ANTHROPOLOGY

Temporal evidence shows *Australopithecus sediba* is unlikely to be the ancestor of *Homo*

Andrew Du* and Zeresenay Alemseged

Understanding the emergence of the genus *Homo* is a pressing problem in the study of human origins. *Australopithecus sediba* has recently been proposed as the ancestral species of *Homo*, although it postdates earliest *Homo* by 800,000 years. Here, we use probability models to demonstrate that observing an ancestor's fossil horizon that is at least 800,000 years younger than the descendant's fossil horizon is unlikely (about 0.09% on average). We corroborate these results by searching the literature and finding that within pairs of purported hominin ancestor–descendant species, in only one case did the first-discovered fossil in the ancestor postdate that from the descendant, and the age difference between these fossils was much less than the difference observed between *A. sediba* and earliest *Homo*. Together, these results suggest it is highly unlikely that *A. sediba* is ancestral to *Homo*, and the most viable candidate ancestral species remains *Australopithecus afarensis*.

INTRODUCTION

Understanding the origin of the genus *Homo* is one of paleoanthropology's most enduring questions. A key element in resolving this question is determining which species may have been ancestral to our genus. Because *Australopithecus sediba* has recently been proposed as a candidate ancestral species (*1–3*), it is essential that we critically evaluate this claim. Fossil specimens from *A. sediba* are currently only known from Malapa, South Africa, which is dated to 1.977 million years (Ma) ago (*2*). These fossils postdate by 800,000 years (0.8 Ma) the only known specimen from the oldest, and currently unnamed, species of *Homo* (hereafter, "earliest *Homo*"), which is dated to 2.8 to 2.75 Ma ago at Ledi-Geraru, Ethiopia (*4, 5*). Most recently, the argument for *A. sediba* being ancestral to *Homo* was continued by Robinson *et al.* (*6*), who discussed how a fossil horizon from an ancestral species could be much younger than a horizon from the descendant and claimed, "On temporal grounds alone one cannot dismiss the possibility that *A. sediba* could be ancestral to the genus *Homo*" (p. 1).

Two conditions must both be met for *A. sediba* to be ancestral to *Homo* and for the recovery of an *A. sediba* fossil horizon that is much younger than an earliest *Homo* horizon (barring severe postdepositional stratigraphic mixing or errors in taxonomic assignment or dating): (i) Because an ancestor's fossil horizon can only postdate a descendant's if there is some overlap in the species' temporal ranges (Fig. 1A), the descendant must have speciated from the ancestor via budding cladogenesis (Fig. 1B). For our study, we assume that *Homo* cladogenetically budded from *A. sediba* because, otherwise, this analysis would be unnecessary, and the argument for *A. sediba* being ancestral to *Homo* would be illogical (because the *A. sediba* fossil horizon postdates the earliest *Homo* horizon). (ii) Given the large amount of time separating the fossil horizons of *A. sediba* and earliest *Homo*, there must have been substantial overlap between the two species' temporal ranges, such that the end of the *A. sediba* range is able to postdate the beginning of the earliest *Homo* range by at least 0.8 Ma (Fig. 2). If range overlap is less than 0.8 Ma, then the *A. sediba* fossil horizon cannot be 0.8 Ma younger than the earliest *Homo* horizon (assuming *A. sediba* was ancestral to *Homo*) (Figs. 1A and 2). As range overlap increases, so does the probability of sampling the end and beginning of the *A. sediba*

and earliest *Homo* ranges, respectively, such that their horizons are at least 0.8 Ma apart (Fig. 2A). This second condition forms the theoretical basis for our probability model.

While Robinson *et al.* (*6*) are correct that it is possible for an ancestor's fossil horizon to be much younger than the descendant's, a more informative question would be, "How likely is this chronological pattern?" We build upon previous work concerning the evolutionary relationships of *A. sediba* (*1–3, 6*) and construct a probability model, which serves as a null hypothesis test, to evaluate whether *A. sediba* is ancestral to *Homo*. We assume that (i) *A. sediba* and earliest *Homo* each had temporal ranges of 0.97 Ma (*6*), (ii) the probability of recovering fossils throughout each species' range is uniform through time (*7, 8*), and (iii) the probability of sampling an *A. sediba* fossil horizon does not affect the probability of sampling an earliest *Homo* fossil horizon, i.e., these are independent events (see Materials and Methods). From these assumptions, we quantify the probability of finding one fossil horizon from *A. sediba* that is at least 0.8 Ma younger than one horizon from earliest *Homo* (i.e., the observed data), assuming *A. sediba* is ancestral to *Homo* (i.e., the null hypothesis). The computed probabilities are equivalent to *P* values, and if they are exceptionally low, this would suggest that *A. sediba* is unlikely to be the ancestor of *Homo* (i.e., the null hypothesis is falsified). We calculate multiple *P* values as a function of the overlap between the two species' true temporal ranges, which is currently unknown. We analyze temporal evidence only (*6*) and do not consider morphological data concerning the evolutionary relationship between *A. sediba* and *Homo* (*1, 9–11*). We also analyze the historical record of hominin discovery and calculate the geological age difference between initial fossil discoveries in purported ancestor and descendant species. The aim here is to corroborate our theoretical probability results and to empirically assess how likely it is for an ancestor's fossil horizon to postdate a descendant's by at least 0.8 Ma.

RESULTS

The probability of finding an ancestor's fossil horizon that is at least 0.8 Ma younger than the descendant's is, by definition, zero when temporal range overlap is less than or equal to 0.8 Ma (Figs. 2A and 3 and Eq. 5c). This probability monotonically increases with range overlap when overlap is greater than 0.8 Ma (Fig. 3 and Eq. 5c) for reasons discussed above (Fig. 2A). However, even when the two species' ranges completely overlap, which is impossible for ancestor-descendant

Department of Organismal Biology and Anatomy, The University of Chicago, Chicago, IL 60637, USA.
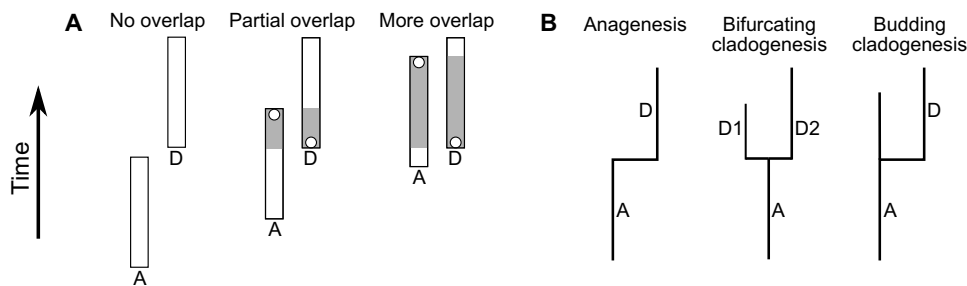*Corresponding author. Email: andrewdu@uchicago.edu

Fig. 1. Conditions where an ancestor's fossil horizon can be younger than the descendant's. For both figures, "A" represents the ancestral species, and "D" represents the descendant species. (**A**) When there is no overlap between the temporal ranges of an ancestor and a descendant, an ancestor's fossil horizon can never be younger than the descendant's. If ranges partially overlap (gray), then an ancestor's fossil horizon can postdate the descendant's (fossil horizons are represented by white circles). The maximum age difference between a younger horizon from an ancestor and an older horizon from a descendant is ultimately constrained by the amount of range overlap, such that the age difference can never be greater than the amount of overlap. (**B**) Three different ways a descendant can speciate from an ancestor. Budding cladogenesis is the only speciation mode that produces ancestors and descendants with overlapping temporal ranges and is therefore the only mode where an ancestor's fossil horizon can postdate the descendant's. "D1" and "D2" represent two sister lineages, which are both descendants of "A." (B) is modified after Fig. 1 in (25).
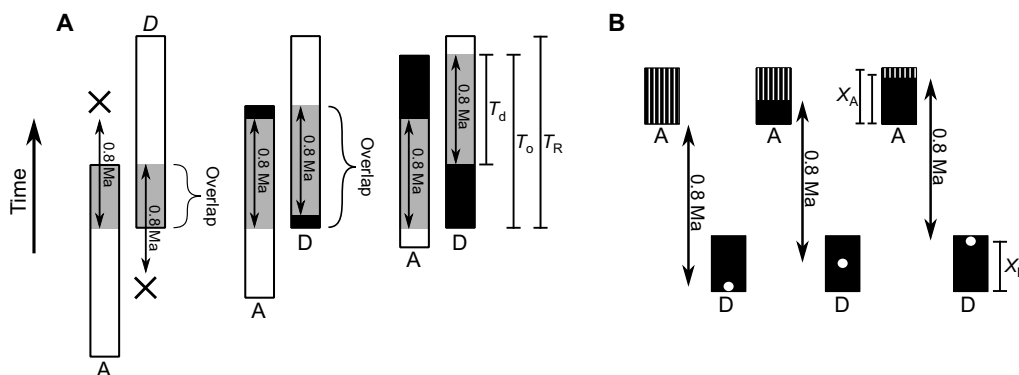

Fig. 2. Schematic used to derive the model for quantifying the probability that an ancestor's fossil horizon postdates the descendant's by at least 0.8 Ma. For both figures, "A" represents the ancestral species, and "D" represents the descendant species. (**A**). The probability of sampling an ancestor's fossil horizon that is at least 0.8 Ma younger than the descendant's is ultimately a function of the amount of overlap between both species' temporal ranges relative to the age difference of interest (which here is 0.8 Ma). When range overlap is less than 0.8 Ma, the ancestor's horizon cannot postdate the descendant's by 0.8 Ma (represented by the Xs in the leftmost example). In the middle example, there is enough range overlap where 0.8 Ma separates the end and beginning of the ancestor's and descendant's ranges, respectively (black), and each species' fossil horizon must be sampled from these black regions. As overlap increases (rightmost example), so does the size of the black regions and the probability of sampling an ancestor's fossil horizon that is at least 0.8 Ma younger than the descendant's horizon. The rightmost example is used to illustrate the three variables from our probability model (Eq. 5c): T_d represents the age difference of interest (i.e., 0.8 Ma), T_o represents the amount of range overlap, and T_R represents the duration of the entire temporal range (i.e., 0.97 Ma). (**B**) Focusing on the black regions, a descendant's fossil horizon (white circles) can sample some time near the species' age of origination (leftmost example), which means that the ancestor's horizon can be sampled anywhere in its own black region and still be at least 0.8 Ma younger than the descendant horizon (white-striped region). If the descendant's horizon is found in the middle of the black region (middle example), the ancestor's horizon must sample the younger half of its own black region. If the descendant horizon samples the end of its black region (rightmost example), the ancestor's horizon must sample the end of its temporal range. The rightmost example is used to illustrate the X_A and X_D variables (Eq. 3), each of which represents the distance from the beginning of the black region to the temporal location of the fossil horizon in the ancestor's and descendant's range, respectively. For the ancestor's horizon to postdate the descendant's by at least 0.8 Ma, X_A must be greater than X_D, and two iterations of this are shown.

species and is only presented as a theoretical upper bound, the computed P value is only 0.016 (Fig. 3 and Eq. 5c). If we treat all possible values of range overlap as equally likely, the mean P value over all overlap values is 0.0009 (Eq. 6c). We have confirmed our probability model results with simulations (fig. S1 and data file S5).

Reviewing the paleoanthropology literature, we recorded 28 hypothesized ancestor-descendant species pairs (table S1). There is only one instance where an ancestor's first-discovered fossil postdated the descendant's: ancestor *Homo erectus sensu lato* (Kedung Brubus 1) dated to 0.8 to 0.7 Ma ago (12) and descendant *Homo antecessor* (ATD6-1) dated to 0.9 to 0.8 Ma ago (13). The age difference between these specimens (i.e., 0.1 Ma) is far less than the age difference observed

between *A. sediba* and earliest *Homo* (i.e., 0.8 Ma) (Fig. 4). When the mean and SD of the 28 observed age differences are used to generate a normal distribution model (bell curve in Fig. 4), 0.8 Ma falls in the >99.9th percentile, which translates to a P value less than 0.001.

DISCUSSION
We have demonstrated using probability models that the null hypothesis of *A. sediba* being ancestral to *Homo* can be falsified. That is, it is very unlikely (about 0.09% on average) to find an *A. sediba* fossil horizon that is at least 0.8 Ma younger than an earliest *Homo* horizon, if the former species is actually ancestral to the latter. The prior record of
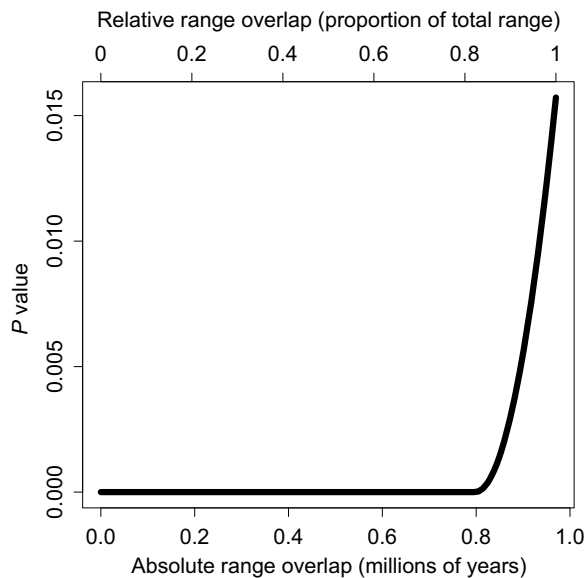
Fig. 3. Probability of finding an ancestor's fossil horizon that is at least 0.8 Ma younger than the descendant's fossil horizon (*P* value). *P* values are plotted as a function of the overlap between the two species' true, unknown temporal ranges, each of which is assumed to be 0.97 Ma in duration (*6*).
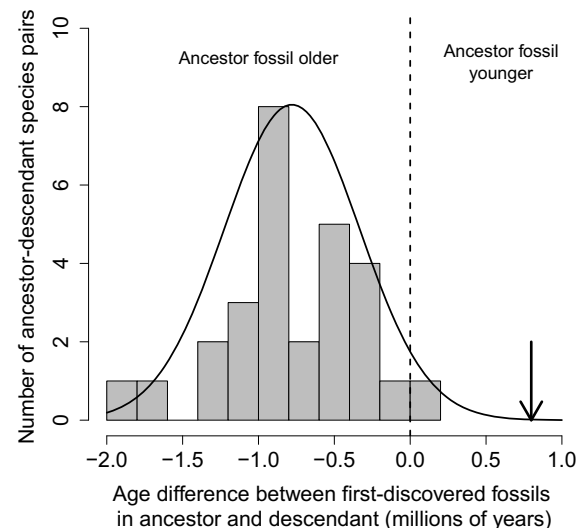

Fig. 4. Histogram of the geological age differences between first-discovered fossils in purported hominin ancestor-descendant species pairs (*n* = 28). Negative age differences represent those species pairs where the ancestor's first-discovered fossil is older than the descendant's, and positive age differences indicate the opposite. The black arrow represents the observed age difference between *A. sediba* (hypothesized ancestor) and earliest *Homo* at Ledi-Geraru (hypothesized descendant). The bell curve represents a normal distribution model, generated using the sample mean and SD of the 28 observed age differences.

paleoanthropological discoveries also reflects the rarity of cases in which this chronological pattern is observed, further supporting that *A. sediba* is unlikely to be ancestral to *Homo*.

We can explore how strongly our assumptions influenced our modeling results. We calculated our *P* values, assuming the 2.8-Ma-old Ledi-Geraru mandible actually belongs to *Homo* (*5*). Some researchers dispute this (*14*), so we also ran our analyses assuming A.L. 666-1 (2.33 Ma-old)—a specimen widely regarded as *Homo*—represents the oldest *Homo* specimen (*15*). Although a handful of researchers argue that all pre–1.9-Ma-old specimens assigned to *Homo* are invalidly named or are poorly dated (*2, 3*), we view this assertion as unlikely [as does Robinson *et al.* (*6*)]. By selecting a younger fossil to represent the oldest *Homo* specimen, we are decreasing the observed age difference between *A. sediba* and earliest *Homo*, which should increase the *P* values overall (Eq. 5c). We also explored whether our choice of 0.97 Ma to represent hominin temporal durations might affect our results because using a longer duration will increase the amount of time associated with a given percentage of range overlap between two species, and this should increase *P* values as well (Eq. 5c). We therefore reran our analyses assuming hominin temporal durations of 2 Ma, which is at the larger end of estimated mean species durations in African large mammals [all African large mammals: 2.3 Ma (*16*); eastern African bovids: 1.4 Ma (*17*); large mammals in the Omo-Turkana Basin, Ethiopia/Kenya: 1.4 Ma (*17*); *Australopithecus anamensis-afarensis*: 1.2 Ma (*7, 8*)]. Results show that calculated *P* values are still small even when relaxing the age of earliest *Homo* to 2.33 Ma ago or hominin temporal durations to 2 Ma. For example, *P* values exceed 0.05 only when range overlap is at least 70%, and the mean and maximum *P* values over all possible overlap values are only 0.04 and 0.20, respectively (Eqs. 5c and 6c, and fig. S2, A and B). When both assumptions are simultaneously relaxed, *P* values exceed 0.05 when overlap is at least 50%, and the mean and maximum *P* values are 0.093 and 0.34, respectively (Eqs. 5c and 6c, and fig. S2C).

For our model, we assumed that the probability of recovering a fossil horizon from each of the *A. sediba* and earliest *Homo* temporal ranges is uniform through time. This assumption is a parsimonious one given that only one horizon each has been sampled from *A. sediba* (*1, 2*) and earliest *Homo* (*5*), and a uniform fossil recovery potential (FRP) (i.e., the probability of finding a fossil horizon) is a good approximation for the one hominin lineage where FRP has been explored, i.e., *A. anamensis-afarensis* (*7, 8*). However, we also have to consider the possibility that FRP is not uniform through time in the *A. sediba* and earliest *Homo* temporal ranges. Our *P* values would only be biased downward if FRP is greater in South Africa and eastern Africa during the geological time periods when *A. sediba* and earliest *Homo* are found, respectively. This is because if FRP is actually higher toward the end and beginning of the *A. sediba* and earliest *Homo* temporal ranges, respectively, then it is more likely that one will recover an *A. sediba* horizon that is much younger than an earliest *Homo* horizon, even if the former species is ancestral to the latter. Using the number of hominin fossil horizons—defined as midpoint ages of hominin-bearing members with age duplicates removed (see data file S3) (*7, 8*)—as a proxy for FRP, we find that FRP is not appreciably higher during the times when *A. sediba* and earliest *Homo* are found in their respective geographic regions (fig. S3). There is the possibility that FRP might be slightly higher in South Africa around the time of *A. sediba* (fig. S3), but even if we double the probability of recovering a fossil horizon in the last 25% of the ancestor's (i.e., *A. sediba*) temporal range, the maximum *P* value is only 0.025 (fig. S4).

Regarding our analysis of the historical record of first-discovered hominin fossils, ancestor-descendant hypotheses might implicitly or explicitly incorporate temporal information, which would potentially render our analysis circular. That is, if ancestor-descendant relationships are proposed at least partly based on the fact that the ancestor's fossil predates the descendant's, it should be no surprise

that ancestors' fossil horizons rarely postdate descendants' horizons. However, incorporating temporal data into ancestor-descendant hypotheses does not necessarily mean that the ancestor's first-discovered fossil must predate the descendant's first-discovered fossil (fig. S5). For example, a newly discovered fossil from the ancestral species may sample the end of its temporal range, and the rest of the range is revealed only after subsequent sampling. A second, more recently found fossil may be proposed as the ancestor's descendant based on the new fossil postdating the ancestor's first appearance, but the new descendant fossil can still predate the younger, first-discovered fossil from the ancestor (see fig. S5 for a discussion about the more complicated scenario when the descendant fossil is found first). Regardless of whether the ancestor or descendant was found first, none of the ancestor's first-discovered fossils ever postdated the descendants by more than 0.8 Ma (i.e., the observed age difference between *A. sediba* and earliest *Homo*) in our literature review (Fig. 4 and table S1).

Robinson *et al.* (*6*) write, "Until such time as additional data on its temporal range are available for *A. sediba*, any inferences about the evolutionary relationship between it and *Homo* should be based primarily on morphological data" (p. 6). More fossils will always strengthen any inference, but we have demonstrated here that even with the scant data relevant to the question at hand (i.e., only one fossil horizon each from *A. sediba* and earliest *Homo*), we can still use temporal evidence to rigorously assess the proposed ancestor-descendant relationship between these two species. This is accomplished by modeling the process/question of interest to generate the probability of obtaining the observed pattern (i.e., an ancestor's fossil horizon that is 0.8 Ma younger than the descendant's), analogous to a null hypothesis test. Our analyses demonstrate that strong inferences can be made even with an incomplete fossil record, so chronological data and tests should not be so quickly discarded.

The issue of the origin of *Homo* is one of the thorniest questions in paleoanthropology and one that has led to myriad proposals and, sometimes, speculations (*2*, *3*, *18*, *19*). Answers to the questions of how, when, and where the earliest representatives of the genus emerged are still in flux, owing especially to the dearth of fossil data from the relevant temporal range (3.0 to 2.5 Ma ago). It is therefore important to use all available lines of evidence when addressing a question as data poor as this one. While fossil remains from the 3.0- to 2.5-Ma-old interval are necessary to reasonably document the morphological patterns surrounding the origin of *Homo*, probabilistic methods such as the one used here are also critical for assessing the chronological evidence for proposed relationships between *Homo* and candidate ancestors. Hypothesized ancestor-descendant relationships must satisfy both temporal and morphological criteria (*7*, *20*). We tested the first criterion here, and the second one has been tested elsewhere (*11*). *A. sediba* fails both benchmarks, and the most viable ancestral candidate for the genus *Homo* remains *Australopithecus afarensis* both on morphological (*5*) and temporal grounds (*7*, *8*).

MATERIALS AND METHODS
Probability model
We are interested in the probability that an ancestor's fossil horizon postdates the descendant's by at least some amount, T_d. Let us denote this probability as $P(H_A - H_D > T_d)$, where H_A and H_D represent the ages of the ancestor's and descendant's fossil horizons, respectively. To have an ancestor's horizon postdate the descendant's, the fossils must

come from the period of temporal range overlap (Fig. 1A). To get an ancestor's horizon that postdates the descendant's by at least T_d, the ancestor's fossil must sample the younger end of the overlap region, and the descendant's fossil must sample the older end (Fig. 2A); let us designate these respective regions as end_A and end_D (i.e., black regions in Fig. 2A), and the probability of sampling these regions is $P(end_A)$ and $P(end_D)$. Because we assume that the ancestor and descendant species have equal temporal ranges, $P(end_A) = P(end_D)$ (Fig. 2A). Assuming sampling probability is uniform throughout a species' temporal range, the probability of sampling a fossil horizon from this region is

$$P(end_A) = P(end_D) = \frac{T_o - T_d}{T_R} \qquad (1)$$

where T_o is the amount of range overlap and T_R is the duration of the entire temporal range (Fig. 2A). We assume here that the probability of selecting a fossil horizon from the ancestor's range is independent from selecting a fossil horizon from the descendant's range. This is a sensible assumption given that the earliest *Homo* specimen is from eastern Africa (*5*), whereas the *A. sediba* specimens are from South Africa (*1*). Therefore, the probability of sampling one fossil horizon each from end_A and end_D is $P(end_A) \times P(end_D)$ or

$$P(end_A \cap end_D) = \frac{(T_o - T_d)^2}{T_R^2} \qquad (2)$$

where "∩" denotes the intersection, i.e., when two events both occur.

Once end_A and end_D are both sampled, Fig. 2B illustrates the necessary conditions that must occur for the ages of the ancestor's and descendant's fossil horizons (i.e., H_A and H_D, respectively) to be separated by at least T_d. Let X_D represent the age difference between the beginning of end_D and H_D (X_A represents the same but for the ancestor) (Fig. 2B). For a given value of X_D, which we will call t, X_A must be greater than X_D, so H_A falls within the white-striped regions in Fig. 2B. The probability of this occurring for all possible values of t (i.e., from zero to infinity) is

$$P(X_A > X_D) = \int_{t=0}^{\infty} P(X_A > X_D | X_D = t) P(X_D = t) dt \qquad (3a)$$

Note that this is the law of total probability (*21*), which states $P(A) = \sum_n P(A|B_n)P(B_n)$, i.e., the probability of event A occurring is equal to the probability of A given event B_n multiplied by the probability of B_n, and all these are summed (or integrated) over all possible instances of B_n in the sample space to get the total probability of A. Because we assume X_A and X_D are independent (i.e., the probability of X_D taking on some value, t, does not affect the value of X_A and whether it is greater than t), the first probability on the right-hand side in Eq. 3a can be simplified, so

$$P(X_A > X_D) = \int_{t=0}^{\infty} P(X_A > t) P(X_D = t) dt \qquad (3b)$$

Because we assume that FRP is uniform throughout a species' temporal range, the probability of sampling a fossil can be modeled as a Poisson process, where X_A and X_D are exponentially distributed (*22*, *23*). The first probability in the integral (i.e., $P[X_A > t]$; Eq. 3b)

can be thought of as the probability that H_A is not found within the interval $(0, t)$ (or one minus the probability that H_A is sampled in this interval). Using the exponential cumulative distribution function, this probability is

$$P(X_A > t) = 1 - (1 - e^{-\lambda t}) = e^{-\lambda t} \tag{3c}$$

The second probability in the integral ($P[X_D = t]$; Eq. 3b) can be calculated using the exponential probability density function (i.e., the probability that X_D takes on some value, t), so

$$P(X_D = t) = \lambda e^{-\lambda t} \tag{3d}$$

Substituting Eqs. 3c and 3d into Eq. 3b, we get

$$P(X_A > X_D) = \int_{t=0}^{\infty} e^{-\lambda t} \lambda e^{-\lambda t} dt \tag{3e}$$

Note that because we are only concerned with sampling one fossil horizon each from the ancestor's and descendant's range, both of which are of equal duration, the sampling rate, λ, for each species is the same. Solving Eq. 3e

$$P(X_A > X_D) = \lambda \int_{t=0}^{\infty} e^{-2\lambda t} dt$$

$$= \lambda \cdot \frac{-e^{-2\lambda t}}{2\lambda} \bigg|_{t=0}^{\infty}$$

$$= \lambda \left(\frac{-e^{-2\lambda\infty}}{2\lambda} + \frac{1}{2\lambda} \right) \tag{3f}$$

The exponential term equals zero given that λ is positive, so

$$P(X_A > X_D) = \frac{\lambda}{2\lambda} = \frac{1}{2} \tag{3g}$$

The same logic and result hold if the roles of X_D and X_A are reversed, i.e., if we instead solve $P(X_D < X_A) = \int_{t=0}^{\infty} P(X_D < X_A | X_A = t) P(X_A = t) dt$.

Therefore, the probability of getting H_A and H_D separated by at least T_d given that H_A and H_D come from end_A and end_D, respectively, is one-half, or using probability notation

$$P(H_A - H_D > T_d | \text{end}_A \cap \text{end}_D) = \frac{1}{2} \tag{4}$$

Putting all the above equations together using the law of total probability (21)

$$P(H_A - H_D > T_d)$$

$$= P(H_A - H_D > T_d | \text{end}_A \cap \text{end}_D) P(\text{end}_A \cap \text{end}_D) +$$

$$P(H_A - H_D > T_d | [\text{end}_A \cap \text{end}_D]^c) P([\text{end}_A \cap \text{end}_D]^c) \tag{5a}$$

where the superscript "c" denotes the complement, i.e., when an event does not happen. We have already established that end_A and end_D need to both be sampled for an ancestor's horizon to postdate a descendant's by

at least T_d (Fig. 2A), so $P(H_A - H_D > T_d | [\text{end}_A \cap \text{end}_D]^c) = 0$. Therefore, the second product in Eq. 5a equals zero and can be dropped. We have already solved the two probabilities in the first product of Eq. 5a with Eqs. 4 and 2, so

$$P(H_A - H_D > T_d)$$

$$= P(H_A - H_D > T_d | \text{end}_A \cap \text{end}_D) P(\text{end}_A \cap \text{end}_D)$$

$$= \frac{1}{2} \times \frac{(T_o - T_d)^2}{T_R^2}$$

$$= \frac{(T_o - T_d)^2}{2T_R^2} \tag{5b}$$

And because $P(H_A - H_D > T_d)$ must be zero when the age difference of interest (T_d) is greater than the amount of range overlap (T_o) (Figs. 1A and 2A), the final model is

$$P(H_A - H_D > T_d) = \begin{cases} 0 & T_d > T_o \\ \dfrac{(T_o - T_d)^2}{2T_R^2} & T_d \leq T_o \end{cases} \tag{5c}$$

For our main analysis (Fig. 3), $T_d = 0.8$ Ma, we assume T_R to be 0.97 Ma (6), and we explored multiple values for T_o, which is currently unknown.

Because T_o (i.e., how much the *A. sediba* and earliest *Homo* temporal ranges overlap) is currently unknown, we also applied uniform prior probabilities over all possible values of T_o to distill the P value function (Eq. 5c) into its mean value (i.e., the expected value) (24). To get the expected P value, we integrate Eq. 5c with respect to T_o over all possible values of T_o (i.e., from zero to T_R) against the probability density function of our T_o uniform prior, which is defined as $1/T_R$ between zero and T_R. Therefore, the expected value is

$$E[P(H_A - H_D > T_d)]$$

$$= \frac{1}{T_R} \left(\int_{T_o=0}^{T_d} 0 \, dT_o + \int_{T_o=T_d}^{T_R} \frac{(T_o - T_d)^2}{2T_R^2} dT_o \right) \tag{6a}$$

Note that because $P(H_A - H_D > T_d)$ is a piecewise function (Eq. 5c), we break the integral into the sum of two integrals separated by T_d (i.e., the value that separates the piecewise function in Eq. 5c). The first integral in Eq. 6a equals zero, and pulling out the $1/2T_R^2$ constant in the second integral gives

$$E[P(H_A - H_D > T_d)] = \frac{1}{2T_R^3} \int_{T_o=T_d}^{T_R} (T_o - T_d)^2 dT_o \tag{6b}$$

Solving Eq. 6b

$$E[P(H_A - H_D > T_d)] = \frac{1}{2T_R^3} \times \frac{(T_o - T_d)^3}{3} \bigg|_{T_o=T_d}^{T_R}$$

$$= \frac{1}{2T_R^3} \left[\frac{(T_R - T_d)^3}{3} - \frac{(T_d - T_d)^3}{3} \right]$$

$$= \frac{(T_R - T_d)^3}{6T_R^3} \tag{6c}$$

which is the expected P value from Eq. 5c, treating all possible values of T_o as equally likely.

Analysis of published fossil ages

We reviewed the literature and recorded the geological ages (lower and upper bracketing ages) and year of discovery of the first fossil found in each species in a hypothesized hominin ancestor–descendant pair [this mirrors the situation in *A. sediba* and earliest *Homo*, both of which currently have only one fossil horizon each (2, 5)]. Because we were only interested in by how much the ancestor's first-discovered fossil postdated the descendant's first-discovered fossil, we were more inclusive than not in our selection (i.e., the accuracy or widespread acceptance of an ancestor-descendant relationship should have no bearing on the age difference between first-discovered fossils). To calculate the age difference, we subtracted the midpoint age of the ancestor's first-discovered fossil from the midpoint age of the descendant's first-discovered fossil, where the midpoint age is defined as (lower bracketing age + upper bracketing age)/2. Negative age differences indicate that the ancestor's first-discovered fossil is older than the descendant's, and vice versa, for positive differences.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/5/eaav9038/DC1

Fig. S1. Confirming our probability model results (Fig. 3) with simulations.

Fig. S2. Same analysis as in Fig. 3 but assuming hominin temporal durations of 2 Ma, A.L. 666-1 (2.33 Ma old) represents the oldest *Homo* fossil, or both.

Fig. S3. Uniform probability plots for 4- to 1-Ma-old hominin fossil horizons in South Africa and eastern Africa.

Fig. S4. Same analysis as in Fig. 3, but the probability of sampling a fossil horizon (i.e., FRP) from the last 25% of the ancestor's range is doubled.

Fig. S5. Schematic illustrating how proposing an ancestor-descendant relationship based on temporal evidence does not necessarily constrain the first-discovered fossil in each species to be in the "correct" order (i.e., where the ancestor's first-discovered fossil predates the descendant's).

Table S1. Previously proposed ancestor-descendant hominin species pairs ($n = 28$), and the year discovered and geological ages of the first-discovered specimen in each species.

Data file S1. Hypothesized hominin ancestor–descendant species pairs.

Data file S2. Geological ages for first-discovered specimens of hominin species.

Data file S3. Four- to 1-Ma-old South African and eastern African hominin-bearing members and their geological ages.

Data file S4. Dataset references.

Data file S5. R code for analyses and creating figures.

References (26, 27)

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Andrew Du and Zeresenay Alemseged

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