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One hominin taxon or two at Malapa Cave? Implications for the origins of *Homo*

A report on the skeletons of two individuals from the Malapa cave site in South Africa attributes them both to a new hominin species, *Australopithecus sediba*. However, our analysis of the specimens' mandibles indicates that *Australopithecus sediba* is not a 'Homo-like australopith', a transitional species between *Australopithecus africanus* and *Homo*. According to our results, the specimens represent two separate genera: *Australopithecus* and *Homo*. These genera are known to have jointly occupied sites, as seen in several early South African caves, so one cannot rule out the possibility that Malapa also contains remains of the two taxa. Our results lead us to additionally conclude that *all* the *Australopithecus* species on which the relevant mandibular anatomy is preserved (not only the 'robust' australopiths but also the 'gracile' – more generalised – ones) are too specialised to constitute an evolutionary ancestor of *Homo sapiens*. Furthermore, given that the Malapa site contains representatives of two hominin branches, one of which appears to be *Homo*, we must seek evidence of our origins much earlier than the date assigned to Malapa, approximately 2 million years before present. Support for this claim can be found in Ethiopian fossils attributed to the genus *Homo* and dated at 2.4 and 2.8 million years before present.

Significance:

- The proposed hominin species *Australopithecus sediba*, from the Malapa Cave in South Africa, seems to actually consist of two species, each of which represents a different hominin genus: *Homo* and *Australopithecus*. If, indeed, this is the case, *Homo* must have originated prior to the Malapa remains, contrary to the scenario suggested in the original report on *Au. sediba*.

Introduction

The proposal of a new hominin species, *Australopithecus sediba*, announced and described by Berger¹, Berger et al.², and de Ruiter et al.³, is based primarily on the analysis of two partial skeletons, MH1 and MH2. The taxon is claimed to exhibit many features that suggest that it represents an intermediate species between *Australopithecus africanus* and *Homo*. This assertion was recently reiterated in a special issue of *PaleoAnthropology* dedicated to *Australopithecus sediba*.^{4,5} However, a careful assessment of the mandibular remains leads us to conclude that the proposed *Au. sediba* species actually encompasses two species representing separate genera – *Australopithecus* and *Homo* – and as such cannot play a role in the origin of the latter. The discovery of two hominin species at one site is not unheard of in South Africa.

The two mandibles from Malapa plainly exhibit different patterns of ramal morphology: MH1 resembles australopith morphology, and MH2 displays the generalised morphology exhibited by *Homo sapiens* and other *Homo* species.

The morphology of the ascending ramus of the mandible in hominins has been found to be a diagnostic character⁶ (note that Wolpoff and Frayer⁷ claim that the upper part of the ramus is not diagnostic enough to distinguish between *H. sapiens* and *H. neanderthalensis*, but they cannot refute our argument because they have not applied our method to their sample); as such, the ramal morphology clearly distinguishes between *Australopithecus* and *H. sapiens*⁸. In the latter, the condylar and coronoid processes are relatively slender in a lateral view, they are similar in size, and they are separated by a broad, scooped out mandibular (sigmoid) notch, whose deepest point lies about halfway between the tips of the two processes (Figure 1). This configuration lends the notch a somewhat symmetrical appearance. In *Australopithecus*, on the other hand, the coronoid process is tall and broad, occupying about three-fourths of the ramal breadth. The process's superior end is rather flat, with a hook-like profile, and overhangs the relatively small mandibular notch, which is shallow in relation to the mandibular condyle. As a result, the outline of the notch is confined and asymmetric.

Similarly, *H. sapiens* and australopith rami seem to differ vis-à-vis the preangular notch. In *H. sapiens*, as in many other primates (i.e. the generalised configuration), the concave anterior margin of the ramus forms this notch, which is also present in MH2 (Figure 1). In the australopiths, as in MH1, the anterior margin of the ramus usually slopes diagonally in a straight line until it meets the mandibular body. Some exceptions to this dichotomy can be noted – for example, the presence of the preangular notch on MLD 40, Sts 52, Sts 7 and SKW 5, despite their assignment as *Au. africanus*. These exceptions somewhat diminish the diagnostic power of the preangular notch.

Because *H. sapiens* shares its ramal morphology with many other primates (for example, chimpanzees, orangutans, vervets and colobines), that morphology is clearly the primitive one, whereas the *Australopithecus* ramal configuration is derived – a synapomorphic character that combines *Au. robustus*, *Au. africanus* and *Au. afarensis* (and possibly other australopiths, such as *Au. anamensis* and *Au. boisei*, neither of which has a ramus that is sufficiently preserved to permit study) into what seems to be a monophyletic group. To suggest that the derived configuration, that of *Australopithecus*, evolved into the modern human configuration violates the principle of parsimony.



Figure 1: Ramal morphology of five hominoid specimens (not shown to scale). From upper right, clockwise: MH1, *Australopithecus robustus* (SK 23), orangutan, *Homo sapiens* and MH2. Note the hook-like shape of the coronoid process and the confined, narrow, and asymmetric mandibular notch in the *Australopithecus robustus* mandible and the notch's similarity to that of the MH1 mandible. The upper part of the ramus in all the other mandibles exhibits the generalised configuration. Also note the absence of a preangular notch on the anterior margin of the specialised ramus and the presence of the notch, indicated by white arrows, on the generalised ramus. The photographs of MH1 and MH2 were adapted from Berger et al.² and de Ruiter et al.³ with permission. Note the parts that we added (reconstructed) on MH2.

Although we are convinced that the discrepancies that we have observed in ramal morphology stem from profound biomechanical differences, elucidation of the functionality at play (of the derived configuration) is a major project and beyond the scope of this study. Because the morphological differences are manifested in very young individuals^{9,10}, as described later, one can be certain that these morphologies are embedded in the genome and not generated by some activity during an individual's lifetime. In any case, the functional issue has no bearing on the taxonomic question treated here.

In this paper, our aim is not to determine which species of *Australopithecus* or *Homo* the Malapa mandibles belong to, but to determine how the two mandibles differ and what those differences mean. To accomplish these goals, we show that the differences are beyond what is expected in a trait's normal range of distribution in a given population. Our null hypothesis is that the two mandibles of *Au. sediba* represent a single taxon (as claimed, for example, by Berger¹; Berger et al.²; de Ruiter et al.³; de Ruiter et al.⁵; Ritzman et al.⁹; and Williams et al.⁴). The alternative hypothesis is that the mandibles of *Au. sediba* represent a mix of taxa; in this scenario, a statistical analysis would classify one mandible with the *Australopithecus* cluster (but not provide any species assignment), and the other mandible with the generalised cluster (bearing a shared morphology). Indeed, our evidence supports this alternative hypothesis.

Materials and methods

Our sample includes 115 mandibles from mature extant primates, both male and female (Supplementary table 1): 41 modern humans, 58 chimpanzees (29 each of *Pan paniscus* and *Pan troglodytes*, grouped into one class following the results of previous analyses⁸), and 16 orangutans (*Pongo pygmaeus*). The *H. sapiens* specimens emanate from geographically varied regions: Australia (Aboriginal peoples), India, the Levant, and northern Canada (Inuit). Regarding the size of the modern *H. sapiens* sample, see the Results section. Fossil hominins in the sample consist of four rami from mature *Australopithecus*

individuals (A.L. 288-1, SK 23, MAK-VP 1/83 and SK 34) and two rami from *Australopithecus* juveniles (SK 63 and A.L. 333-43). The juvenile specimens help increase the sample and were added after it became apparent that no ontogenetic change occurs in ramal morphology^{9,10} (Figures 2–4). Another young individual, DIK11, from the Ethiopian Dikika site, exhibits the same ramal morphology, as seen on a photograph of the specimen (no cast has been available to us as yet). In addition, one *Ardipithecus ramidus* ramus, specimen GWM5sw/P56¹¹ (Figure 3), was included as an unknown. Five *Homo* fossils (three *H. erectus* specimens from Choukoutien, restored by Franz Weidenreich¹²; KNN-WT 15000 – *H. ergaster*; and ATD696, a mandible from Gran Dolina, Spain) were also analysed, although they proved to be of limited value (see Discussion).

Gorillas were excluded from our analysis. It was demonstrated in a 2007 study that the ramal morphology of gorillas is similar – although not identical – to that of *Australopithecus*.⁸ As noted in that study:

given a phylogeny in which chimpanzees and modern humans are sister groups, parsimony dictates that we view the similarity in ramal morphology between Australopithecus afarensis [in fact, all the australopithecids that provide ramal evidence] and gorillas as a homoplastic character, a character that appears independently and as such has no phylogenetic value.^{8(p.6570)}

The similarity between the gorilla ramus and that of *Au. robustus* may well stem from the very tall ramus in both groups.

Regarding reconstruction, MH1 requires none. In MH2, the tip of the coronoid process is damaged; nevertheless, its reconstruction is straightforward, as seen in Figure 5. The three dotted white lines on the superimposed images were added by us. The lines demonstrate that there is no way to reconstruct the coronoid process in MH2 to resemble the robust configuration.



Figure 2: Comparison of ramal morphology in three specimens, left to right (not shown to scale): A.L. 33343 (infant), SK 34 (mature individual), and modern *Homo sapiens* (mature individual). Note that the two australopith rami are virtually identical in shape despite their difference in individual age, and their shape differs from that of the generalised (i.e. shared) configuration, which is seen in *H. sapiens*.

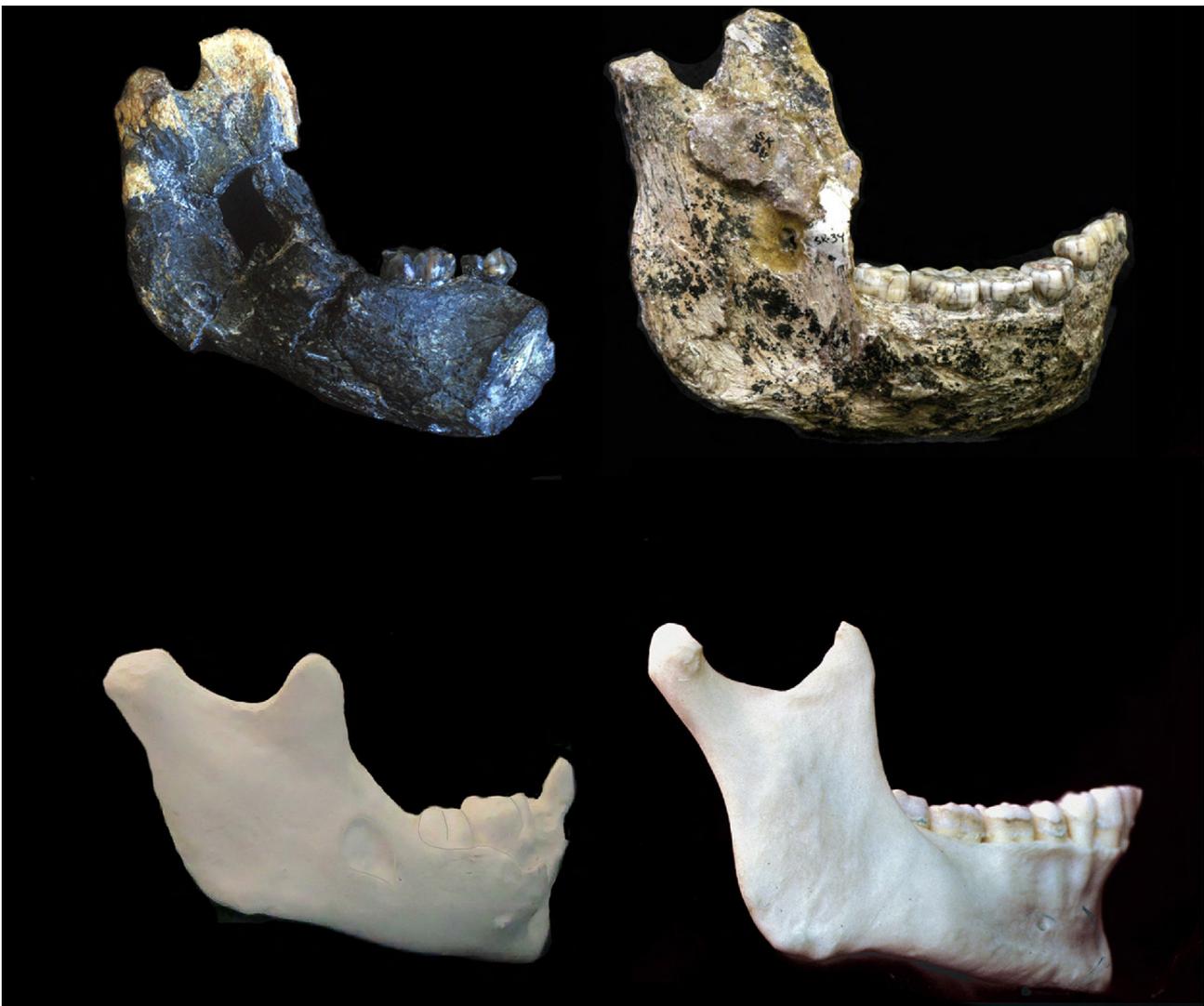


Figure 3: Comparison of ramal morphology in four mandibles (not shown to scale). Upper: juvenile *Australopithecus* specimen A.L. 33343 (left) and adult *Australopithecus* specimen SK 34 (right). Lower: juvenile *Homo sapiens* mandible (left) and adult *H. sapiens* mandible (right). Note that the upper part of the ramal morphology is the same in the juvenile specimen and its corresponding mature specimen in both pairs. In the *Australopithecus* mandibles, the coronoid process is taller than the condylar process; the mandibular notch between them is confined and asymmetric; and its deepest point is very close to the condylar process. This configuration is quite different from that of *H. sapiens*, in which the two processes are the same size in the juvenile and the adult; the mandibular notch is wide; and the deepest point of the notch is midway between the condylar and coronoid processes.



Figure 4: A juvenile *Au. robustus* specimen, SK 63 (flipped), exhibiting the ramal configuration typical of *Australopithecus*.

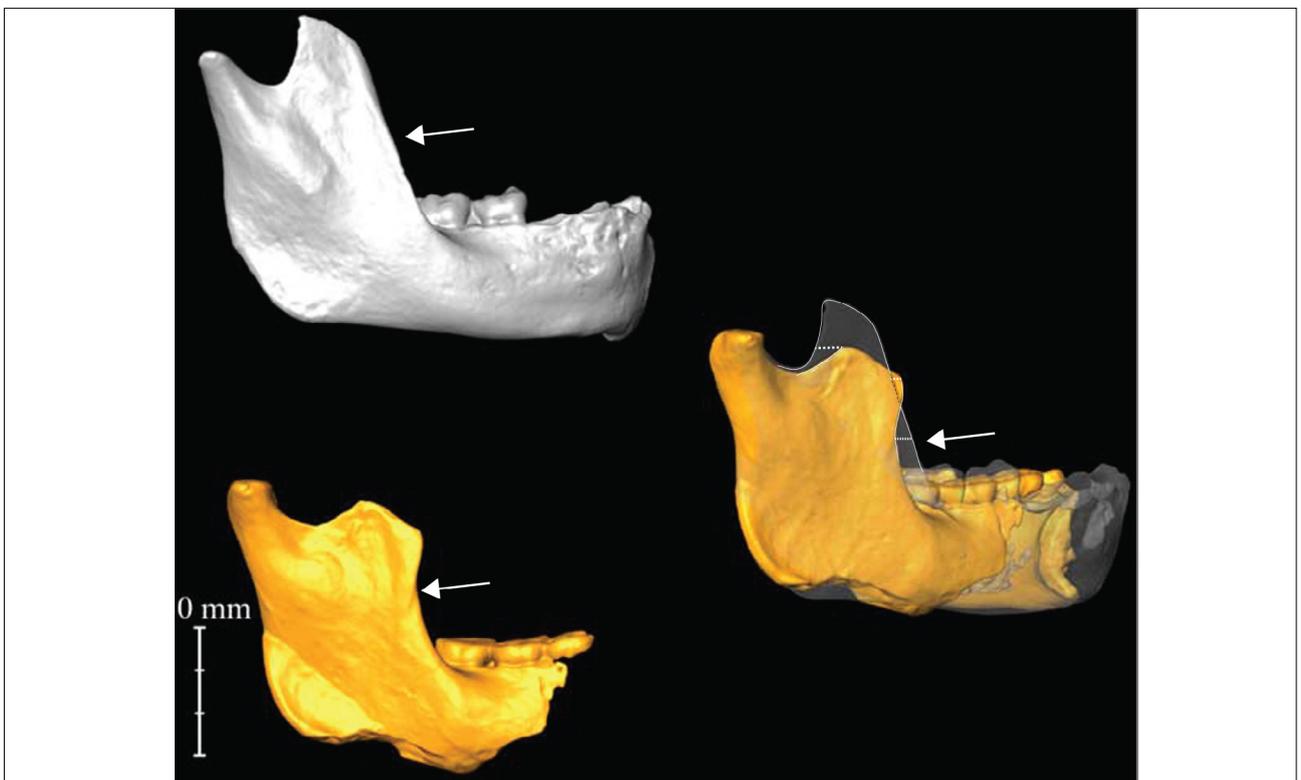


Figure 5: A portion of Berger et al.'s figure S2² showing MH1 (upper) and MH2 (lower). Berger et al.² have superimposed MH1 on MH2 (right), resulting in a vivid illustration of the morphologies that we claim distinguish between *Australopithecus* and *Homo*. For best viewing, enlarge the image. Note the three dotted white lines that we added to the right-hand image. These three lines indicate the differing morphologies of the upper part of the ramus. The white arrows point to the preangular notch or its absence.

We quantified the upper ramal contours of the specimens through a simple method described by Rak et al.^{8(p.6571)}:

To convey the anatomical differences in the upper ramal contour, we adopted a method... which consisted of capturing a digital image of the mandibular ramus with the camera centred at the vertical level of the mandibular notch and held perpendicular to the lateral surface of the ramus. ... We traced the digital image of each ramus from the tip of the condylar process to the anterior margin of the ramus. ...

...We stretched the contour proportionally on the vertical and horizontal axes by dragging the contour's lower right corner until it occupied the entire width of the area of the fixed coordinates in the background template. This part of the procedure eliminated differences in size in the analysis [leaving shape only]. The posterior margin [of the ramus] was aligned with the vertical line at 0, and the anterior margin was aligned at T. The posterior ramal margin in the entire sample exhibits a slight concavity between the posterior end of the condyle and the insertion site of the posterior fibres of the masseter and medial pterygoid muscles; using these two posteriorly protruding structures, we were able to orient the posterior margin on a vertical line throughout the sample. The intersection of the ramal contour with each of the vertical lines, A through T, yielded 20 numeric variables for each ramus.^{8(p.6571)}

We define variable T as the maximum *horizontal* distance between the condyle and two-thirds of the anterior ramal margin's height. In this way, we accentuate the most diagnostic part of the ramal outline (A–T). Note that the use of the point defining T (or any other point on the ramus) does not affect the height measurement of the coronoid process in the mandibles under study.

The intersection of each contour with a vertical line and a horizontal line (i.e. coordinates) is assigned a value representing the distance of the intersection point from the zero horizontal line (for example, 10, 20 or 30) (Figure 6). These are the numerical values used for the statistics. Note that as long as all the contours are on the same grid, units of measure are irrelevant, as is the distance between the lines (provided that it is constant).

We chose the same orientation for the posterior margin of all the rami in our sample because that orientation seems to be *fixed* in relation to the base of the skull, the Frankfurt horizontal, and the zygomatic arch (indicating functional significance), as demonstrated in Figure 7. Alternatively, positioning all the mandibles with a horizontal orientation of the occlusal plane or of the base of the mandibular body would introduce variation in the shape of the mandibular notch.

The 20 (AT) variables served as independent variables in a general discriminant analysis to classify two unknown fossil specimens (MH1 and MH2). We used Jump version 15 software for all analyses. General discriminant analysis applies the general linear model approach to discriminant analysis and can use both continuous and categorical independent variables. Our reference classes consisted of *Australopithecus*, *Pan*, *Pongo pygmaeus* and *H. sapiens* mandibles. The prior probability of classification was set as equal. The key assumption in discriminant analysis is that the variables used are not completely redundant.

To reduce dimensionality and eliminate the dependence between the variables, we used two independent approaches. First was the best-subset approach. Of 1 048 556 possible models, we inspected the 100 models that accounted for most of the variation (i.e. that exhibited the lowest misclassification rate) (Supplementary figure 1). Out of those models, we selected the one with the least number of parameters and used its functions to predict the state of unknowns. This approach considerably reduces the number of variables in the analysis and

keeps the power of classification nearly the same. Thus, the retained variables are those that are most multidimensionally informative for the classification.

Our second approach was a principal component analysis to accommodate the effects of collinearity among the variables. All 20 variables were collapsed into principal components. Five components – those with an eigenvalue greater than or equal to 1 (after varimax rotation) – were retained. We used the components' scores as independent variables in the general discriminant analysis, and the resulting discriminant functions served to classify the unknown fossil specimens. For cross-validation, we applied the leave-one-out procedure. Through the two approaches just described, we classified the unknown fossil specimens. We also reran the analysis under a two-class model: *Australopithecus* and taxa with a generalised ramus (*Pan*, *Pongo* and *Homo*).

Results

Even in the absence of the coronoid process on MH2, the differences between it and MH1 are readily visible, as was shown in 2010 by Berger et al.² themselves (reproduced and modified here in Figure 5). The unreconstructed outline of the mandibular (sigmoid) notch in MH2 diverges quite clearly from the comparable area in MH1. When the two specimens are adjusted to the same scale (Figure 6), the deepest part of the notch in MH2 is situated much more anteriorly than in MH1 and descends much farther relative to the zero point, i.e. the mandibular condyle, as in the generalised configuration. The statistical analysis tells us that the difference between the height of the two coronoid processes, reconstructed or not, is of less importance than the outline of the mandibular notch itself and has little effect on the results.

The best-subset approach yielded a classification success ranging from 94.6% to 92.5%. Most of these models share variables A, G, H, I, P, R and T (Figure 8). The smallest subset model consists of eight effects (A, F, G, I, O, P, R and T; Figure 8), which correctly classify 93.3% of the cases (the leave-one-out cross-validation classification success is 87.4%). According to the posterior probabilities ($p(k_j)$) from the smallest subset model, MH2 falls in the generalised group (assigned as most likely an orangutan, with $p(k_j) = 0.76$), whereas MH1 is assigned as most likely *Australopithecus* ($p(k_j) = 1.00$). Finally, when only *Australopithecus* and the generalised ramus group are considered, the two best models consist of a single variable (I or J) that correctly classifies all cases (100%) (Figure 6). This variable corresponds to the deepest point of the notch in the generalised group; compare with the position of the homologous point in the specialised group (Figure 6). According to this model, MH1 is assigned to the *Australopithecus* cluster ($p(k_j) = 0.98$) and MH2 to the generalised ramus group ($p(k_j) = 1.00$). The ramus of the *Ar. ramidus* mandible¹¹ (Figure 3) falls in the generalised cluster, with a probability of 0.98.

Note that the size of the *H. sapiens* sample (41 individuals) is not what counts; rather, the statistical analysis regards the entire generalised sample, consisting of 115 individuals, as one group, because the real issue is whether the Sediba mandibles fall in the generalised cluster, the specialised one, or both.

In the principal component approach, the four factors with an eigenvalue greater than or equal to 1 together accounted for 91.7% of the variation in the data. (The first four principal components accounted for 50%, 17%, 17% and 8% of the variance, respectively, totalling 92%.) The eigenvalues of the factors were 9.9 (49.7%), 3.4 (17.2%), 3.4 (17.2%) and 1.5 (7.6%). All four factors were significantly different from each other (Bartlett test, $p < 0.0001$ for each of the factors).

The general discriminant analysis correctly classifies 74.2% of cases (with the leave-one-out crossvalidation classification success at 69.7%). Posterior probabilities of this model assign MH1 as *Australopithecus* ($p(k_j) = 1.0$) and MH2 as most likely an orangutan ($p(k_j) = 0.755$). The latter is in contrast to a probability of 0 as *Australopithecus*. *Ar. ramidus* is classified as most likely a chimpanzee ($p(k_j) = 0.49$) or orangutan ($p(k_j) = 0.49$). Finally, when only *Australopithecus* and the generalised ramus group are considered, MH2 and *Ar. ramidus* are assigned to the generalised ramus group ($p(k_j) = 1.00$ in both cases) and MH1 is classified as *Australopithecus* ($p(k_j) = 1.00$).

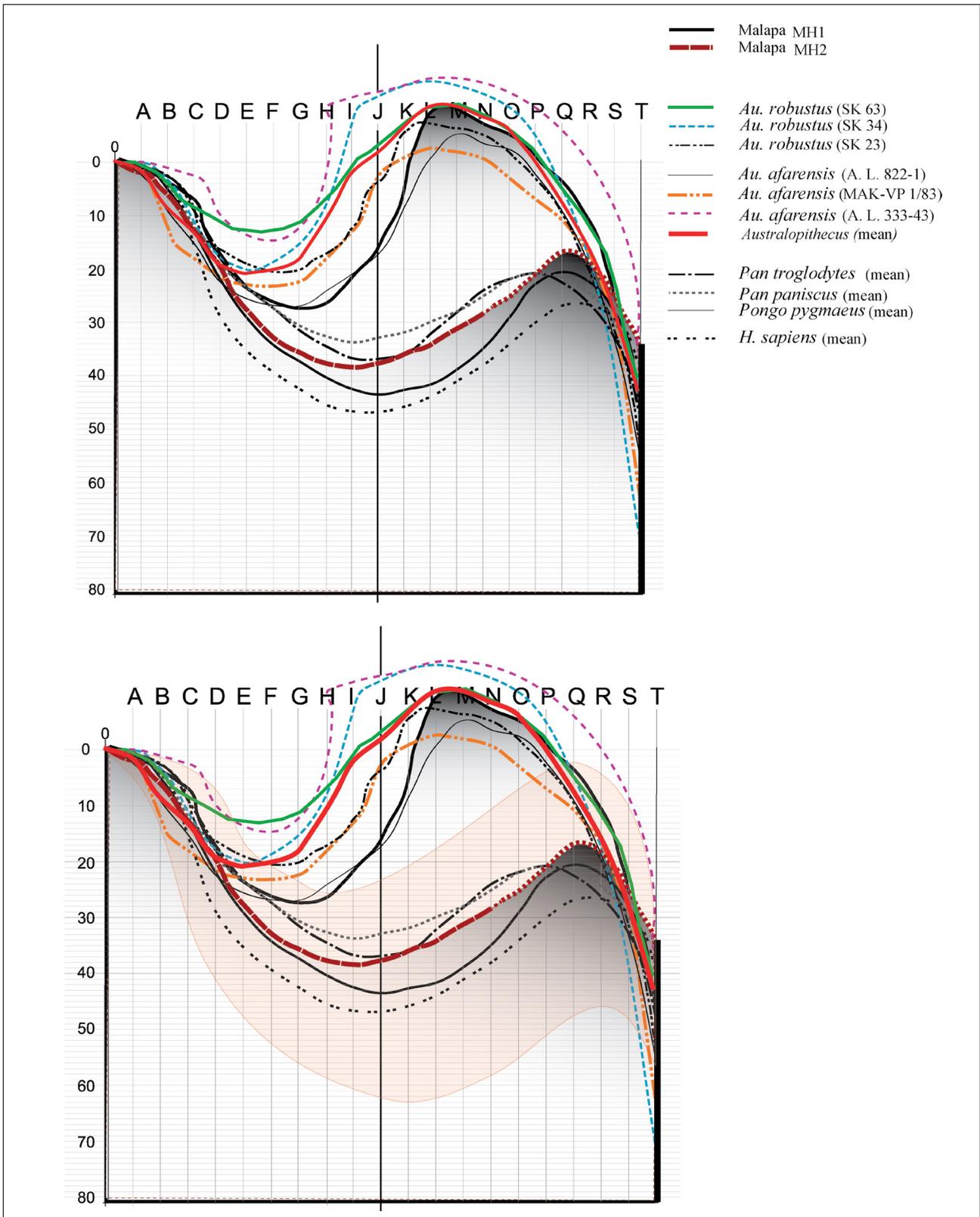


Figure 6: Ramal outlines of fossil specimens and mean ramal outlines of extant hominoid groups, stretched proportionally to fit the distance zero to T. The outlines form two distinct assemblages. Upper graph: the grey-shaded area in the upper portion of the graph represents the MH1 ramus. The lower grey-shaded area represents the MH2 ramus, delineated by the MH2 outline itself (thick, dashed maroon line). The vertical line J represents a variable that is alone sufficient to distinguish between the *Australopithecus* and generalised assemblages. Note that the variable J does not intersect the dotted maroon line, which represents the reconstructed coronoid tip in MH2; i.e. the reconstruction has no influence on the results. Lower graph: this graph is the same as the upper one, with the addition of the range of variation in the *Homo sapiens* sample (light-red shaded area). Note that the means of the extant hominoid sample fall within the range of *H. sapiens*.

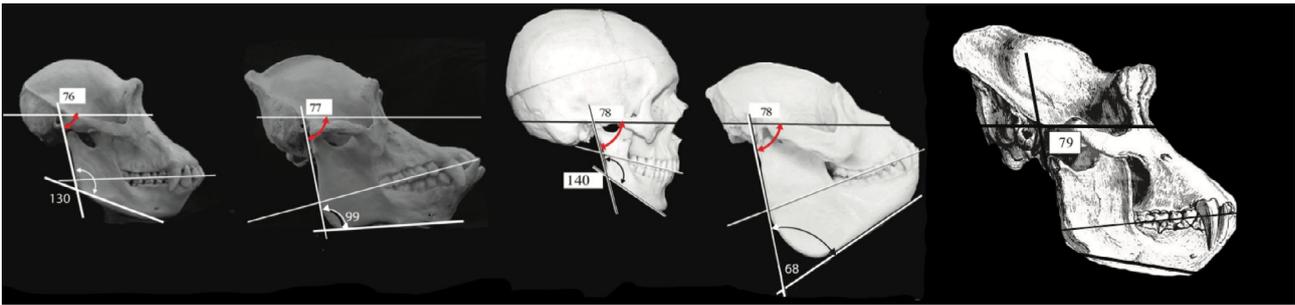


Figure 7: The angle, in degrees, between the posterior margin of the mandibular ramus and the Frankfurt horizontal (which coincides more or less with the zygomatic arch), demonstrating the rationale for using a fixed orientation of the mandibular ramus. From left to right (not shown to scale): chimpanzee, orangutan, *Homo sapiens*, howler monkey and gorilla. Note the similar angle, at 78°, in even the most extreme cases – *H. sapiens* and the howler monkey. In contrast, note the variation in the orientation of the occlusal plane and the inferior margin of the mandibular body.

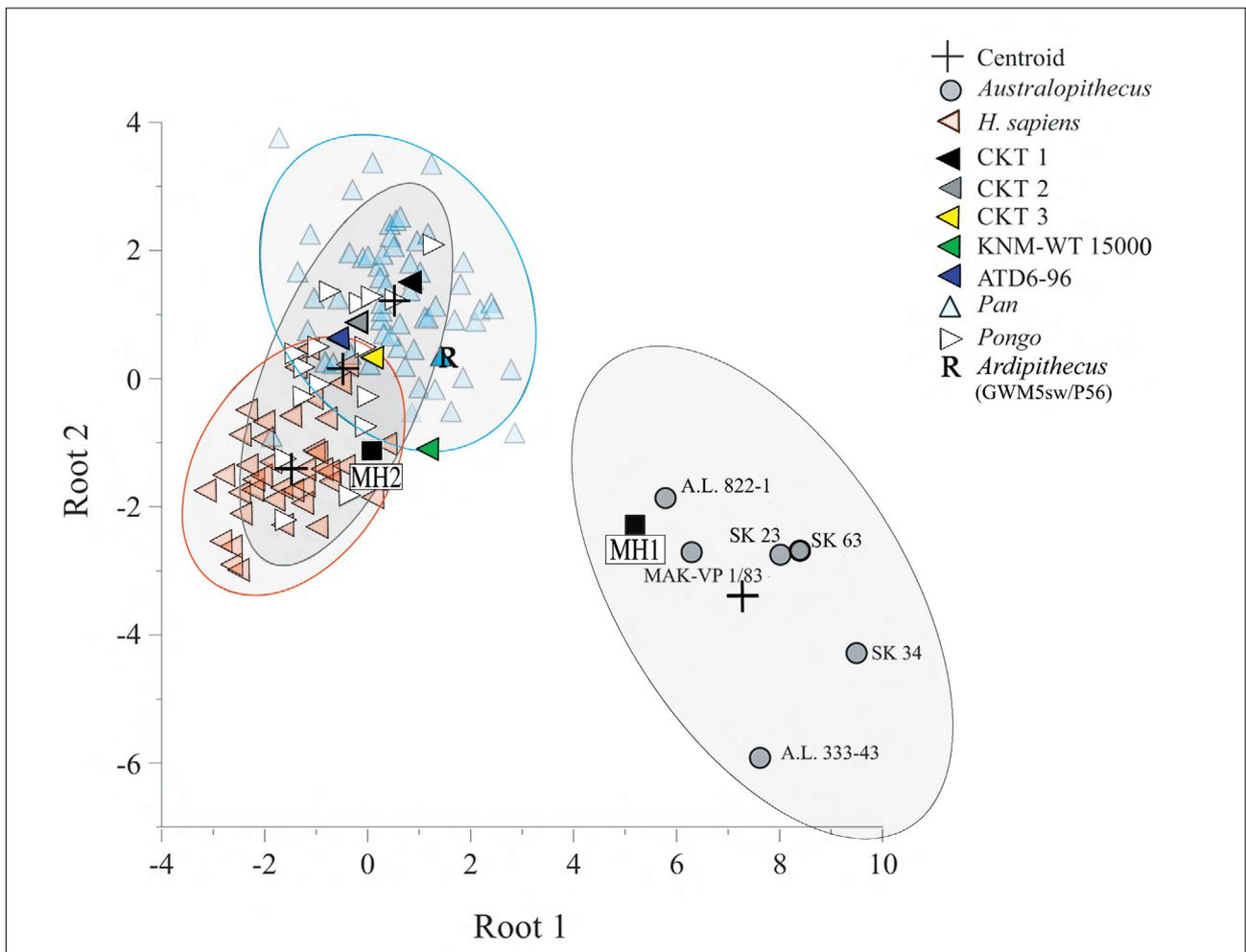


Figure 8: Discriminant function plot including CKT, Choukoutien; KNM-WT 15000, *Homo ergaster*; ATD696, a mandible from Gran Dolina, Spain. Roots 1 and 2 account for 59% and 34% of the variation, respectively. MH1 falls within the *Australopithecus* cluster (with a probability of 0.98), as do the infants A.L. 33343 and SK 63. MH2 falls within the generalised ramus group (with a probability of 1.0), as does *Ardipithecus ramidus* (with a probability of 0.98). The ellipses represent a confidence level of 95%.

The morphological overlap between the comparative taxa is high only in the groups displaying the generalised morphology (not surprisingly, given that ‘generalised’, by definition, is shared). On the other hand, there is no overlap whatsoever between the generalised group and the derived one (Figure 6 and Figure 8). Note that no attempt has been made to assign MH1 and MH2 to particular species (because one of these configurations is synapomorphic and the other is generalised). The fact

that MH2 is classified as most likely an orangutan is of little relevance, nor does it come as a surprise. What counts is that MH2’s generalised configuration puts it in the generalised cluster.

Discussion

The data, as seen in both the distribution of the actual contours (Figure 6) and the plot of the discriminant analysis (Figure 8), clearly demonstrate

that the MH2 mandible falls in the group that exhibits the generalised configuration, a group that includes *H. sapiens*. The MH1 mandible, on the other hand, is clearly clustered with the australopiths.

Although we were limited to specimens that are complete enough to be included in our analysis, other, more fragmentary, specimens of *Australopithecus* (A.L. 333100, A.L. 333w15, A.L. 333n1, A.L. 333108, A.L. 4381g, A.L. 288–1i and DNH 8) exhibit what is undoubtedly the derived configuration of the ramus. Although not a single ramus of *Au. africanus* is complete enough to be included in the analyses, one can clearly see the derived morphology on a forgotten fragment, Sts 7, that is still embedded in matrix (Supplementary figure 2). (Note that Kimbel and Rak's study¹³ of the face of MH1 led them to conclude that the specimen is *Au. africanus*.)

Not surprisingly, the fossil *Homo* specimens that were included in the sample fall in the same cluster as the generalised hominoids (Figure 8). Nevertheless, the *Homo* fossils are of little value to the analysis because in order to serve as an outgroup, they must be assigned to a branch that predates the emergence of the so-called *Au. sediba* species (i.e. fossils that are nested between the *H. sapiens* branch and the *Australopithecus* clade are of no use in this context) – a scenario that we find hard to accept. *Ar. ramidus* is the only hominin that is helpful in this respect; indeed, like chimpanzees and orangutans, *Ar. ramidus* displays a generalised configuration of the ramus (Figure 8).

A recent study⁹ examines a claim that has been presented in several forums^{14–16} and that we offer here in detail: that two taxa are present in the *Au. sediba* hypodigm. In their analysis, Ritzman et al. state that^{9(p.54)}:

while the difference between MH1 and MH2 is large relative to within-species comparisons, it does not generally fall outside of the confidence intervals for extant intraspecific variation. However, the MH1–MH2 distance also does not plot outside and below the between-species confidence intervals. Based on these results, as well as the contextual and depositional evidence, we conclude that MH1 and MH2 represent a single species and that the relatively large degree of variation in this species is due to neither ontogeny nor sexual dimorphism.

Ritzman et al. do, however, acknowledge that ‘the possibility that it [*Au. sediba*] samples two taxa cannot be completely refuted’^{9(p.62)}.

The reason that Ritzman et al.⁹ cannot clearly distinguish between the gorilla cluster and that of modern humans, for example, nor between MH1 and MH2, is rather simple: in their study's method, a large percentage of the variables (semi-landmarks) are identical in humans, gorillas, and all the other groups in their sample because of the straight anterior outline of the rami in all. In other words, only a small percentage of the semi-landmarks are of diagnostic value and worth comparing. The Ritzman et al.⁹ analysis is thus incompatible with our analysis, which takes into consideration only the relevant, more diagnostic, part of the anatomy.

Furthermore, the absence of an australopith sample in Ritzman et al.'s⁹ study seriously detracts from their conclusions. Indeed, the inclusion of australopiths as a distinct known group in our statistical analysis demonstrates clearly that MH1, when treated as unknown, falls in the australopith cluster, whereas MH2, when treated as unknown, falls in the generalised group, as noted earlier (Figure 8). (An additional factor affecting the analysis by Ritzman et al.⁹ is their inclusion of gorillas, due to the different goals of their study.)

The discovery of a hypodigm represented by only two individuals whose morphologies fall at the extreme opposite ends of the range of a population with a normal distribution is highly unlikely. Is it possible that, in keeping with the common primate pattern, the specialised mandible (MH1) represents a male, exhibiting more specialised cranial anatomy, and MH2, with its generalised mandible, represents a female? This scenario

is also unlikely, given that primate mandibles usually do not exhibit sexual dimorphism to such magnitude in characters other than size (see also Ritzman et al.⁹). Even species with pronounced sexual dimorphism, such as the gorilla, demonstrate no sexual dimorphism in ramal shape. The specialised cluster in our study includes specimens that are clearly female (for example, A.L. 822), as well as young individuals, which, although expected to display the generalised anatomy, are nevertheless characterised by a specialised morphology. Most important – even if MH1 and MH2 do represent one highly dimorphic, transitional species – the presence of a specialised mandible (as commonly defined) in that hypodigm would be sufficient to invalidate Berger et al.'s³ original claim that the proposed species is part of our ancestry. Hence, the credibility of the MH2 reconstruction is of no relevance to the phylogenetic issue once we recognise that the complete MH1 mandible is specialised. (See also Du and Alemseged¹⁷.)

Regarding the question of the *Homo* species at play, note that the main concern is the distinction between *Australopithecus* at large and *Homo*. Hence, we do not deal with nomenclature on a species level; it is sufficient to demonstrate that one of the Malapa mandibles belongs to the genus *Homo* and the other to the genus *Australopithecus* – that is, that representatives of both genera existed at Malapa.

The presence at one site of two hominin species of two genera ought not to be surprising. The coexistence of *Homo* and *Australopithecus* at South African cave sites has already been documented. In the mid-20th century, a *Homo* mandible with small teeth was discovered in Swartkrans Cave, which has yielded specimens that are mostly *Au. robustus*.¹⁸ Later, Clarke and Howell¹⁹ recognised that the Swartkrans specimens SK 80 and SK 47 actually constitute one *Homo* specimen, SK 847. In the nearby Sterkfontein site, the presence of both *Homo* and *Au. africanus* was acknowledged with the discovery of the *Homo* specimen StW 53²⁰, although admittedly, the latter specimen may be several hundred thousand years younger than the *Au. africanus* specimens from Sterkfontein. The StW 53 skull includes a neglected fragment of a badly preserved ramus, whose morphology supports the claim by Hughes and Tobias²⁰ that the specimen represents *Homo*. However, Sts 19, a controversial specimen that emanates from the Sterkfontein type site itself along with numerous *Au. africanus* specimens, has been identified by some researchers as *Homo* rather than *Australopithecus*.^{21–24} The Sterkfontein group of *Homo* specimens probably includes the immature individual StW 151 as well.²⁵ Another South African site, Drimolen, provides additional evidence of the coexistence of these two taxa.^{26,27} For a meticulous discussion of the chronology of the hominin-bearing layers in South Africa, see Herries et al.²⁸ and Herries and Shaw²⁹.

Conclusions

The phylogenetic scenario that Berger¹ and Berger et al.² propose, in which *Au. sediba* is a link in our evolutionary chain, ought to be ruled out because one of the Malapa mandibles is too derived to be positioned in the human lineage. Furthermore, one need not dismiss *in limine* the presence of *Homo* at sites contemporary with Malapa or even earlier, or question their geological age, as does Berger in his discussion of a 2.4-million-year-old *Homo* specimen par excellence, A.L. 666, from the Afar in Ethiopia.¹ Malapa itself clearly contains a generalised specimen, and *Homo*, given the size and shape of the fossil, is the only candidate. The split between *Homo* and the robust clade must have occurred earlier than the occupation of Malapa.

Hence, *Au. sediba* is not a species that ‘shares more derived features with early *Homo* than any other australopith species’, as claimed by Berger et al.² In fact, their *Au. sediba* seems to represent a mixture of two hominin taxa, leading Berger et al. to refer to the new species as a transitional one (Figure 5). Moreover, by viewing *Au. sediba* as an ideal link between *Au. africanus* and *H. habilis*, they ignore all the synapomorphic features that the former already shares with the robust clade and to which attention was drawn many years ago (for example, by Aguirre³⁰, Johanson and White³¹ and Rak³²) (Figure 9).

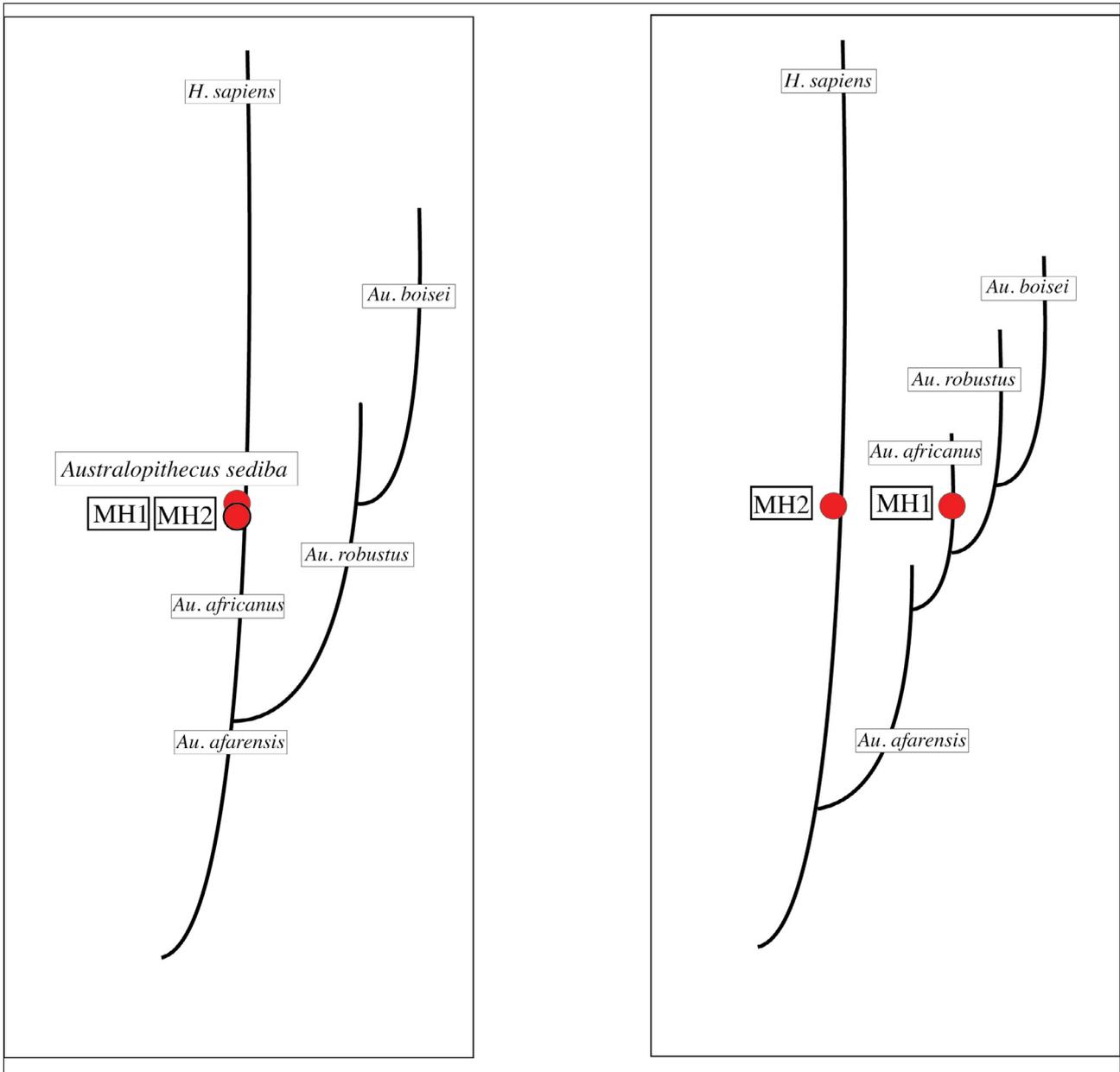


Figure 9: Two proposed phylogenetic trees. The left tree depicts Berger et al.'s 2010 proposal², in which *Australopithecus sediba* is a link in the chain between *Au. africanus* and *Homo sapiens*. The right tree depicts our proposal, in which MH1 lies on the robust clade and MH2 is on the *Homo* lineage. In addition, an analysis of the MH1 skull indicates that there is no reason to exclude it from the *Au. africanus* hypodigm.²³ The *Au. afarensis* mandibular ramus is too derived to allow us to place it on the *Homo* lineage. We have placed *Au. africanus* on the robust lineage, based on facial synapomorphies that it shares with the robust australopithecids.³²

All the australopithecids on which the relevant ramal morphology is preserved (*Au. afarensis*; *Au. africanus*, including the *Australopithecus* specimen at Malapa; and certainly *Au. robustus*) are actually too derived to play the role of a *H. sapiens* ancestor. Given that Malapa already contains representatives of two hominin branches, one of which appears to be *Homo*, we must seek the latter's origin in geological layers that are earlier than those at Malapa, which are dated at approximately 2 million years before present.³³ Support for such a scenario can be found in earlier Ethiopian fossils attributed to the genus *Homo*: A.L. 666, dated at 2.4 million years³⁴, and LD 3501, dated at 2.8 million years³⁵.

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Competing interests

We declare that there are no competing interests.

Authors' contribution

Y.R.: Study conception and design, acquisition of data, analysis and interpretation of data, drafting of manuscript. W.H.: Study conception and design, critical revision. E.B.: Study conception and design, critical revision. A.G.: Acquisition of data, analysis and interpretation of data. E.G.: Analysis and interpretation of data, drafting of manuscript.



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