

# Temporal ranges and ancestry in the hominin fossil record: The case of *Australopithecus sediba*

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In attempting to resolve the phylogenetic relationships of fossil taxa, researchers can use evidence from two sources – morphology and known temporal ranges. For most taxa, the available evidence is stronger for one of these data sources. We examined the limitations of temporal data for reconstructing hominin evolutionary relationships, specifically focusing on the hypothesised ancestor–descendant relationship between *Australopithecus sediba* and the genus *Homo*. Some have implied that because the only known specimens of *A. sediba* are dated to later than the earliest fossils attributed to *Homo*, the former species is precluded from being ancestral to the latter. However, *A. sediba* is currently known from one site dated to 1.98 Ma and, thus, its actual temporal range is unknown. Using data from the currently known temporal ranges of fossil hominin species, and incorporating dating error in the analysis, we estimate that the average hominin species' temporal range is ~0.97 Myr, which is lower than most figures suggested for mammalian species generally. Using this conservative figure in a thought experiment in which the Malapa specimens are hypothesised to represent the last appearance date, the middle of the temporal range, and first appearance date for the species, the first appearance date of *A. sediba* would be 2.95, 2.47 and 1.98 Ma, respectively. As these scenarios are all equally plausible, and 2.95 Ma predates the earliest specimens that some have attributed to *Homo*, we cannot refute the hypothesis that the species *A. sediba* is ancestral to our genus based solely on currently available temporal data.

### Significance:

- We correct a common misconception in palaeoanthropology that a species currently known only from later in time than another species cannot be ancestral to it.
- On temporal grounds alone one cannot dismiss the possibility that *A. sediba* could be ancestral to the genus *Homo*.

## Introduction

In evaluating competing phylogenetic hypotheses there are two primary sources of data available to palaeontologists for most fossil taxa: the morphology of the taxa under investigation and their known temporal ranges. For many taxonomic groups, however, the quality of these two sources of data differs substantially. Some taxa are well known morphologically, yet are spatially and temporally restricted. Other taxa are well sampled across sites and through time, yet are represented by limited and/or fragmentary anatomical elements. While some researchers have argued that the incomplete nature of the fossil record makes temporal information unreliable for reconstructing phylogenetic relationships<sup>1,2</sup>, and that using 'age to define...ancestry is eminently circular'<sup>3(p.439)</sup>, morphological evidence regarding evolutionary relationships among fossil taxa can also be equivocal, such as when there are multiple equally parsimonious phylogenetic trees or when there is the potential that homoplasy has substantially influenced phylogenetic interpretations (see Wood and Harrison<sup>4</sup> for a discussion of the latter in hominins). Consequently, it is important to consider the relative strengths of these sources of data when evaluating phylogenetic hypotheses.

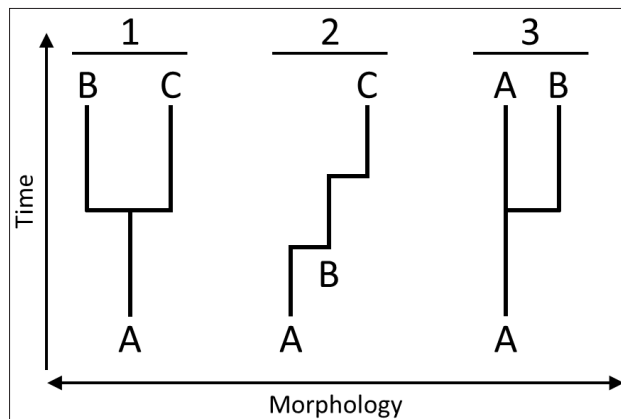
Here, we focused on the limitations of temporal data for reconstructing evolutionary relationships in the hominin fossil record, using *Australopithecus sediba* as a case study. Originally proposed as the probable ancestor of the genus *Homo*<sup>5,6</sup>, some have contended that this scenario is unlikely based on both morphological<sup>7-9</sup> and, either directly or implicitly, temporal grounds (e.g. see comments by White in Balter<sup>10</sup>, Grine in Cherry<sup>11</sup> and Richmond in Gibbons<sup>12</sup>). Leaving aside the morphological arguments for others to debate, here we examine the suggestion that the currently understood first appearance date (FAD) for *A. sediba* of ~1.98 Ma (million years ago)<sup>5,6</sup>, in and of itself, negates it as a potential ancestor of the genus *Homo* because putative fossils of early *Homo* appear earlier in the geological record<sup>13,14</sup>. As these critiques derive from news pieces rather than scholarly articles it is possible that the quotes have been taken out of context and do not reflect what the researchers intended to say. However, they give the impression that at least some in the field of palaeoanthropology, like many in the general public and popular press (see Gibbons<sup>15</sup> for a recent example), think that if all representatives of one taxon are found later in time than at least one specimen attributed to another taxon, it implies that the former cannot be members of the ancestral lineage from which the latter evolved. This issue is especially relevant as these misconceptions are currently being presented in college anthropology textbooks.<sup>16(p.154)</sup>

As noted by Spoor<sup>7</sup>, two scenarios have been proposed that are consistent with the hypothesis that *A. sediba* is ancestral to *Homo*. First, Berger et al.<sup>5</sup> hypothesised that the Malapa specimens represent late surviving members of the species that gave rise to *Homo* earlier in time. Second, Pickering et al.<sup>6</sup> questioned the validity of specimens attributed to *Homo* that had been recovered from strata predating the Malapa deposits, and suggested that *A. sediba* cannot be precluded as a potential ancestor of *Homo* based on the age of the fossils from Malapa. Notwithstanding the difficulties in recognising early members of the genus *Homo*, we concur with Spoor<sup>7</sup> that the first scenario is more likely. Therefore, in this paper we explore the question of whether it is plausible for *A. sediba* to be the ancestor of the genus *Homo* based on the FADs of specimens currently attributed to these two taxa.

## Research methods and data

### Contemporaneous ancestors and descendants in the fossil record

Depending on the mode of speciation, it may or may not be possible for ancestral and descendant taxa to coexist in the fossil record. Speciation resulting from bifurcating cladogenesis or anagenesis (Figure 1: Modes 1 and 2) precludes ancestors from being contemporaneous with their descendants because in both cases the entire ancestral species evolves into one or more descendant species. Alternatively, under a budding cladogenesis model of speciation (Figure 1: Mode 3) ancestors and descendants do co-occur.<sup>17</sup> In budding cladogenesis, a subset of a species, usually a geographically isolated population, differentiates from the rest of the species and forms a new descendant taxon. Within the fossil record this is seen as a change in morphology in one population, while the remaining populations retain the ancestral form. Thus, as far as can be perceived, the ancestral species persists after giving rise to its descendant. Recent studies of animal and plant biogeography suggest that this mode of speciation is relatively common<sup>18</sup>, and there is genetic evidence that some ancestral species are extant, living contemporaneously with their descendants<sup>19</sup>. Some have even argued that budding cladogenesis is the primary mode by which species arise, with most ancestral taxa existing contemporaneously with their descendants for some time.<sup>20,21</sup>



**Figure 1:** Modes of speciation: (1) bifurcating cladogenesis, (2) anagenesis and (3) budding cladogenesis. In both Modes 1 and 2, ancestors cannot be contemporaneous with their descendants as the entire ancestral species evolves into one or more descendant species. In Mode 3, ancestral and descendant taxa can coexist as a, typically geographically isolated, population speciates from the main population, which retains its species integrity.

The coexistence of ancestral and descendant species, which would imply that the latter species evolved via budding cladogenesis, has been hypothesised to be present in the fossil record for a variety of invertebrate groups including bryozoans, ostracods and mollusks (see citations in Gould<sup>22</sup>). Additionally, budding cladogenesis has been suggested, either explicitly or implied through the hypothesised coexistence of ancestors and descendants, in phylogenetic reconstructions of numerous mammalian groups spanning almost the entire range of body sizes including rodents<sup>23</sup>, suids<sup>24,25</sup>, equids<sup>25</sup>, hippopotamids<sup>26</sup> and proboscideans<sup>25,27</sup>.

Among hominins, examples of putative ancestral and descendant species existing contemporaneously include *Homo habilis* and *Homo erectus*, *H. erectus* and most later *Homo* species, and *Australopithecus afarensis* and *Australopithecus africanus*.<sup>4,28,29</sup> Even the transition of *Australopithecus anamensis* into *A. afarensis* via anagenesis – generally considered to be the strongest example of this mode of speciation in the early hominin fossil record<sup>30,31</sup> – has been questioned based on a critical reevaluation of the morphological differences between the older *A. afarensis* material from Laetoli and specimens from the younger

Hadar deposits<sup>32</sup>. Moreover, fossils tentatively assigned to *A. afarensis* from the site of Fejej in southern Ethiopia (e.g. Fleagle et al.<sup>33,34</sup> but see Ward<sup>35</sup> for an alternative view) overlap with the currently known temporal range of *A. anamensis*.<sup>36</sup> If this diagnosis holds, then the evolution of *A. afarensis* from *A. anamensis* must have also occurred via budding cladogenesis. Although some have argued that the evidence for hominins rarely meets the criteria for budding cladogenesis, specifically that there are few examples of ancestors and descendants overlapping in time<sup>30</sup>, if we accept that speciation in hominins can occur via this mechanism, as appears to be common in many other taxa, then contemporaneity in and of itself cannot be used to refute a potential ancestor–descendant relationship between *A. sediba* and the genus *Homo*, just as the proposed ~250 kyr of temporal overlap between *H. erectus* and *H. habilis* in East Africa does not preclude the latter taxon from being the progenitor of the former.<sup>29,37</sup>

Recognising budding cladogenesis requires documenting that ancestors and descendants co-occur in the fossil record. It is of course implicit that any specimens utilised are correctly identified to taxon. As an analysis of hominin alpha taxonomy is beyond the scope of this paper, we rely on the analyses of the experts working on the species in question for the identification of the earliest and latest examples of each taxon. Detailed criteria for identifying ancestors in the fossil record are set out by Delson<sup>3</sup>. If, for example, one seeks to test whether it is plausible that *A. sediba* is the ancestor of the genus *Homo* it would first be necessary to provide evidence that *A. sediba* is the sister taxon of the genus *Homo* (i.e. that it shares synapomorphies with *Homo* that other hominin taxa do not possess). A sister group relationship has been suggested in an extensive recent phylogenetic analysis of hominins<sup>38</sup> and in the original description of *A. sediba*<sup>5</sup>; however, as with any phylogenetic hypothesis, it must withstand further testing by other researchers, especially when additional evidence is obtained. For *A. sediba* to be ancestral to the genus *Homo* it would also have to exhibit more primitive hominin features (plesiomorphies) than *Homo* and cannot exhibit any uniquely derived characters (autapomorphies) as these would indicate that it is also a descendant of the ‘true ancestor’ of both groups. If these criteria are met then one could argue that *A. sediba* corresponds to the ancestral morphotype of the node shared with *Homo* that links them as sister taxa. Moreover, Delson<sup>3(p.440)</sup> cogently argues that only after morphological criteria are met should one then consider other data such as a taxon being ‘widespread, polytypic, anatomically well known and perhaps of “correct” geographic and chronological age’.

### The incomplete nature of the fossil record

The known fossil record likely represents fewer than half of the species that have lived<sup>39</sup>, albeit with large differences in representation among taxonomic groups, as a result, at least partly, of differential preservation<sup>40</sup>. With respect to primates, it is estimated that between about 3.8% and 7% of taxa have been sampled in the fossil record.<sup>41,42</sup>

Although it is implicit in evolutionary theory that some portion of an ancestral taxon necessarily preceded its descendants<sup>3</sup>, palaeontologists have long recognised that ancestors can potentially be found in strata dated to later in time than those of their descendants as a consequence of the incomplete nature of the fossil record<sup>3,43</sup>. For example, even after accounting for the known temporal ranges of the ‘abundant and heavily studied’ North American fossil hipparionines, Alroy<sup>44(p.167)</sup> notes that the most parsimonious phylogenetic hypothesis has two ancestral species that, based on the available evidence, arose one million years after their descendants, and two additional ancestral taxa that have the same FAD as their descendants. In other examples, the possibility of descendant taxa preceding their ancestors was explored by researchers studying graptoloids and echinoids.<sup>45,46</sup> Although these researchers ultimately judged those scenarios as less likely than alternative phylogenetic hypotheses, they did not dismiss them based solely on descendants being present in the known fossil record prior to their ancestors.

One might argue that the intensive focus on recovering hominins over the past ~100 years at sites in East and South Africa would have resulted in a relatively complete fossil record. However, hominins make up very small percentages of most Plio-Pleistocene faunal assemblages

when compared to other medium- and large-sized mammals. Although published percentages are not fully comparable as different research teams include different taxonomic groups and body size subsets of the overall mammalian assemblages in their data sets, hominins are nonetheless relatively rare at most African sites from this time period. For instance, hominins make up only 5.3% of the reported mammalian assemblages at sites yielding robust australopithecids in South Africa,<sup>47</sup> and even this figure is likely to be an overestimate given the enhanced scrutiny that they receive relative to non-hominins. Hominins are even less common (<2%) at sites in East Africa such as Omo, Hadar and Laetoli<sup>48–50</sup>, although they make up a greater percentage (9% of the vertebrate fauna) of the smaller sample of mammalian fossils from Kanapoi<sup>51</sup>.

If we accept that hominin fossils are rare, their recovery is likely to be more strongly influenced by stochastic factors than is the case for other mammals (e.g. bovids or suids). Consequently, current FADs and last appearance dates (LADs) for hominins are likely not representative of their actual temporal ranges<sup>52,53</sup>, and the FADs of hominins that are not known from long stratigraphic sections in particular are 'subject to substantial error'<sup>54(p.10375)</sup>. Moreover, some have noted that the hominin record has 'a disproportionate contribution from the East African Rift Valley' and, accordingly, have contended that this 'precludes firm conclusions regarding immigration or speciation events'<sup>50(p.178)</sup>. It is entirely possible that earlier (or later) populations of hominin species that are currently only known from one or a few localities and from a limited temporal range will be identified in under-sampled regions of Africa. Depending on how many distinct hominin species one recognises, there are as many as seven that are currently known from only one locality (i.e. they are arguably 'single hits') (Table 1). As Foote and Raup<sup>55(p.136)</sup> argue, 'a very high frequency of single hits suggests the possibility of a poor fossil record which should be analyzed with caution'. The implications of the above are that hominins are not as well known as might be expected based on the number of published articles on this group, and that a substantial amount of the hominin fossil record may be unknown. This claim is bolstered by the relatively large number of new hominin taxa named over the past 25 years, which has nearly doubled the number of putative hominin species (see citations in Wood and Boyle<sup>56</sup>). As such, it is likely that even the more generous estimates for hominin species durations significantly underestimate the true temporal ranges of these taxa, and this needs to be considered when evaluating hypotheses of ancestor–descendant relationships.

### Species temporal ranges

Numerous methods have been developed to estimate 'true' temporal ranges for fossil taxa,<sup>45,57–59</sup> but none of these methods can be applied to *A. sediba* because they require that specimens be known from more than a single stratum. Thus, calculating confidence intervals for the FAD and LAD of *A. sediba* using these methods is not possible and we must use indirect methods for estimating its temporal range.

One million years (Myr) has been cited as the typical mammalian species longevity (e.g. Martin<sup>41</sup> and references therein), a value that can be traced back through several studies to Kurtén's<sup>60</sup> analysis of the Pleistocene mammals of Europe. In contrast, recently compiled average species durations from a survey of published data sets of Cenozoic mammals ranged from 0.8 to 6.3 Myr.<sup>61</sup> Although these types of estimations are highly dependent on the group of mammals under consideration (e.g. large versus small mammals) and the data set used, most of the studies yielded average species durations between 2 and 4 Myr.<sup>61</sup> Taxonomic practices (e.g. tendencies to 'lump' or 'split') also influence estimates of species longevity and vary between groups. Given that related taxonomic groups tend to share similar preservation potential<sup>17,58</sup>, and similar risks of extinction<sup>40</sup>, it seems most appropriate to use the temporal ranges of fossil primate species in general, and hominins in particular, as models for hominin species durations.

Unfortunately, few estimates of overall primate species longevity can be found in the literature (e.g. Martin<sup>41</sup>). Based on published hominin species temporal ranges from a recent study,<sup>56</sup> the estimated average hominin species longevity is 0.43 Myr, which is substantially lower than that of other mammalian groups. However, these estimates include taxa that are recorded from only one locality. Given that species known

from a single locality cannot provide an estimate of the temporal range of that species, unless that locality samples a range of time within well-defined strata, removing them from these calculations seems appropriate. By removing these taxa, and *Homo sapiens*, which lacks an LAD at the time of writing, the average hominin species duration would be 0.50 Myr using published hominin species range data, and 0.80 Myr when the estimates of dating error from Wood and Boyle<sup>56</sup> are incorporated (Table 1). Furthermore, if we group hominin species that many researchers 'lump' together (e.g. those that are listed as 'low confidence' in Table 2 of Wood and Boyle<sup>56</sup>), the average published, and with dating error, species durations for hominins rise to 0.62 and 0.97 Myr, respectively (Table 1). We acknowledge that the choice of which taxa to retain may not be agreed upon by all researchers, but note that the larger 0.97 Myr average hominin species duration utilising the data set with error is still on the low end of the ranges reported for other groups of mammals,<sup>61</sup> and is very close to the 1.0±0.25 Myr range suggested by Wood and Boyle<sup>56</sup>. As such, we will use this estimate to assess the possibility that, based on their currently estimated temporal ranges, *A. sediba* could be ancestral to the genus *Homo*.

Using 0.97 Myr as the average species duration for hominins, we estimate three temporal distributions for *A. sediba* by assuming that the Malapa specimens represent either the LAD, midpoint or FAD of the species (Scenarios 1, 2, and 3) (Figure 2). If we assume the Malapa specimens represent the LAD (Scenario 1), then the species would have originated around 2.95 Ma and gone extinct at 1.98 Ma. Alternatively, if Malapa is at the midpoint of the temporal range for the species (Scenario 2), then *A. sediba* can be estimated to have arisen at around 2.47 Ma and gone extinct at around 1.49 Ma. Finally, the possibility that the Malapa specimens represent early members of the species, chronologically closer to or at the speciation event (FAD) (Scenario 3), yields a potential temporal range of 1.98–1.01 Ma.

Thus, Scenarios 1, 2 and 3 would date the FAD of *A. sediba* to 2.95, 2.47 and 1.98 Ma, respectively, with all three being equally plausible based on currently available temporal data. The earliest specimen that some have attributed to the genus *Homo* is the partial mandible LD 350-1 from Ledi-Geraru, which is dated to 2.75–2.8 Ma.<sup>14</sup> Under Scenarios 2 and 3 in which the Malapa specimens represent the midpoint of the temporal range or the FAD of *A. sediba* it would not be possible for that species to be the ancestor of the genus *Homo* based on the estimate we are using for the average hominin temporal range. However, under Scenario 1 (i.e. the Malapa specimens represent the LAD for *A. sediba*), this ancestor–descendant relationship would be possible even if we incorporate the 'with error' FAD estimates from Wood and Boyle<sup>56</sup> for LD 350-1 (Figure 2).

It is important to carefully examine whether the first scenario is plausible, because if it is not, then the possibility that *A. sediba* is ancestral to the genus *Homo* would be considered unlikely given the parameters discussed above. In this regard, we make several observations. First, if the Malapa specimens are correctly identified as part of an 'australopithecine adaptive grade'<sup>15</sup> then these deposits likely contain some of the latest surviving members of the gracile form of this grade of early hominin. As such, the dates for the Malapa deposits may be close to the LAD for *A. sediba*. Second, given the mosaic nature of the morphology of *A. sediba*<sup>5</sup> and, thus, the difficulty of determining whether the taxon is represented by other, more incomplete specimens in the hominin fossil record, it may be that researchers have already recovered, or will recover at a later date, other fossils from earlier (or later) in time that should be attributed to this taxon. Furthermore, we note that some researchers have questioned the taxonomic attribution of LD 350-1.<sup>62</sup> If the specimen does not belong to the genus *Homo*, the earliest putative specimens of our genus would be dated to ~2.4 Ma using published hominin species range data,<sup>13</sup> and 2.6 Ma utilising the 'with error' data (Table 1). As such, both Scenarios 1 and 2 would be possible if 2.4 Ma accurately reflects the FAD for *Homo*, although again, only Scenario 1 remains possible at a 2.6 Ma FAD for *Homo*. Recall, however, that the 0.97 Ma average hominin duration used to generate a FAD for *A. sediba* is only an estimate based on current temporal range data from other hominins that also suffer from incomplete sampling. It is entirely possible that this figure underestimates the true temporal range for *A. sediba*.

**Table 1:** Data from Wood and Boyle<sup>56</sup> used to calculate average hominin species duration estimates. The first series represent the ‘conservative’ data with corresponding first appearance date (FAD), last appearance date (LAD) and temporal ranges, while the second series represents the ‘with error’ data. Calculated average hominin durations are provided in bold, with those in brackets generated using a lumping approach. Taxa that were grouped together are indicated by footnotes. Taxa below the dashed line are considered single hits and were not used in average hominin species duration calculations.

Taxon	Observed range <sup>a</sup>			Dating error incorporated <sup>b</sup>		
	FAD	LAD	Range	FAD	LAD	Range
<i>Orrorin tugenensis</i>	6	5.7	0.3	6.14	5.52	0.62
<i>Ardipithecus kadabba</i>	6.3	5.2	1.1	6.7	5.11	1.59
<i>Ardipithecus ramidus</i>	4.51	4.3	0.21	4.6	4.262	0.338
<i>Australopithecus anamensis</i>	4.2	3.9	0.3	4.37	3.82	0.55
<i>Australopithecus afarensis</i>	3.7	3	0.7	3.89	2.9	0.99
<i>Kenyanthropus platyops</i>	3.54	3.35	0.19	3.65	3.35 <sup>c</sup>	0.3
<i>Australopithecus deyiremeda</i> <sup>d</sup>	3.5	3.3	0.2	3.596	3.33	0.266
<i>Australopithecus africanus</i>	3	2.4	0.6	4.02	1.9	2.12
<i>Paranthropus aethiopicus</i>	2.66	2.3	0.36	2.73	2.23	0.5
<i>Paranthropus boisei</i>	2.3	1.3	1	2.5	1.15	1.35
<i>Paranthropus robustus</i>	2	1	1	2.27	0.87	1.4
<i>Homo habilis</i>	2.35	1.65	0.7	2.6	1.65 <sup>c</sup>	0.95
<i>Homo rudolfensis</i>	2	1.95	0.05	2.09	1.78	0.31
<i>Homo erectus</i>	1.81	0.027	1.783	1.85	0.027 <sup>c</sup>	1.823
<i>Homo ergaster</i> <sup>e</sup>	1.7	1.4	0.3	2.27	0.87	1.4
<i>Homo antecessor</i> <sup>f</sup>	1	0.936	0.064	1.2	0.936 <sup>c</sup>	0.264
<i>Homo heidelbergensis</i>	0.7	0.1	0.6	0.7 <sup>c</sup>	0.1 <sup>c</sup>	0.6
<i>Homo helmei</i> <sup>f</sup>	0.26	0.08	0.18	0.26 <sup>c</sup>	0.08 <sup>c</sup>	0.18
<i>Homo neanderthalensis</i>	0.13	0.04	0.09	0.197	0.03922	0.15778
<i>Homo rhodesiensis</i> <sup>f</sup>	0.6	0.3	0.3	0.6 <sup>c</sup>	0.3 <sup>c</sup>	0.3
<b>Average</b>			<b>0.501 (0.620)</b>			<b>0.800 (0.969)</b>
<i>Sahelanthropus tchadensis</i> <sup>g</sup>	7.2	6.8	0.4	7.43	6.38	1.05
<i>Australopithecus bahrelghazali</i> <sup>h</sup>	3.58	3.58	–	3.85	3.31	0.54
<i>Australopithecus garhi</i> <sup>h</sup>	2.5	2.45	0.05	2.5 <sup>h</sup>	2.488	0.012
<i>Australopithecus sediba</i> <sup>h</sup>	1.98	1.98	–	2.05	1.91	0.14
<i>Homo georgicus</i> <sup>g</sup>	1.85	1.77	0.08	1.85 <sup>c</sup>	1.77 <sup>c</sup>	0.08
<i>Homo floresiensis</i> <sup>g</sup>	0.074	0.017	0.057	0.108	0.016	0.092
<i>Homo sapiens</i> <sup>g</sup>	0.195	0	0.195	0.2	0	0.2
<i>Homo naledi</i> <sup>h</sup>	0.286	0.286	–	?	?	?

<sup>a</sup>Conservative estimates reported in Wood and Boyle<sup>56</sup>(table 1).

<sup>b</sup>Estimates with dating error reported in Wood and Boyle<sup>56</sup>(table 1).

<sup>c</sup>No ‘with error’ date provided in original publication; this value represents those reported in the ‘conservative estimate’.

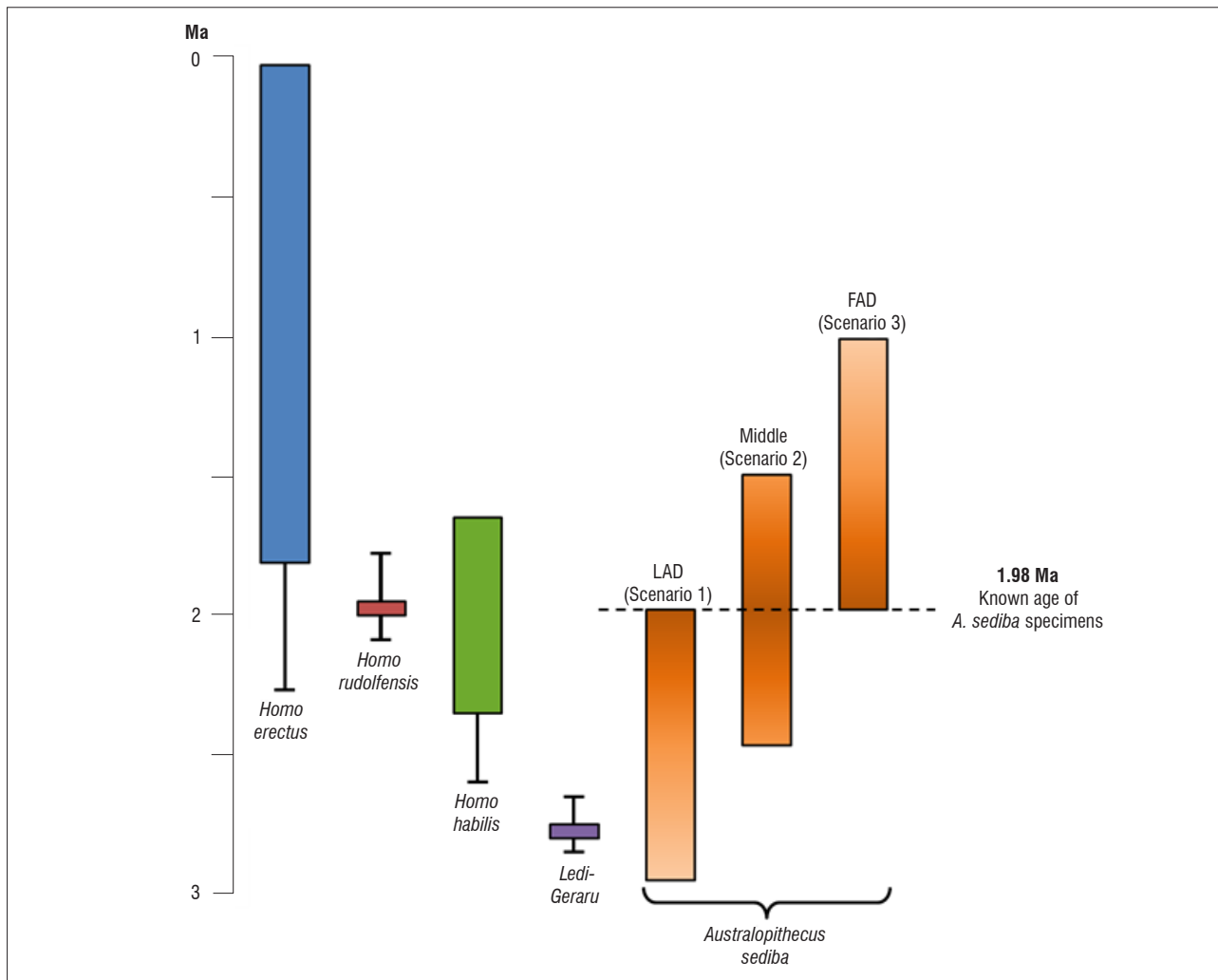
<sup>d</sup>Taxon and associated dates lumped with *A. afarensis* in calculation of temporal range.

<sup>e</sup>Taxon and associated dates lumped with *H. erectus* in calculation of temporal range.

<sup>f</sup>Taxon and associated dates lumped with *H. heidelbergensis* in calculation of temporal range.

<sup>g</sup>‘Single hit’ taxa not considered in calculating average hominin duration.

<sup>h</sup>Mid-range of most parsimonious age estimates reported in Dirks et al.<sup>67</sup>



**Figure 2:** Estimates of the temporal ranges of the earliest species attributed to the genus *Homo* and potential durations for *Australopithecus sediba* assuming the Malapa specimens represent the last appearance date (LAD; Scenario 1), the middle of the species actual temporal range (Scenario 2) or first appearance date (FAD; Scenario 3) using an average hominin temporal duration of 0.97 Myr. Data used to generate the figure are from Table 1. Solid bars represent ranges using the ‘conservative’ data set while error bars incorporate both the ‘with error’ data and a lumping of the ‘low confidence’ taxa from Wood and Boyle<sup>56</sup>. Graded shading on the bars for *A. sediba* indicates the greater degree of uncertainty that the taxon existed at the time indicated.

Thus, although arguments can be made against Scenarios 2 and 3, we find insufficient evidence to refute Scenario 1, and, as a result, would argue that it is not implausible that *A. sediba* is the ancestor of the genus *Homo* based on our analysis of the dates of specimens currently attributed to these and other hominin taxa.

## Conclusions

While some researchers have critiqued the hypothesis that *A. sediba* is ancestral to the genus *Homo* on morphological grounds, others have based their criticism, at least partly if not largely, on the date of the Malapa specimens. Although the known temporal range of a fossil species can be an important piece of evidence in testing ancestor–descendant hypotheses, palaeontologists do not typically dismiss the possibility that a fossil species is the ancestor of another based solely on the two species’ currently recognised FADs.<sup>44–46</sup> Echoing previous researchers<sup>3,63,64</sup>, Foote<sup>17(p.147)</sup> argues, ‘whether species are preserved in the ‘wrong’ order does not affect the facts of their genealogical relationships, which we must attempt to reconstruct regardless of where we find the species stratigraphically’. This does not mean that temporal data cannot be informative, particularly for taxa that have a well-sampled fossil record, such as deep-sea microplankton.<sup>43</sup> However, if a taxon is not well known in the fossil record and/or is only known from a highly

localised area, such as is the case for *A. sediba* and many other hominins (Table 1), the likelihood that its known record is an accurate reflection of the entire temporal range during which that taxon lived is substantially reduced. This limitation is demonstrated by the specimens attributed to *Homo floresiensis* and *Homo naledi* that are both suggested to have ghost lineages extending back much earlier in time based on their more primitive morphological features.<sup>65,66</sup> FADs and LADs are especially likely to be inaccurate for taxa like early hominins that had low population densities and ‘relatively sparse fossil records’<sup>53(fig.1)</sup>. Therefore, it is difficult to have confidence in hypothesised evolutionary relationships that are based on the dates attributed to a handful of specimens.

Criticisms of the putative relationship of *A. sediba* and *Homo* based on their relative temporal ranges may be related, in part, to a dispute over the mode by which hominin species arose, with some taking the view that budding cladogenesis occurred rarely, if at all, in hominin evolution (e.g. White et al.<sup>30</sup>). However, as discussed above, this mode of speciation appears to be relatively common in mammalian, including hominin, evolution. Given that there is no theoretical reason to suspect that human evolution was any different than the evolution of any other mammal, we would argue that it would not be unusual to find evidence for contemporaneous ancestors and descendants in the human fossil record (e.g. Spoor et al.<sup>29</sup>).

Finally, we stress that the date for the Malapa deposits containing the *A. sediba* specimens should be interpreted for what it is – evidence of one particular moment in time when the species existed, but which cannot provide an accurate estimate of the lineage's temporal range (i.e. absence of evidence is not evidence of absence). In this paper, we are neither advocating for the position that *A. sediba* is the ancestor of the genus *Homo*, nor are we addressing questions about the taxonomic attribution of the Malapa specimens. We are merely pointing out that the critiques of *A. sediba* as a potential ancestor of the genus *Homo* based on temporal criteria are at the very least premature and are prone to misinterpretation by the media and general public. 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. While the arguments presented here have specifically revolved around one taxon, they are germane to studies of all hominin taxa in the fossil record, particularly 'single hit' taxa (Table 1) for which we have no clear understanding of the species' true temporal range. As such, we urge caution for all scientists involved in studies of human evolution to carefully think about how temporal data can, and should be, used in assessing phylogenetic hypotheses.

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## Authors' contributions

C.R. and D.J.d.R. conceptualised the project with contributions to the research goals later provided by T.L.C. and S.C. T.L.C. developed the methodology and collected and analysed the data on fossil hominin first and last appearances. C.R. and T.L.C. wrote the initial draft with the table and figures created by T.L.C. Later contributions and revisions of the text were provided by D.J.d.R. and S.C. Revisions to the first submission were primarily written by T.L.C. and C.R.

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