Au. africanus* and for aligning the former taxon with specimens attributed to early *Homo*. This is particularly the case with the adult specimen MH2.

To better understand the nature of differentiation between early hominin taxa in both size and shape of mandibular corpora, we replicated the approach of Lague and colleagues (2) using specimens attributed to species of *Australopithecus* and early *Homo* in Africa and Georgia (15). Seven of the eight measures originally used (2) could be replicated in the reassembled mandible of MH2 and form the basis of our analyses. Randomization of “distinctness values” (RDV) (2, 16) reveals that within-group variance is less than between-group variance; thus, it appears that the mandibles of *Australopithecus* and *Homo* that we examined do indeed reflect a taxonomic signal. We therefore investigated the size and shape of the mandibular corpus of *Au. sediba* in relation to other hominins. We performed a multivariate analysis of variance (MANOVA) (15), the overall results of which can be visualized as a plot of between-group differences, scaled to within group variances (Fig. 3A). The major result illustrated in this plot is that *H. sapiens* are clearly distinct from early hominins, especially the robust australopithecids, whereas *Au. sediba* clusters with the nonrobust australopithecids and early *Homo*. This major axis indicates that human mandibles are small overall, have relatively narrow corpora, and relatively mesiodistally (MD) elongated (though small overall) canine alveoli (table S2).

Among the early hominins, *Au. sediba* most closely matches this pattern. A planned contrast within the MANOVA results explicitly comparing *Au. sediba* and *Au. africanus* revealed a significant difference between them ( $F_{8,23} = 2.55$ ,  $P = 0.037$ ). The difference between these two taxa primarily involved the smaller overall size of the mandible, the relatively deeper mandibular corpus, and the relatively MD elongated premolar row in *Au. sediba* when compared with that of *Au. africanus* (table S3). In other words, the mandibles of *Au. sediba* are not only scaled differently than those of *Au. africanus*, they are also shaped differently. Removal of humans from the ordination resulted in a primary axis that principally defined differences between the robust australopithecids and the remaining early hominins (Fig. 3B). However, the secondary axis—approximately one-third the magnitude of the first—separated *Au. sediba* clearly from all other early hominins (planned contrast,  $P = 0.034$ ). This effect was due to *Au. sediba* having a relatively MD elongated canine alveolus (table S3). Excluding size as a variable results in ordinations similar to those in Fig. 3, demonstrating that size is not unduly influencing the analysis (fig. S1).

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# Australopithecus sediba

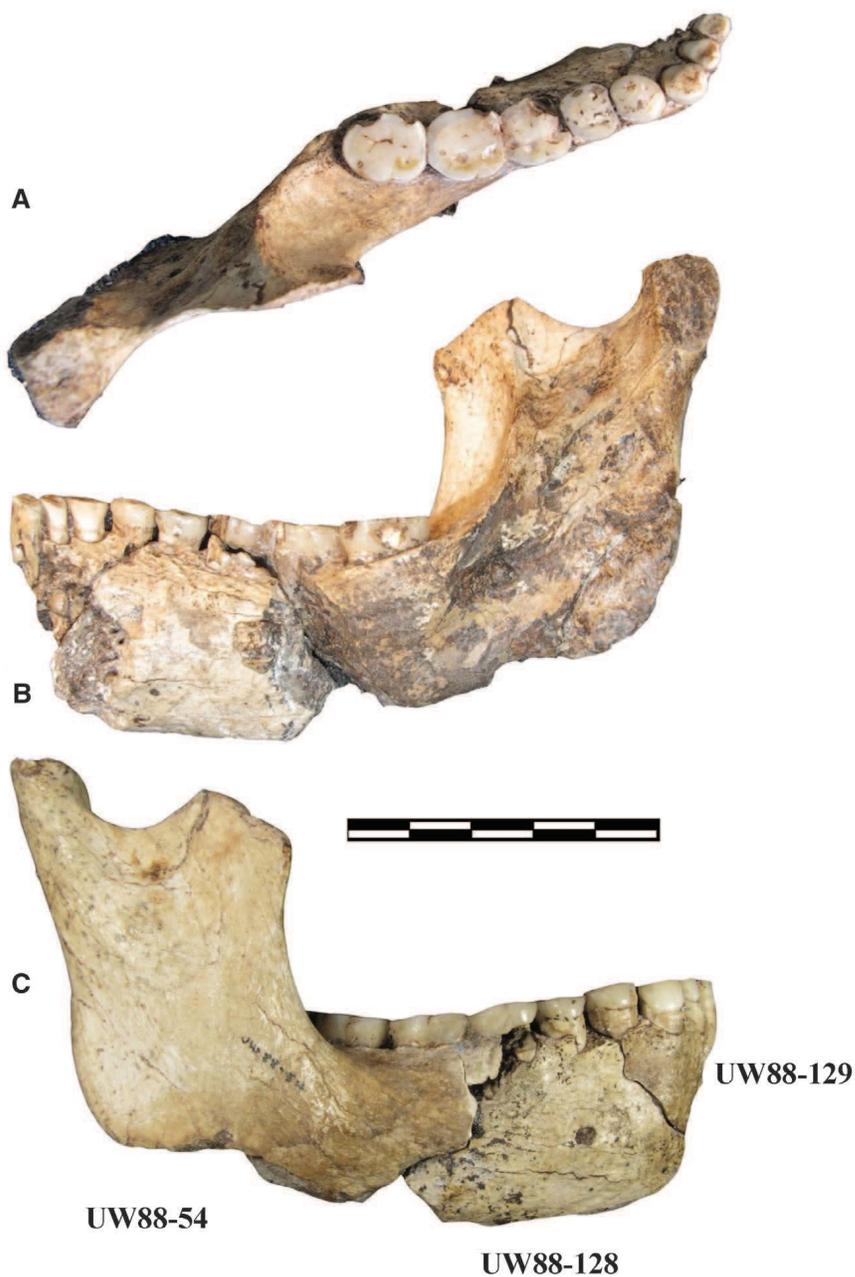
The mandibular molars of *Au. sediba* were recorded as being small, similar to specimens attributed to early *Homo* (1), and we now have data on the remaining mandibular dentition from MH2 (figs. S2 and S3). Although the incisors of MH2 are too worn to reliably reconstruct their mesiodistal (MD) MD lengths, the buccolingual (BL) breadth of the  $I_1$  plots at the lowest end of the range of *Au. africanus* and *H. erectus* but within the range of *Au. robustus* and *H. sapiens*. The BL breadth of the  $I_2$  plots at the lowest end of the range of *Au. africanus*, but within the range of *Au. robustus*, *Au. boisei*, *H. erectus*, and *H. sapiens*. The only specimen of *Au. africanus* that overlaps with MH2 in the BL breadth of both incisors is Stw 151, a specimen described as more derived toward *Homo* than are the remainder of the Sterkfontein Member 4 sample (17). As in MH1 (1), the MD length of the canine of MH2 is small, plotting below the range for *Au. africanus* and *H. habilis*, and within the range of *H. erectus* and *H. sapiens*. In BL breadth, the canine of MH1 plots near the lowest end of the range for *Au. africanus* and close to the mean for *H. habilis* and *H. erectus*, whereas the canine of MH2 falls below the range of these early *Homo* taxa as well as *Au. africanus*. Indeed, the canine of MH2, and to a lesser extent of MH1, is among the smallest in the hominin fossil record. Likewise, the premolars of MH2 are small and generally plot at or below the lower end of the ranges seen in *Au. africanus* and *H. habilis*, appearing especially MD shortened; where the  $P_4$  of *Au. sediba* overlaps with *Au. africanus*, only a single specimen attributed to *Au. africanus*, Stw 112, appears smaller than MH2. Conversely, the premolars of *Au. sediba* plot within the ranges of *H. erectus* and *H. sapiens* dentitions.

The shape of the premolars is also diagnostic; occlusal outline analysis of both the  $P_3$  and the  $P_4$  by using elliptical function Fourier analysis (EFFA) positions them as outliers relative to both *Au. africanus* and *Au. robustus*, demonstrating that these teeth differ in both size and shape from other South African australopiths (fig. S4) (15). Although the complete dentition of MH2 appears small in size similar to that of *Homo*, it shares with *Australopithecus* a pattern of increasing tooth size along the molar row (fig. S5).

Using mandibular molars, it was originally estimated that the dentition of MH1 was between 8.1 and 10.7% larger than that of MH2 (1). We can now extend this to include canines: The canine of MH1 is ~9.6% larger than the canine of MH2 in MD length and ~20.0% larger in BL breadth. Converting this to a square root of the basal crown area, the canine of MH1 is ~15% larger than that of MH2. This can be compared with canine dimorphism levels derived for other hominins by using the “mean” method of estimation (15, 18). With a value of 1.15, *Au. sediba* is intermediate between taxa such as *Au. afarensis* (1.21) and *Au. boisei* (1.21) on the one hand and taxa such as *Au. africanus* (1.11), *Au. robustus* (1.11), *H. erectus* (1.13), and *H. sapiens* (1.07)

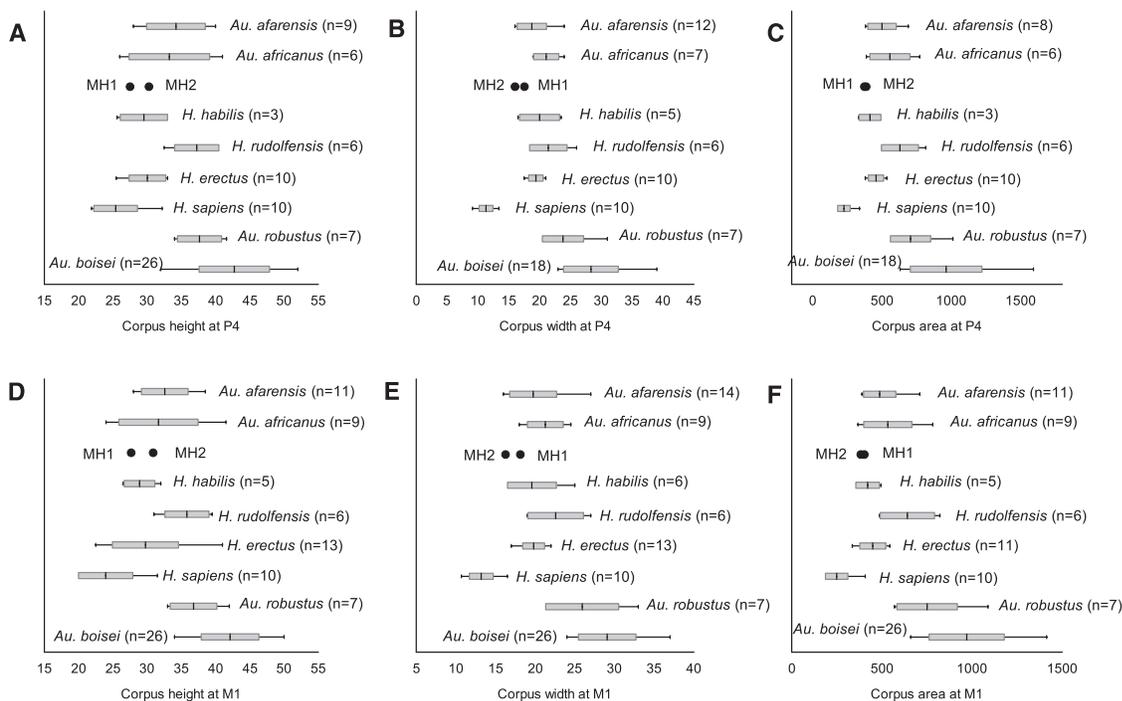
on the other. Although the “mean” method tends to overestimate dimorphism in fossil species for which sex is generally unknown (18), with probable male and female individuals *Au. sediba* provides a known sample. Sample sizes are small for the hominin taxa, although these data nonetheless serve to highlight the dimorphism evident in the otherwise small canines of *Au. sediba*. Although the canines of *Au. sediba* are small and lack the diagnostic lingual relief seen in *Au. africanus*, a pattern shared with early *Homo*, they reveal a degree of canine dimorphism that approaches levels seen in several other australopith taxa and that is also close to that of *H. erectus*.

Last, we tested whether *Au. sediba* shares a common pattern of development with *Au. africanus* using Euclidean distance matrix analysis (EDMA) (15). We examine the ontogeny of mandibular shape in the fossil species *Au. sediba*, *Au. africanus*, and *H. erectus* and in the extant species *H. sapiens* and *Pan troglodytes*. Juvenile samples are roughly the same developmental age as MH1 (pre- $M_3$  eruption), and therefore by necessity this comparison captures only one stage of development. EDMA was performed on mean forms of extant samples and on individual fossil juvenile and adult specimens as representatives of their respective species (table S4) (19–22). In addition, simulated hypothetical juvenile *Au.*



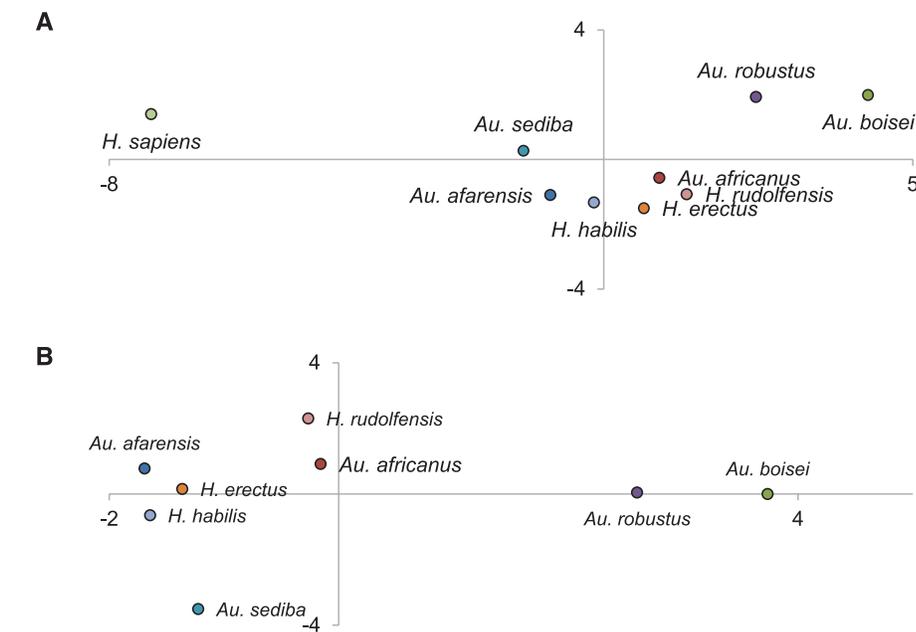
**Fig. 1. Right hemi-mandible of adult probable female individual MH2 from Malapa.** Conjoined fragments UW88-128 and UW88-129 refit to UW88-54 in (A) occlusal view, (B) medial view, and (C) lateral view. The coronoid process is truncated because of damage. Scale bar, 5 cm.

**Fig. 2. Mandibular corpus measures of *Au. sediba* compared with other early hominin taxa.** (A) Corpus height at P<sub>4</sub>. (B) Corpus width at P<sub>4</sub>. (C) Corpus area at P<sub>4</sub> computed by using the formula for an ellipse [ $\pi(\text{height}/2) * (\text{width}/2)$ ]. (D) Corpus height at M<sub>1</sub>. (E) Corpus width at M<sub>1</sub>. (F) Corpus area at M<sub>1</sub> computed by using the formula for an ellipse [ $\pi(\text{height}/2) * (\text{width}/2)$ ]. Measures for *Au. afarensis*, *Au. boisei*, *H. habilis*, *H. rudolfensis*, and *H. erectus* specimens are from (23–25); measures of *Au. africanus*, *Au. sediba*, *Au. robustus*, and *H. sapiens* specimens were taken by D.J.d.R. on original materials.



*sediba* forms were created by using species-specific growth patterns derived from *Au. africanus* and *H. erectus* in order to explore the effect of these respective growth patterns when applied to *Au. sediba* (15). The overall EDMA results can be visualized in a principal coordinates plot (PCOORD) (Fig. 4) and show that *Au. sediba* displays a pattern of growth that differs from *Au. africanus*, *P. troglodytes*, and *H. sapiens* [further discussion is available in (15)]. Rather, the growth pattern of *Au. sediba* is most similar to *H. erectus*. *Au. sediba* also differs in magnitude of growth from *Au. africanus* and *H. erectus* as well as both of the extant taxa (Fig. 4). Because these data are scaled to facilitate cross-species comparisons, the magnitude of change should be interpreted as the magnitude of shape change during growth rather than absolute size. Additionally, the simulated hypothetical juvenile forms and their associated growth trajectories further support a distinction between mandibular growth in *Au. sediba* versus both fossil hominin species [further discussion is available in (15)], with neither a *H. erectus*-like nor an *Au. africanus*-like pattern or magnitude of growth resulting in simulated final juvenile forms similar to the actual MH1 juvenile, which further suggests that ontogenetic change in the mandible of *Au. sediba* is unique.

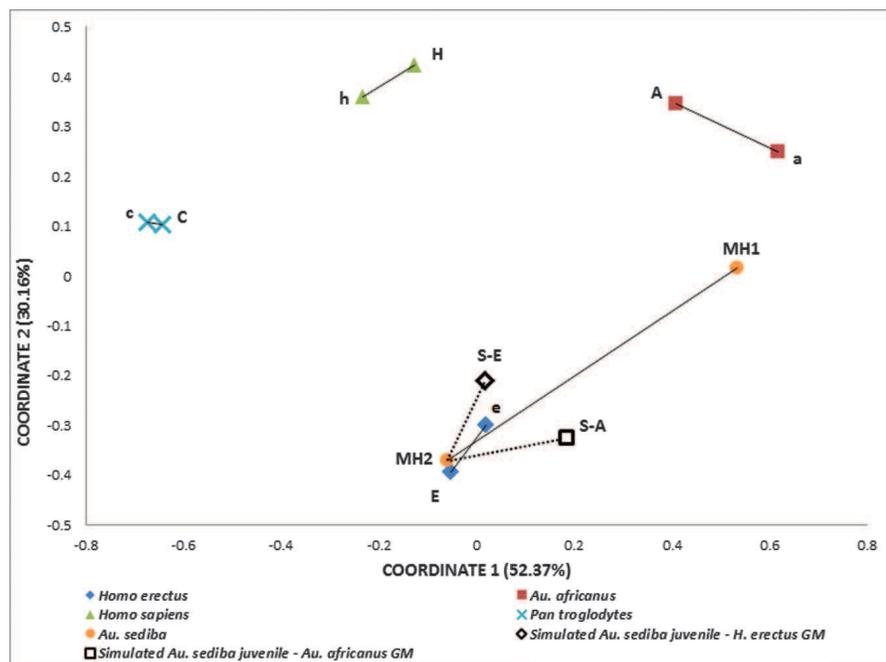
The small size of the newly recovered mandibular corpus of *Au. sediba*—combined with its reduced dentition, in particular of the canines and premolars—separate it from its otherwise close morphological affinity, *Au. africanus*. The distinction between *Au. sediba* and *Au. africanus* extends to more than just a size difference; the two taxa differ in shape as well, with *Au. sediba* possessing a relatively smaller and deeper corpus, and a relatively elongated premolar row when compared



**Fig. 3. Visualization of the first two canonical axes from the MANOVA on form.** (A) Including humans. (B) Excluding humans. Details of canonical plot interpretation are available in the text, and computation is available in supplementary text S1. Measures for *Au. afarensis*, *Au. boisei*, *H. habilis*, *H. rudolfensis*, and *H. erectus* specimens are from (23–25); measures of *Au. africanus*, *Au. sediba*, *Au. robustus* and *H. sapiens* specimens were taken by D.J.d.R. on original materials. Plot aspect ratio indicates the relative magnitude (eigenvalues) of the respective canonical axes.

with those of *Au. africanus*. Likewise, the premolars of *Au. sediba* differ in occlusal outline shape from those of *Au. africanus* and *Au. robustus*, plotting as distinct outliers relative to the South African australopiths. The divergent growth trajectory of *Au. sediba* compared with those of both extant and fossil taxa further highlights the singular nature of the mandible of *Au. sediba*.

We interpret these substantial size and shape differences as upholding the taxonomic distinction initially proposed for *Au. sediba* (1), in particular as compared with specimens of *Au. africanus*. And where the *Au. sediba* mandibles differ from those of *Au. africanus*, they appear most similar to representatives of early *Homo* in both size and shape.



**Fig. 4. Ontogenetic trajectories of mandibular shape variability for *Au. sediba* (MH1, MH2), *Au. africanus* (A, a), *H. erectus* (E, e), *H. sapiens* (H, h), *P. troglodytes* (C, c), and two simulated trajectories for *Au. sediba* (S-A, S-E). Upper- and lowercase labels indicate adults and juveniles, respectively, and are connected by a line that indicates a “growth trajectory” in shape space. Black dotted lines denote simulated growth trajectories connecting MH2 with “hypothetical” juvenile forms. Details of interpretation are available in the text. Details of the samples and analysis can be found in (15). Linear measurements for all specimens are derived from laser surface scans taken by L.S. and K.B.C. on original material.**

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## Supplementary Materials

[www.sciencemag.org/content/340/6129/1232997/suppl/DC1](http://www.sciencemag.org/content/340/6129/1232997/suppl/DC1)  
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Supplementary Text  
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References (26–33)

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