

New discoveries of *Australopithecus* and *Homo* from Ledi-Geraru, Ethiopia

Corresponding Author: Kaye Reed

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

This manuscript reports four new hominin specimens from Ledi-Geraru, and concludes that both *Homo* and a thus far unknown species of *Australopithecus* were present in the Afar region between 2 and 3 Ma (in addition to *A. garhi*). New hominin fossils from this time period in eastern Africa are important, but interpreting the evidence is complicated by the fact that it concerns isolated teeth. The current manuscript is too 'casual' and has substantial problems that are mostly related to practical issues. It is critically important that these are addressed before it can be assessed in full whether the authors make a convincing case or not.

Here are four issues to consider.

1. No customary methods section is included, which is indicative of how little information is provided about the 'materials and methods' that underpin the analyses and conclusions.

With respect to the new fossils themselves, there needs to be a section providing some more detail of how specimens were found. Most important in this context is a justification of why the upper and lower dental elements of LD 760 are considered to be a single individual, given that they are part of a large sample (i.e. they were not found in isolation). Note that Table 1 does not include the two incisors.

Essential information about the comparative samples is missing. A long generic list of species and sites is given in Extended Data Table 1, making reference to 58 studies, without any differentiation. The same applies to various captions of figures. It needs to be known which specimens are included in the samples and what the source is of metrics. If unpublished Authors' data are included these should be given. In fact, these days most studies will simply provide the data underpinning the graphs as Supplementary Information.

There is a suggestion that the authors assessed the holotype of *A. garhi*, and made original observations, but images are all attributed to Tim D. White. Given the importance here of this species (i.e. single attributed specimen) the 'methods' aspect of this part of the comparative analysis needs to be clarified.

2. Figures:

- Some specimens have an unconventional orientation (Ext Data Fig 4)
 - Orientation of teeth is not indicated
 - Some show left and right specimens making comparison difficult (but some matched by flipping)
 - Comparisons shown are not always meaningful or even mentioned in the text (Ext Data Fig 4, right)
 - Non-matching specimen orientation makes it difficult to interpret (Fig 4 bottom row)
 - Extended Data Fig 7 outlines anterior fovea without mention, but does not illustrate the measurements used on the right.
- In short, for each of the four specimens there should be comprehensive comparative figure which demonstrates the similarities and differences with known taxa. Nature's Extended Data Figures format provides plenty of space to make this possible (consult Formatting guide).

3. The four phylogenetic scenarios are a little lengthy, and could perhaps contemplate that hominin evolution not only took place in the Afar region but elsewhere in Africa as well (see also my comment about *A. africanus* below).

4. Comparative observations – taxonomic attributions

The value of this submission largely depends on the reliability of the taxonomic attributions, and whether they warrant the

conclusions. As the checkered history of interpreting the isolated Omo teeth has shown (especially non-*Paranthropus* specimens), the authors have a difficult job with their sample, and this means comprehensive and reliable analyses. As will be clear from the comments below (two general ones, followed by four specimen-specific ones), I am not convinced that the authors make a credible case for each of the specimens. Typically this is because of incomplete evidence provided, and not necessarily because I disagree with the conclusions as such.

- As written the comparisons lack a clearly argued conclusion regarding the affinities, apart from a specific attribution of LD 302-23 to *Homo*. I assume that the verdict regarding the other three can be picked up from Table 1, but this approach does not help with making a convincing case.

- At present comparisons with *A. africanus* are practically absent, apart from some plots of dental dimensions (noting that Ext Data Figure 15 shows just two *africanus* M2s when about 25-30 are available for this species). I appreciate that there is no evidence for *A. africanus* in eastern Africa, but in all current cladistic analyses the species forms a clade with *Homo*. Hence, in any discussion of a possible 'direct' link between *A. afarensis* and *Homo* the status of *A. africanus* cannot be ignored.

LD 302-23

- No actual MD and BL dimensions are given, and the shape is not metrically analysed. There is a statement that the crown is MD compressed (line 124), but Ext Data Fig 5 does not show this (specimen falls along the average trend of *afarensis* and *Homo*, and within *Paranthropus* range).

- It departs in shape from unicuspid specimens of *A. afarensis* (line 132-133), but how it compares to other P3 specimens of this species is not commented on (not all *afarensis* P3s are the same; see Delezenne & Kimbel 2011).

- Regarding size (line 131-132) "falls in the upper range of the *A. afarensis* size distribution" is incorrect; the area falls in the middle of the *A. afarensis* distribution, and in the upper range of early *Homo*. It may just be outside the boisei hull, but I doubt this is statistically significant.

- In line 136-137 the specimen is attributed to *Homo*. This diagnosis seems largely based negatively on what it is not, rather than positively on what it is similar to. This needs an informative figure (replacing Ext Data Fig 4) which illustrates the diagnostic features in comparison with *Homo*, *Paranthropus* and *A. afarensis* (latter not only a unicuspid P3).

LD 750-115670

- Figure 2: compares the specimen with AL 128-23, but this is the very smallest among about 30 *A. afarensis* P4s and not representative (some might call this 'misleading').

- No specific comparisons are made with early *Homo*. LD 750 falls just within its MD and BL ranges (Ext. Data Fig 6), even if KNM-ER 5431 is not included as having 'earliest' *Homo* affinities. Any morphological reasons this is not *Homo*?

LD 760

- Comparison with *Homo* (line 199-202): the australopith pattern of relative molar size $M1 < M2 < M3$ is also seen in early *Homo* (KNM-ER 730, 1802, 60000, OH 13), and even in younger KNM-BK 8518. Hence, if there is M3 reduction it is meaningful, but in this context absence of M3 reduction is not.

- Comparison with *A. afarensis* (line 204-211): Where is it shown how the MD and BL dimensions fall in the *A. afarensis* distribution? The three ways of difference need to be demonstrated, visually and/or metrically.

- Comparison with *Paranthropus* (line 213-214): is the wear gradient really all to go by to distinguish the LD 760 molars?

- Comparison with *A. garhi* (line 214-230): the BOU-VP-12/130 wear pattern is an interesting observation. However, this would need better documentation because what the authors describe does not seem to match Figure 3CD of Asfaw et al (1999). Moreover, the notion that this pattern is only seen in a single individual in the early hominin record should be reason for caution. This especially as it represents an acquired character (through normal or abnormal mastication) rather than dental morphology. What could that complementary pattern on the mandibular teeth (line 224) look like, and what would the associated masticatory motion be? Any other primate showing this pattern? Certainly interesting but not as a decisive, taxonomically diagnostic feature until it is replicated as taxon specific rather than an individual anomaly/pathology.

- Canine comparison: (line 240-241) "...puts this specimen in the upper range of *Australopithecus* and *Homo*". No; it is in the middle (M1) to lower (M2) range of *Homo*.

AS 100-1

- The M1 (AS 100-1a) is not shown at all, which is not acceptable. Apart from simply documenting the evidence, the glimpse in Fig 5 suggests that it may well be informative, especially in combination with the M2. The M1-M2 can be shown jointly in comparison with AL 666, BOU-VP-12/130 and a suitable *afarensis* specimen (replacing Fig 5 or as an Extended Data Figure).

Lastly, and I realize that this is a sensitive issue, but is honoring Charlie Lockwood really best served by making him co-author well over a decade after his untimely death. He was not there to scrutinize the fossils and how they are interpreted, and I am not sure this is good (ethical) practice in science writing.

Referee #2

(Remarks to the Author)

The human fossil record in East Africa in the time interval between 3.0 and 2.5 Ma is very limited, with only a handful of fossil specimens attributed to the genera *Australopithecus*, *Paranthropus* and *Homo*. Thus, any new discovery marks an important addition to the picture of the evolutionary events that happened in this critical time frame that saw the emergence of the genera *Paranthropus* and *Homo*.

In this regard, the ms by Villmoare et al contributes in several ways to this picture. The significant points of the ms include:

1. The new fossils attributed to Homo from Gurumaha (2.78 Ma) and Asboli (2.58 Ma), confirm the deep antiquity of the Homo lineage well into the late Pliocene before the Pliocene/Pleistocene boundary (set at 2.58 Ma) as previously suggested by the Ledi Geraru mandible LD 350-1 (2.8 – 2.75 Ma). The dates of the Homo fossils also match the dates of the oldest Paranthropus fossils from Kenya (2.7 Ma) and Tanzania (c. 2.66 Ma), suggesting a comparable antiquity for the origin of the two lineages.

This evidence seems to support the model that describes the origin of the Homo and Paranthropus lineages as the result of a cladogenetic event that occurred in the final phase of the evolution of the species *A. afarensis*, whose most recent fossils are dated at 2.95 Ma.

2. At the same time, as noted by the authors, the occurrence of fossils from Ethiopia attributed to a separate species of *Australopithecus* (*A. garhi*) at 2.5 Ma rendered this interpretation more complex: now, the new fossils from Lee Adoyta described in the ms suggest the occurrence, at 2.63 Ma, of a new species of *Australopithecus*, different from *A. garhi*. This new evidence puts further into question the simple model of an evolutionary crossroad Homo-Paranthropus and suggests that the high diversity of australopith species documented in the middle Pliocene was only partially decimated by the events that led to the origin of the Homo and Paranthropus lineages.

3. The present evidence thus establishes the occurrence of four separate species of hominins in East Africa between 2.8 and 2.5 Ma.

4. In a model where Homo and Paranthropus (whose oldest fossils now are dated respectively at approx. 2.8 Ma and 2.7 Ma) are derived from *A. afarensis* (whose most recent fossils are dated at 2.95 Ma) the cladogenetic event must have occurred in a relatively short time frame (geologically speaking). As such, the time range between 3.0 and 2.8 Ma, and fossils deriving from it, now become critical for interpreting the origins of the Homo and Paranthropus lineages - the new frontier for field research for the next generation of paleoanthropologists.

General comments

The ms is well structured and well written. The description of the specimens is accurate and the analysis is appropriate. A few details can be added – see below. The reasons given for suggesting a new species of *Australopithecus* are well argued, and, wisely enough, the authors refrain from naming a new species. The references cited are appropriate.

It contradicts the usual adagio that “more fossils will help to clarify our picture of human evolution”: the new fossils from Ethiopia make more complex our view of our distant past. Also, the new fossils help to narrow the gap between the last *A. afarensis* and the earliest Homo and Paranthropus fossils.

My concern is relative to the position of the figures showing the new specimens. Some are presented in the main text, whereas others are presented in the extended data. This requires the reader to jump from the main text to the extended data, and back, to see how they look like.

My suggestion is putting in the main text all the photos of the new specimens, and in some cases, where relevant, also showing the specimen in different view. All this can be combined in a single figure or two. The figures comparing the new specimens with published specimens should all go in the extended data, and in this case more comparative photos can be added.

Although separated by almost 500 ka, comparisons with *A. deyiremeda* specimens should be added, since these derive from an area not far from that of the sites described in the ms and one may expect some kind of regional continuity between *A. deyiremeda* and the new *Australopithecus* species. Alternatively, reasons for not comparing the new specimens with *A. deyiremeda* should be given.

The ms can be accepted after revisions indicated.

Specific comments:

p. 4 line 79

79 Gurumaha Tuff, a light gray lapilli tuff dated to 2.782 ± 0.006 Ma (1σ sd; recalculated from ref.

Add “(GT)” after Gurumaha Tuff

Page 7, table 1.

In the table add the two incisors mentioned in the text (p. 14, line 232).

In the table and in the text fossil specimens are sometimes referred to with the locality number only, whereas in other occasions the complete labelling system is employed. Only one system should be used for consistency.

p. 7 Gurumaha hominins

Following the same logic used for the specimens described later, a comment should be made on the possibility that the specimen LD 302-23 belongs to *Australopithecus* sp. n. or why this possibility has not been considered.

p. 8 -10 Lee Adoyta hominins

Specimen LD 750-115670, LP4. In this case also reasons for excluding this specimen from Homo should be given.

p. 15. Line 250.

Given that the teeth from 750 represent the same individual a sentence of this kind should be added : “Taken together, the combined evidence of the molars and the canines suggests differences of this individual from *A. afarensis*, *A. garhi*, Homo and *Paranthropus* ... “ or something along this line.

No description is given of the two incisors. This should be added at least for the I2.

p. 17 line 262.

Here the fossils are referred to as “Asboli hominins” whereas the other specimens have been referred to with the name of the sedimentary package, thus in this case “Golden Sands”. Modify throughout the text for consistency, in one way or another.

p. 17 line 263.

A figure showing AS 100-1a should be added – if it is worth showing it.

p. 17 – 18.

Again, also in the case of AS 100-1b reasons for excluding the specimen from *Paranthropus* and *Australopithecus* sp.n. should be given.

Extended data

In the extended data the following tables would be useful:

1. A table with a list of the specimens attributed to early Homo, or putative early Homo - all or the most relevant – discovered in East Africa in the time range 3.0 – 2.3 Ma. For example,

Mille-Logya
Nachukui
LD 350-1
Omo 75-14
KNM ER 5431

This will give a good idea of how limited the fossil evidence in this time range is, but I leave the final decision of inserting the table to the authors.

2. A table with all the dental metrics of the specimens described. Presently, the reader has to go through text and figure captions to collect this information. Having all of them in a single place would be helpful.

Also, bivariate plots of MD vs BL of all the new specimens (beside those already presented) would be useful, at least as composite images. This will give a good perception of the size of the teeth.

Referee #3

(Remarks to the Author)

This paper reports on new fragmentary dental remains recovered from the Ledi-Geraru research area, which contains sediments representing a critical and poorly sampled time range (3 to 2.5 Ma) in the hominin fossil record. The authors suggest that early Homo and *Australopithecus* were sympatric in the Afar. If indeed borne out by the data, the paper would be of great relevance to multiple questions in human evolution ranging from phylogeny to paleoecology to mode of evolution of early hominins and the origin of the genus Homo.

The major claim of the paper is predicated upon demonstrating that the Lee Adoyta dental remains do indeed belong to *Australopithecus* because, in the Afar, only Homo and *A. garhi* are known from the 3 – 2.5 Ma interval. While the addition of another *Australopithecus* taxon would increase diversity, the same will also raise new palaeobiological and palaeoecological questions.

The attribution of LD 302-23 P3 to the genus Homo, while it does not affect the main thrust of the paper, their assertion: “departs strongly in shape from the unicuspid specimens of *Au. afarensis* (e.g., A.L. 128-23, A.L. 288-1)” needs to be tempered as P3 morphology in *A. afarensis* tends to bimodal or is at least variable. The above cited specimens represent the

more primitive condition and not the mean. Some *A.afarensis* P3s are more derived though not to the extent seen in the new specimen. A.L. 822 for example has a more differentiated occlusal surface with a metaconid that is more developed than what is seen in A.L. 288.

Furthermore the configuration seen in A.L. 288 (the primitive condition) is seen in some *Homo* specimens including the holotype of *H.habilis*, OH 7 in addition to OH16, OH 13 and OH22. What we learn from variation in *A.afarensis* is that it is the frequency of many of these traits and not their "discrete nature" that characterizes the species. Their sample size does not lend hand to examine frequency hence the need for caution.

I must also note that wear on LD 302 makes the occlusal morphology difficult to observe, offering less confidence in statements like "LD 302 differs from *Au. afarensis* in having a metaconid situated well anterior to the protoconid and in having a reduced anterior fovea". Given all these caveats, I would place LD 302 in cf. or aff. *Homo*. Since LD 350 comes from the same time period, the status of the former will not affect their main conclusion. I suggest that the description of the specimen be revised to reflect these comments.

The Attribution of the Asboli specimen from 2.59 Ma to *Homo* is convincing and the new teeth expand known sample size of *Homo* prior to 2.5 Ma, which is much needed. AS 100-1b also gives another line of evidence to show that what they have at this site is not *Au. garhi*. Can they provide an image of AS 100-1a?

The Lee Adoyta premolar and molars that are central to the main conclusion of the paper are well described, demonstrably separated from *A.garhi* and *Homo* and are reasonably attributed to *Australopithecus* but differ from *A.afarensis* in some aspects. 1) they are BL broad relative to their MD length, 2) the M2 and M3 do not taper distally to the extent seen in *Au. afarensis*, and 3) the LD 760 molars lack the distinct bilobate buccal contour seen in *Au. afarensis*.

Based on this, the authors outline four possibilities for the taxonomic attribution of the Lee Adoyata dentition. They have evidence to show that the specimens do not belong to *A. garhi* or the *Paranthropus* lineage. Given the limited sample size it is difficult to clearly demonstrate if the specimens represent some late survivors of *Au. afarensis* or may belong to an unknown *Australopithecus* species. While the authors lean toward the latter, more fossils are needed to better characterize the difference from *A. afarensis* given that changes (over 350kys) within this species could have introduced what is being observed. Whatever the case might be, the presence of *Australopithecus* this late in geologic time changes our understanding of the genus albeit based on shaky evidence. This paper is well written, and the authors have done their best to squeeze as much information as possible from the fragmentary evidence. The latter is a weakness but still suggests the possibility of the presence of *Australopithecus* by 2.63 Ma. With great caution, what is being proposed can be accepted as a hypothesis that can be tested through further fieldwork.

Q. Fig. 4: (Top row) in order of appearance from left to right it should be lingual and Labial and NOT Labial and lingual.

I recommend publication of the ms with the above suggestions included in a revised version.

Zeray Alemseged

Referee #4

(Remarks to the Author)

The manuscript by Villmoare reports new fossil discoveries in Ledi-Geraru (Afar, Ethiopia) and assigns the fossils to *Australopithecus* spp. The authors provide a general description of the current chronology and species assemblages existing in the eastern African hominin record between ~3-2 Ma and present the geologic, chronologic, and fossil descriptions to constrain the ages and taxonomy of the new specimens.

The paper has a well-summarized introduction and provides a detailed geologic figure to show the stratigraphic context of the fossils. The Ar/Ar age data recalculations from published data are necessary and will be helpful to readers who do not understand the complexities of standardization in Ar/Ar dating. I have a few specific comments and recommend minor revisions, provided there is another reviewer to assess the fossil assignment to *Australopithecus* spp. Rather than assigning these materials to an already established taxon.

This reviewer is not an expert in hominin paleontology, so my comments will be mostly restricted to the geological and geochronological portions of the paper. Having collaborated on hominin paleontology research projects, I find it odd that a collection of isolated teeth is sufficient to assess that these elements cannot be of any already-established taxon, given the many comparative specimens that were studied (based on the list in lines 112-115). Especially given the similarities with other *Australopithecus* dentitions, and some evidence being mesowear patterns to refute associating the new materials with other established species, it seems likely that there is simply not sufficient fossil material in the new LD assemblages to rule out their assignment to *A. afarensis* or *A. garhi*. Given my shallow ability to evaluate this data, however, I would recommend at least one reviewer can adequately evaluate the results and discussion pertaining to the fossil materials, since I cannot carefully assess that portion of the presented work.

Line-by-line comments:

i.e., point 3, lines 338-345: If there are very few specimens of *A. garhi* (one?), is this sufficient to exclude the association of new fossils based on different tooth wear patterns?

Lines 352-355: what evidence is being presented to demonstrate the habitat of these materials? There is no information on the sediments in the manuscript. I don't see any isotope data or faunal assemblage analysis. This point seems to be added at the end and not well supported.

Supplementary Information contains all of the supporting data for the ages of tephra.

For the Ar/Ar methods, can you please provide a one-sentence explanation for how the blank correction was applied to the samples?

Supp Fig. 1: the apparent and plateau age of one crystal is significantly younger and more imprecise than others sample 27361-20. Any reason why? This was also the grain excluded in the probability distribution function age from plateaux. Since it is unusual to omit younger grains than the mode, unless there is a clear reason, why is this grain omitted? The same question goes for the two younger grains omitted for the isochron ages. In this case, are there two omitted (rather than one) for a particular reason? It seems like including the second youngest one may bring the MSWD closer to 1, as well, so it isn't clear why this grain is omitted there. And if it is included, does it bring the isochron-based mean age closer to the plateau-based mean age? Based on the Ca/K plot, it appears the second omission is not the second youngest in the plateau age diagram, implying the age and precision does shift significantly with the isochron approach.

Extended Data contains additional supporting materials on the fossils. I have no significant comments on this section.

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The revised manuscript is much improved, but needs some final revision as indicated below. I can't emphasize enough that all figures should be easy to interpret. This especially as Nature is not a specialists' journal, although all my Figure comments would equally apply in a journal like Journal of Human Evolution.

Line 149 "at a similar stratigraphic level". Confusing because in Line 120-121 we learn that LD 302 is 6m stratigraphically below LD 350.

Line 181-190: as written I can't see the justification why attribution to Homo is excluded, and the conclusion is aff. Australopithecus rather than Homo or Australopithecus, but not Paranthropus. Please be clearer, or modify.

Line 229-231: "The LD 760 molars depart from the typical feature set of Au. afarensis in three ways: 1) the M1s are BL broad relative to their MD length...".

Looking at Supplementary Figs. 8, 9 my conclusion is that the LD 760 M1s fall well within the range of variation of A. afarensis in this respect, but among the BL wider specimens. Just considering 'typical afarensis proportions' as the exact mean of the sample, as apparently done here, is biologically not realistic (majority of afarensis specimens would also be 'atypical'). Please moderate statement.

Line 325-327: I assume the authors refer to species diversity before 3.0 Ma (i.e. A. deyiremeda, K. platyops, possibly A. Prometheus). If so, they should cite some relevant references making this clear.

Line 382: Should that also include 'southern Ethiopia (i.e. Member C, Omo Shungura Formation)?

As a technical comment, and the editor will correct me if I am wrong, but my reading of the Formatting Guide is that essential Methods information should be part of the article text, rather than having all methods in the Suppl Materials ("The 'Methods' section is in the main text file, following the figure legends"). This is important because Supplementary Materials is generally less thoroughly reviewed (cheer bulk often), not edited at all, and available separately. Of course the Methods can be expanded into the Suppl Materials.

Figures

Figure 2: it is helpful to have this overview figure (with orientation indicated). However, I would recommend to use the most conventional orientation with mesial to the top (as in some other figures). And be consistent: why is Ext Data Fig 3 oriented differently from Figure 2?

Anatomical orientation. Is only indicated in Figure 2, and this should be done for all other figures (incl. Ext. Data Figs and Suppl Figs). This can be done in the figure itself or in the legend stating something like 'mesial to the top, buccal to the right'.

Figure 4 (Line 275-276): "Images are oriented differently to emphasize the distinctive relevant morphology". Regarding the lower three images: it would be helpful if at least AL 200-1 and BOU-VP-12/130 would be oriented in the same way (and if the legend would indicate the orientation).

Figure 5. What is the point of when we have Figure 2 (top right) showing the same view? Supplementary Figure 12 may well be a good replacement, because the average reader may struggle to visualize 'distal taper and bilobate contour', whereas it is critical for identifying LD 760 as non-afarensis.

Currently, many of the Extended Data Figures are greatly underusing the full A4 size that is available (e.g. 3, 4, 8). These can be combine with multiple images in a single Extended Data Figure, as long as they share a theme of sorts. For example, Ext Data Figs 3-5 can easily be combined. Doing so frees up space and the most important Suppl Figures can be moved to Extended Data Figs.

Referee #2

(Remarks to the Author)

Review of the paper

New discoveries of Australopithecus and Homo from Ledi-Geraru, Ethiopia – R1

By B. Villmoare et al.

The authors have made a commendable effort to address the concerns raised by the reviewers. I believe that the revised version is much improved, and it can accepted with minor reviosions indicated below.

Minor comments on the R1.

Figure 2. LD 760 assemblage.

The authors have chosen an unusual position for the upper teeth. The I1, I2, upper canine must be rotated by 90° clockwise (or counter-clockwise, if they prefer).

Figure 3. line 207. Reference to Table 1 is present. Shouldn't this be Supplementary online dental metrics ?

Extended Data Fig 4. Indicate mesial and distal.

Supplementary Figures 4, 6, 9, 10, 11, 16, deyiremeda is incorrectly spelled "deyiremida"

Notes on the hominin dental metrics table:

Cell L1 : mandibular P3 MD has no subscript in 3

Cell A243 : Stw 19 is listed as A. africanus, but in cell A511 the same specimen is listed as Homo sp. Please sort this out.

Cell A438 : KT 12/H40 : Guy et al. () is not in the references

Cell A 453 : KNM-ER 1813 : Zaim et al. (2011)/Wood (1991). Zaim et al is not in the references

Cell A612: Peninj 1: is not given in Moggi-Cecchi et al 2010. see Wood 1991

Data for the specimen KNM-ER 5431 are not present in the table. Please add - see Wood 1991.

I hope that the data are in the plots, since this is a critical specimen.

Measurements of the specimens labelled Stw are indeed published in Moggi-Cecchi et al. JHE 2006, so it is more appropriate to refer to that paper. As for the other A. africanus specimens the (JMC pers. comm.) can stay.

A matter of style:

Many specimens in column A, for each species, are sorted as 'text' (see specimens labelled Sts, Stw, MLD, OH, KNM-ER, DNH, KW, SK, SKW, SKX) - it is preferable having them sorted as 'number'.

Jacopo Moggi-Cecchi

Referee #3

(Remarks to the Author)

The authors have addressed the specific concerns I had in my initial review.

Referee #4

(Remarks to the Author)

since this is a review for the revision, I will keep it short. The authors have satisfied my comments and correction suggestions related to the Ar/Ar dating. If the other reviewers who evaluated the fossil material consider those revisions appropriate, then I consider this manuscript ready for publication.

Version 2:

Reviewer comments:

Referee #1

(Remarks to the Author)

The second revision has again improved and I have just three points for consideration. I look forward to seeing this paper published. Congratulations to the authors.

Methods issue

In their rebuttal the author cite an unspecified source:

“.....Specialized methods that require chemical structures, figures or tables, or methods requiring equations, cannot be accommodated in the Methods section of the main text file. If such information is part of the Methods, the entire Methods section must instead be included within a Supplementary Information text file.”

And conclude:

“Our methods do include specialized figures related to the $^{40}\text{Ar}/^{39}\text{Ar}$ analysis so we chose to keep the methods in the Supplementary Information”.

I could not find this stipulation in the latest version of the Nature Formatting Guide (<https://www.nature.com/nature/authors/formatting-guide>), or anywhere on the web. In my mind it seem a strange rule that if some individual method requires a figure or table that cannot be accommodated in the article this implies that absolutely everything should be moved to the Suppl Info.

Hence, I suggest to the editor that it is important in an article like this one that the core methods are part of the actual article rather than squirreled away in unedited Supplementary Info. Thus, summary statements about where, when and how the fossils were found, how (to what) were they compared, in what way were they dated etc. The details of all of this (comparative samples, dating and geology details etc) should obviously be in the Suppl. Info.

Two other comments:

Line 182: “Since LD 182 750-115670 lacks any clear Homo synapomorphies”
Can we please have a reference where these synapomorphies are specified?

Extended Data Fig. 3: please reorient the A.L. 333w-1 P3 along the correct mesiodistal axis (see Figure 6C in Deleuzene & Kimbel 2011). It currently looks like a rather strange tooth.

Referee #2

(Remarks to the Author)

The authors have addressed my observations and comments. The manuscript to me can now be accepted pending the very minor formatting issues indicated below.

My comment : Cell L1: mandibular P3 MD has no subscript in 3
Authors reply: We corrected this.

I still don't see the subscript in what is now cell E1. Please check

My comment : A matter of style: Many specimens in column A, for each species, are sorted as ‘text’ (see specimens labelled Sts, Stw, MLD, OH, KNM-ER, DNH, KW, SK, SKW, SKX) - it is preferable having them sorted as ‘number’.

Authors reply: We corrected this and now the table has a more straightforward sorting function.

Unfortunately, this is not the case. I paste below an example for part of the StW specimens to explain what I meant:

Stw 147

Stw 179

Stw 18 - this is not in numerical order

Stw 183
Stw 188
Stw 189
Stw 19 - this is not in numerical order
Stw 193
Stw 196
Stw 2 - this is not in numerical order
Stw 204
Stw 208
Stw 212
Stw 213
Stw 220
Stw 23 - this is not in numerical order
Stw 234
Stw 237
Stw 246

I have downloaded the table and tried to sort them as numbers, but Excel does not allow to do this.

Since this is just a matter of style, I leave to the Editor the decision on whether to leave the list as it is now or ask the authors to reformat it (which probably implies moving manually each single row not in numerical order into the exact position, FOR EACH OF THE SITES indicated above).

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Responses to referees' comments:

Referees comments in italics and our responses in bold face.

Referee #1 (Remarks to the Author):

This manuscript reports four new hominin specimens from Ledi-Geraru, and concludes that both Homo and a thus far unknown species of Australopithecus were present in the Afar region between 2 and 3 Ma (in addition to A. garhi). New hominin fossils from this time period in eastern Africa are important, but interpreting the evidence is complicated by the fact that it concerns isolated teeth. The current manuscript is too 'casual' and has substantial problems that are mostly related to practical issues. It is critically important that these are addressed before it can be assessed in full whether the authors make a convincing case or not.

Here are four issues to consider.

1. No customary methods section is included, which is indicative of how little information is provided about the 'materials and methods' that underpin the analyses and conclusions. With respect to the new fossils themselves, there needs to be a section providing some more detail of how specimens were found. Most important in this context is a justification of why the upper and lower dental elements of LD 760 are considered to be a single individual, given that they are part of a large sample (i.e. they were not found in isolation). Note that Table 1 does not include the two incisors.

We have added a more formal methods section (in the Supplemental Material, per journal instructions) of how and where the specimens were found and recovered. We discuss in depth the depositional relationship between the upper and lower teeth of LD 760 starting in lines 193 in the main text and also show a spatial view of the teeth as discovered in Extended Figure 7. We have also added the incisors to the table and Figure 2.

Essential information about the comparative samples is missing. A long generic list of species and sites is given in Extended Data Table 1, making reference to 58 studies, without any differentiation. The same applies to various captions of figures. It needs to be known which specimens are included in the samples and what the source is of metrics. If unpublished Authors' data are included these should be given. In fact, these days most studies will simply provide the data underpinning the graphs as Supplementary Information.

We have added a supplementary table (available to download as a CSV) for the data used in this analysis, with citations for all metrics not measured directly by the authors. We also differentiated the references to refer directly to relevant species. Measurements are also in text and figure legends.

There is a suggestion that the authors assessed the holotype of A. garhi, and made original observations, but images are all attributed to Tim D. White. Given the importance here of this

species (i.e. single attributed specimen) the ‘methods’ aspect of this part of the comparative analysis needs to be clarified.

Two of the authors (BV, LD) directly examined and measured the *A. garhi* holotype (Extended Figure 9 caption). However, Tim White declined to give permission to take photographs, so all images of that specimen were necessarily provided by him, using photographs taken at perspectives we requested. We trust the reviewer is aware of the sensitivity surrounding examination of some specimens in the Ethiopian National Museum.

2. Figures:

- *Some specimens have an unconventional orientation (Ext Data Fig 4)*
- *Orientation of teeth is not indicated*
- *Some show left and right specimens making comparison difficult (but some matched by flipping)*
- *Comparisons shown are not always meaningful or even mentioned in the text (Ext Data Fig 4, right)*
- *Non-matching specimen orientation makes it difficult to interpret (Fig 4 bottom row)*
- *Extended Data Fig 7 outlines anterior fovea without mention, but does not illustrate the measurements used on the right.*

In short, for each of the four specimens there should be comprehensive comparative figure which demonstrates the similarities and differences with known taxa. Nature’s Extended Data Figures format provides plenty of space to make this possible (consult Formatting guide).

We have reoriented specimens and provide anatomical orientations. Figure 2 now shows all specimens analyzed in the manuscript (at the request of another reviewer) oriented and to scale. All comparative specimens now have the same orientation. The measurements and importance of the P₄ anterior fovea (now Extended Figure 6) is explained in the legend for that figure.

3. The four phylogenetic scenarios are a little lengthy, and could perhaps contemplate that hominin evolution not only took place in the Afar region but elsewhere in Africa as well (see also my comment about *A. africanus* below).

The phylogenetic arguments are somewhat complex, so we are reluctant to reduce them too much. We agree of the importance of South African taxa and have included them in our comparative analyses but no current phylogenetic analyses place *A. africanus* as a sister taxon to *Homo* or other East African australopiths and so may not be directly relevant to the taxonomic issues raised in this manuscript, which only makes attribution to the level of the genus.

4. Comparative observations – taxonomic attributions

*The value of this submission largely depends on the reliability of the taxonomic attributions, and whether they warrant the conclusions. As the checkered history of interpreting the isolated Omo teeth has shown (especially non-*Paranthropus* specimens), the authors have a difficult job*

with their sample, and this means comprehensive and reliable analyses. As will be clear from the comments below (two general ones, followed by four specimen-specific ones), I am not convinced that the authors make a credible case for each of the specimens. Typically this is because of incomplete evidence provided, and not necessarily because I disagree with the conclusions as such.

- As written the comparisons lack a clearly argued conclusion regarding the affinities, apart from a specific attribution of LD 302-23 to Homo. I assume that the verdict regarding the other three can be picked up from Table 1, but this approach does not help with making a convincing case.

We have made explicit the taxonomic attributions of our material in the text, and more importantly, why we make these attributions. Our arguments and conclusions can be found in and around the following lines 143 (LD 302-23), line 190 (LD 750), line 288 (LD 760), line 317 (AS 100).

- At present comparisons with A. africanus are practically absent, apart from some plots of dental dimensions (noting that Ext Data Figure 15 shows just two africanus M2s when about 25-30 are available for this species). I appreciate that there is no evidence for A. africanus in eastern Africa, but in all current cladistic analyses the species forms a clade with Homo. Hence, in any discussion of a possible 'direct' link between A. afarensis and Homo the status of A. africanus cannot be ignored.

Thank you for noticing the absence of A. africanus on Extended Data Figure 15 – those specimens were not appearing because of a formatting error on that figure, which is now Supplementary Figure 16. This has been fixed and A. africanus is now on all relevant figures, including additional figures added.

We disagree about the phylogenetic placement of *Au. africanus* as the sister to *Homo*. Though its position is not stable, most recent analyses place *Au. africanus* as the sister to a *Paranthropus*+*Homo* clade (i.e., Mongle et al., 2019, 2023), while others position *Au. africanus* in a clade with *Paranthropus* (i.e., Dembo et al., 2016). We do not attribute the *Australopithecus* teeth to a species, and instead prefer only a genus-level diagnosis given current evidence. We have added a sentence to the manuscript stating that we cannot exclude *africanus* on a morphological basis.

LD 302-23

- No actual MD ad BL dimensions are given, and the shape is not metrically analysed. There is a statement that the crown is MD compressed (line 124), but Ext Data Fig 5 does not show this (specimen falls along the average trend of afarensis and Homo, and within Paranthropus range).

- It departs in shape from unicuspid specimens of A. afarensis (line 132-133), but how it compares to other P3 specimens of this species is not commented on (not all afarensis P3s are the same; see Deleuzene & Kimbel 2011).

- Regarding size (line 131-132) "falls in the upper range of the Au. afarensis size distribution" is

incorrect; the area falls in the middle of the A afarensis distribution, and in the upper range of early Homo. It may just be outside the boisei hull, but I doubt this is statistically significant.

- In line 136-137 the specimen is attributed to Homo. This diagnosis seems largely based negatively on what it is not, rather than positively on what it is similar to. This needs an informative figure (replacing Ext Data Fig 4) which illustrates the diagnostic features in comparison with Homo, Paranthropus and A. afarensis (latter not only a unicuspid P3).

The specimen's measurements are now in the Supplementary Data Table (along with all measurements used in this manuscript, including comparative specimens). We have also added a Figure (Extended Figure 4) with relevant comparative specimens in occlusal view. Supplemental Figures 4 and 5 provide metric analyses of this specimen relative to comparative species. We have revised and clarified in the morphological description (lines 131-150) to explain our taxonomic conclusion.

LD 750-115670

- Figure 2: compares the specimen with AL 128-23, but this is the very smallest among about 30 A. afarensis P4s and not representative (some might call this 'misleading').

- No specific comparisons are made with early Homo. LD 750 falls just within its MD and BL ranges (Ext. Data Fig 6), even if KNM-ER 5431 is not included as having 'earliest' Homo affinities. Any morphological reasons this is not Homo?

We have added additional specimens to the comparative photograph (now Extended Figure 5) to show comparative occlusal anatomy in temporally relevant eastern African taxa. We have also added detailed comparative morphology (lines 165-190) but we also note that our taxonomic identification is based on plesiomorphic anatomy and that we regard it as therefore provisional and probabilistic (see also our taxonomic discussions starting line 338).

LD 760

- Comparison with Homo (line 199-202): the australopith pattern of relative molar size $M1 < M2 < M3$ is also seen in early Homo (KNM-ER 730, 1802, 60000, OH 13), and even in younger KNM-BK 8518. Hence, if there is M3 reduction it is meaningful, but in this context absence of M3 reduction is not.

True with regard to the M1-M3 size gradient, but the absence needs to be reported since it is taxonomically informative if present (see lines 217-220)

- Comparison with A. afarensis (line 204-211): Where is it shown how the MD and BL dimensions fall in the A. afarensis distribution? The three ways of difference need to be demonstrated, visually and/or metrically.

We now have Supplementary Figures 9-11 that show the metric variation for each molar.

- Comparison with *Paranthropus* (line 213-214): is the wear gradient really all to go by to distinguish the LD 760 molars?

No, as seen in Supplementary Figures 8 and 13, LD 760 falls outside the range of variation of eastern African *Paranthropus*.

- Comparison with *A. garhi* (line 214-230): the BOU-VP-12/130 wear pattern is an interesting observation. However, this would need better documentation because what the authors describe does not seem to match Figure 3CD of Asfaw et al (1999). Moreover, the notion that this pattern is only seen in a single individual in the early hominin record should be reason for caution. This especially as it represents an acquired character (through normal or abnormal mastication) rather than dental morphology. What could that complementary pattern on the mandibular teeth (line 224) look like, and what would the associated masticatory motion be? Any other primate showing this pattern? Certainly interesting but not as a decisive, taxonomically diagnostic feature until it is replicated as taxon specific rather than an individual anomaly/pathology.

We have added description of a fragmentary upper molar that clearly and effectively discriminates LD 760 from BOU-VP-12/130 (Extended Figure 8 and lines 235-245). We have also moved the description of the wear pattern on that specimen from the main text to the Extended Data Figure 9).

- Canine comparison: (line 240-241) "...puts this specimen in the upper range of *Australopithecus* and *Homo*". No; it is in the middle (M1) to lower (M2) range of *Homo*.

Description clarified/modified (line 139).

AS 100-1

- The M1 (*AS 100-1a*) is not shown at all, which is not acceptable. Apart from simply documenting the evidence, the glimpse in Fig 5 suggests that it may well be informative, especially in combination with the M2. The M1-M2 can be shown jointly in comparison with AL 666, BOU-VP-12/130 and a suitable *afarensis* specimen (replacing Fig 5 or as an Extended Data Figure).

We have added the fragmentary molar to Figure 2 and Extended Figure 8.

Lastly, and I realize that this is a sensitive issue, but is honoring Charlie Lockwood really best served by making him co-author well over a decade after his untimely death. He was not there to scrutinize the fossils and how they are interpreted, and I am not sure this is good (ethical) practice in science writing.

We have removed his name.

Referee #2 (Remarks to the Author):

The human fossil record in East Africa in the time interval between 3.0 and 2.5 Ma is very limited, with only a handful of fossil specimens attributed to the genera Australopithecus, Paranthropus and Homo. Thus, any new discovery marks an important addition to the picture of the evolutionary events that happened in this critical time frame that saw the emergence of the genera Paranthropus and Homo.

In this regard, the ms by Villmoare et al contributes in several ways to this picture. The significant points of the ms include:

1. The new fossils attributed to Homo from Gurumaha (2.78 Ma) and Asboli (2.58 Ma), confirm the deep antiquity of the Homo lineage well into the late Pliocene before the Pliocene/Pleistocene boundary (set at 2.58 Ma) as previously suggested by the Ledi Geraru mandible LD 350-1 (2.8 – 2.75 Ma). The dates of the Homo fossils also match the dates of the oldest Paranthropus fossils from Kenya (2.7 Ma) and Tanzania (c. 2.66 Ma), suggesting a comparable antiquity for the origin of the two lineages.

This evidence seems to support the model that describes the origin of the Homo and Paranthropus lineages as the result of a cladogenetic event that occurred in the final phase of the evolution of the species A. afarensis, whose most recent fossils are dated at 2.95 Ma.

2. At the same time, as noted by the authors, the occurrence of fossils from Ethiopia attributed to a separate species of Australopithecus (A. garhi) at 2.5 Ma rendered this interpretation more complex: now, the new fossils from Lee Adayta described in the ms suggest the occurrence, at 2.63 Ma, of a new species of Australopithecus, different from A. garhi. This new evidence puts further into question the simple model of an evolutionary crossroad Homo-Paranthropus and suggests that the high diversity of australopith species documented in the middle Pliocene was only partially decimated by the events that led to the origin of the Homo and Paranthropus lineages.

3. The present evidence thus establishes the occurrence of four separate species of hominins in East Africa between 2.8 and 2.5 Ma.

4. In a model where Homo and Paranthropus (whose oldest fossils now are dated respectively at approx. 2.8 Ma and 2.7 Ma) are derived from A. afarensis (whose most recent fossils are dated at 2.95 Ma) the cladogenetic event must have occurred in a relatively short time frame (geologically speaking). As such, the time range between 3.0 and 2.8 Ma, and fossils deriving from it, now become critical for interpreting the origins of the Homo and Paranthropus lineages - the new frontier for field research for the next generation of paleoanthropologists.

General comments

The ms is well structured and well written. The description of the specimens is accurate and the analysis is appropriate. A few details can be added – see below. The reasons given for suggesting a new species of Australopithecus are well argued, and, wisely enough, the authors refrain from naming a new species. The references cited are appropriate.

*It contradicts the usual adagio that “more fossils will help to clarify our picture of human evolution”: the new fossils from Ethiopia make more complex our view of our distant past. Also, the new fossils help to narrow the gap between the last *A. afarensis* and the earliest *Homo* and *Paranthropus* fossils.*

My concern is relative to the position of the figures showing the new specimens. Some are presented in the main text, whereas others are presented in the extended data. This requires the reader to jump from the main text to the extended data, and back, to see how they look like. My suggestion is putting in the main text all the photos of the new specimens, and in some cases, where relevant, also showing the specimen in different view. All this can be combined in a single figure or two. The figures comparing the new specimens with published specimens should all go in the extended data, and in this case more comparative photos can be added.

All of the described specimens are now illustrated in the main text in a composite figure (Figure 2). Due to spatial constraints in the main text, we illustrate the two isolated premolars in more detail in the Extended Data, reserving space in the Main Text for the more complete *Australopithecus* dentition from LD 760 and the two Asboli molars attributed to *Homo*.

*Although separated by almost 500 ka, comparisons with *A. deyiremeda* specimens should be added, since these derive from an area not far from that of the sites described in the ms and one may expect some kind of regional continuity between *A. deyiremeda* and the new *Australopithecus* species. Alternatively, reasons for not comparing the new specimens with *A. deyiremeda* should be given.*

We have added published *Au. deyiremeda* data to all of the bivariate plots to provide metric comparisons to that species. We have also added a note on P3 morphology, indicating that that the LD 302-23 P3 is derived relative to the *Au. deyiremeda* paratype. However, our taxonomy is only to the generic level so our main analyses focus on discrimination at that level.

The ms can be accepted after revisions indicated.

Specific comments:

p. 4 line 79

79 Gurumaha Tuff, a light gray lapilli tuff dated to 2.782 ± 0.006 Ma (1σ sd; recalculated from ref.

Add “ (GT) “ after Gurumaha Tuff

Done

Page 7, table 1.

In the table add the two incisors mentioned in the text (p. 14, line 232).

Added to the table.

In the table and in the text fossil specimens are sometimes referred to with the locality number only, whereas in other occasions the complete labelling system is employed. Only one system should be used for consistency.

We have made these consistent.

p. 7 Gurumaha hominins

Following the same logic used for the specimens described later, a comment should be made on the possibility that the specimen LD 302-23 belongs to Australopithecus sp. n. or why this possibility has not been considered.

Lines 130-150 detail the taxonomic argument with regard to *Australopithecus*.

p. 8 -10 Lee Adoyta hominins

Specimen LD 750-115670, LP4. In this case also reasons for excluding this specimen from Homo should be given.

Lines 176-190 detail the arguments for the taxonomy for this specimen (which are emphatically provisional)

p. 15. Line 250.

Given that the teeth from 750 represent the same individual a sentence of this kind should be added : “Taken together, the combined evidence of the molars and the canines suggests differences of this individual from A. afarensis, A. garhi, Homo and Paranthropus ... ” or something along this line.

This is now in summary at the end of the manuscript.

No description is given of the two incisors. This should be added at least for the I2.

Lines 247-252 present details of the lateral incisor (the central incisor is fragmentary). Images of these teeth are now in Figure 2.

p. 17 line 262.

Here the fossils are referred to as “Asboli hominins” whereas the other specimens have been referred to with the name of the sedimentary package, thus in this case “Golden Sands”. Modify

throughout the text for consistency, in one way or another.

The text is now modified throughout for consistency. Also, we have now used the word for gold in the Afar language (Giddi) for what was previously referenced as the Golden Sands and Golden Sands Tuff.

p. 17 line 263.

A figure showing AS 100-1a should be added – if it is worth showing it.

The fragment is now in Figure 2 and Extended Figure 10.

p. 17 – 18.

*Again, also in the case of AS 100-1b reasons for excluding the specimen from *Paranthropus* and *Australopithecus* sp.n. should be given.*

Lines 299-318 provide morphological details of why the specimen is not attributed to *Australopithecus*. As Supplementary Figure 16 shows, the AS 100 M² falls well outside the range of variation for eastern African *Paranthropus*.

Extended data

In the extended data the following tables would be useful:

1. A table with a list of the specimens attributed to early Homo, or putative early Homo - all or the most relevant – discovered in East Africa in the time range 3.0 – 2.3 Ma. For example,

*Mille-Logya
Nachukui
LD 350-1
Omo 75-14
KNM ER 5431*

This will give a good idea of how limited the fossil evidence in this time range is, but I leave the final decision of inserting the table to the authors.

2. A table with all the dental metrics of the specimens described. Presently, the reader has to go through text and figure captions to collect this information. Having all of them in a single place would be helpful.

Also, bivariate plots of MD vs BL of all the new specimens (beside those already presented) would be useful, at least as composite images. This will give a good perception of the size of the

teeth.

We have added bivariate plots of all occlusal dimensions of postcanine teeth, as well as comparative data used in these bivariate plots. The taxonomic status of all specimens is included in this table.

Referee #3 (Remarks to the Author):

This paper reports on new fragmentary dental remains recovered from the Ledi-Geraru research area, which contains sediments representing a critical and poorly sampled time range (3 to 2.5 Ma) in the hominin fossil record. The authors suggest that early Homo and Australopithecus were sympatric in the Afar. If indeed borne out by the data, the paper would be of great relevance to multiple questions in human evolution ranging from phylogeny to paleoecology to mode of evolution of early hominins and the origin of the genus Homo.

The major claim of the paper is predicated upon demonstrating that the Lee Adoyta dental remains do indeed belong to Australopithecus because, in the Afar, only Homo and A.garhi are known from the 3 – 2.5 Ma interval. While the addition of another Australopithecus taxon would increase diversity, the same will also raise new palaeobiological and palaeoecological questions.

The attribution of LD 302-23 P3 to the genus Homo, while it does not affect the main thrust of the paper, their assertion: “departs strongly in shape from the unicuspid specimens of Au. afarensis (e.g., A.L. 128-23, A.L. 288-1)” needs to be tempered as P3 morphology in A.afarensis tends to bimodal or is at least variable. The above cited specimens represent the more primitive condition and not the mean. Some A.afarensis P3s are more derived though not to the extent seen in the new specimen. A.L. 822 for example has a more differentiated occlusal surface with a metaconid that is more developed than what is seen in A.L. 288.

Furthermore the configuration seen in A.L. 288 (the primitive condition) is seen in some Homo specimens including the holotype of H.habilis, OH 7 in addition to OH16, OH 13 and OH22. What we learn from variation in A.afarensis is that it is the frequency of many of these traits and not their “discrete nature” that characterizes the species. Their sample size does not lend hand to examine frequency hence the need for caution.

I must also note that wear on LD 302 makes the occlusal morphology difficult to observe, offering less confidence in statements like “LD 302 differs from Au. afarensis in having a metaconid situated well anterior to the protoconid and in having a reduced anterior fovea”. Given all these caveats, I would place LD 302 in cf. or aff. Homo. Since LD 350 comes from the same time period, the status of the former will not affect their main conclusion. I suggest that the description of the specimen be revised to reflect these comments.

We have modified this text to clarify exactly this (lines 131-150) point and added comparative specimens to the figure (Supplementary Figure 4 and 5). The position of the metaconid relative to the protoconid is clear because dentine is exposed at apices of both cusps and the crown bulges out slightly mesiolingually where the metaconid sits. Further, dentine exposure continues from the protoconid along the transverse crest to about the midpoint between the protoconid and metaconid, making the orientation of the transverse crest apparent in occlusal view. No specimen of early *Australopithecus* that we have examined matches LD 302 in the spatial relationship between the metaconid and protoconid.

The Attribution of the Asboli specimen from 2.59 Ma to Homo is convincing and the new teeth expand known sample size of Homo prior to 2.5 Ma, which is much needed. AS 100-1b also gives another line of evidence to show that what they have at this site is not Au. garhi. Can they provide an image of AS 100-1a?

Figure 2 and Extended Figure 10 now have the fragmentary M¹. Extended Data Figure 10 also shows additional comparative specimens, including the Bouri M¹ and M².

The Lee Adoyta premolar and molars that are central to the main conclusion of the paper are well described, demonstrably separated from A.garhi and Homo and are reasonably attributed to Australopithecus but differ from A.afarensis in some aspects. 1) they are BL broad relative to their MD length, 2) the M2 and M3 do not taper distally to the extent seen in Au. afarensis, and 3) the LD 760 molars lack the distinct bilobate buccal contour seen in Au. afarensis.

Based on this, the authors outline four possibilities for the taxonomic attribution of the Lee Adoyata dentition. They have evidence to show that the specimens do not belong to A. garhi or the Paranthropus lineage. Given the limited sample size it is difficult to clearly demonstrate if the specimens represent some late survivors of Au. afarensis or may belong to an unknown Australopithecus species. While the authors lean toward the latter, more fossils are needed to better characterize the difference from A. afarensis given that changes (over 350kys) within this species could have introduced what is being observed. Whatever the case might be, the presence of Australopithecus this late in geologic time changes our understanding of the genus albeit based on shaky evidence. This paper is well written, and the authors have done their best to squeeze as much information as possible from the fragmentary evidence. The latter is a weakness but still suggests the possibility of the presence of Australopithecus by 2.63 Ma. With great caution, what is being proposed can be accepted as a hypothesis that can be tested through further fieldwork.

Q. Fig. 4: (Top row) in order of appearance from left to right it should be lingual and Labial and NOT Labial and lingual.

This figure explanation has been corrected.

I recommend publication of the ms with the above suggestions included in a revised version.

Referee #4 (Remarks to the Author):

*The manuscript by Villmoare reports new fossil discoveries in Ledi-Geraru (Afar, Ethiopia) and assigns the fossils to *Australopithecus* spp. The authors provide a general description of the current chronology and species assemblages existing in the eastern African hominin record between ~3-2 Ma and present the geologic, chronologic, and fossil descriptions to constrain the ages and taxonomy of the new specimens.*

*The paper has a well-summarized introduction and provides a detailed geologic figure to show the stratigraphic context of the fossils. The Ar/Ar age data recalculations from published data are necessary and will be helpful to readers who do not understand the complexities of standardization in Ar/Ar dating. I have a few specific comments and recommend minor revisions, provided there is another reviewer to assess the fossil assignment to *Australopithecus* spp. Rather than assigning these materials to an already established taxon.*

*This reviewer is not an expert in hominin paleontology, so my comments will be mostly restricted to the geological and geochronological portions of the paper. Having collaborated on hominin paleontology research projects, I find it odd that a collection of isolated teeth is sufficient to assess that these elements cannot be of any already-established taxon, given the many comparative specimens that were studied (based on the list in lines 112-115). Especially given the similarities with other *Australopithecus* dentitions, and some evidence being mesowear patterns to refute associating the new materials with other established species, it seems likely that there is simply not sufficient fossil material in the new LD assemblages to rule out their assignment to *A. afarensis* or *A. garhi*. Given my shallow ability to evaluate this data, however, I would recommend at least one reviewer can adequately evaluate the results and discussion pertaining to the fossil materials, since I cannot carefully assess that portion of the presented work.*

Line-by-line comments:

*i.e., point 3, lines 338-345: If there are very few specimens of *A. garhi* (one?), is this sufficient to exclude the association of new fossils based on different tooth wear patterns?*

We have provided several morphology features that distinguish *Au. garhi* from the Ledi-Geraru *Australopithecus* material - see line 237 and following, and Figure 4. These include the presence of a 'talon' on the *Au. garhi* maxillary canine and a highly reduced hypocone on *garhi* maxillary molars, which is reflected in the lingual profile of the *garhi* crowns and probably contributes to the indistinct lingual groove. The features observed in the *Au. garhi* holotype are derived relative to *Au. afarensis* and Ledi-Geraru *Australopithecus*. Thus, the plesiomorphic nature of the Ledi-Geraru teeth, relative to *Au. garhi*, provides no positive support for the hypothesis that they are *Au. garhi*. Expanded samples of both Bouri and Ledi-Geraru *Australopithecus* will be necessary to determine if the currently available samples represent typical individuals of each population or not. Further discoveries may necessitate a

reevaluation of the taxonomic affinities of the two samples vis-a-vis each other. As such, we only attribute the Ledi-Geraru *Australopithecus* teeth to the genus level.

Lines 352-355: what evidence is being presented to demonstrate the habitat of these materials? There is no information on the sediments in the manuscript. I don't see any isotope data or faunal assemblage analysis. This point seems to be added at the end and not well supported.

Descriptions of the sedimentary packages including a brief summary of the lithofacies are provided in the main text and Figure 1B. However, the interpretation of drier open habitat is not a conclusion of this paper but rather supported by the Vrba, DiMaggio, et al., 2015, and Robinson, et al., 2017 citations. Supplementary Information contains all of the supporting data for the tephra ages.

For the Ar/Ar methods, can you please provide a one-sentence explanation for how the blank correction was applied to the samples?

Blanks are run every fourth sample and applied to unknowns as a running-average time series. This text was added to the methodology section for Ar/Ar dating.

Supp Fig. 1: the apparent and plateau age of one crystal is significantly younger and more imprecise than others sample 27361-20. Any reason why? This was also the grain excluded in the probability distribution function age from plateaux. Since it is unusual to omit younger grains than the mode, unless there is a clear reason, why is this grain omitted?

The same question goes for the two younger grains omitted for the isochron ages. In this case, are there two omitted (rather than one) for a particular reason? It seems like including the second youngest one may bring the MSWD closer to 1, as well, so it isn't clear why this grain is omitted there. And if it is included, does it bring the isochron-based mean age closer to the plateau-based mean age? Based on the Ca/K plot, it appears the second omission is not the second youngest in the plateau age diagram, implying the age and precision does shift significantly with the isochron approach.

Generally, the elimination procedure includes eliminating those grains greater than three normalized deviations from the median. However, in both the calculation of the plateau weighted mean age (Supplementary Fig. 2) and the isochron weighted mean age (Supplementary Fig. 3), the inclusion of the previously omitted one or two grains, respectively, did not change the calculation of age or the error in either case. We have decided to include the grains and the figures and text have been updated.

Extended Data contains additional supporting materials on the fossils. I have no significant comments on this section.

Responses to formatting recommendations and referees' comments:

We have addressed all of the referee comments, as described below, as well as followed the overall formatting guidelines provided by the editor. We tracked changes and have described all revisions here. Line numbers refer to when viewing the document in "Simple Markup."

Formatting recommendations are in italics and our revisions are in bold face.

FIGURE LEGENDS: These should be listed sequentially after the main text references and not in the figure files; they should not exceed 300 words each. Each legend should begin with a brief title for the whole figure and continue with a short description of each panel and the symbols used.

We have moved the main text figures into separate files for submission, revised the figure legends where appropriate, and moved them all to the correct location after the main text references (lines 511-552).

METHODS: After the main text figure legends there should be a section entitled "Methods", which provides the full, step-by-step instructions that would allow other researchers to replicate the results.... Specialized methods that require chemical structures, figures or tables, or methods requiring equations, cannot be accommodated in the Methods section of the main text file. If such information is part of the Methods, the entire Methods section must instead be included within a Supplementary Information text file.

Our methods do include specialized figures related to the $^{40}\text{Ar}/^{39}\text{Ar}$ analysis so we chose to keep the methods in the Supplementary Information. We are happy to adjust this if the editors prefer we format it differently.

MAIN TEXT STATEMENTS

Required main text statements have been added where appropriate.

DISPLAY ITEMS

Figures were formatted according the guidelines for the main text, Extended Data, and supplementary information. We created panels of figures in order to accommodate most

data figures in the Extended Data rather than the supplementary information. We also uploaded the main text figures as separate files rather than leaving them in the main text.

EXTENDED DATA: ... All Extended Data must be referred to in the main text, and their legends should be listed sequentially at the end of the main text, not in the Extended Data files. The Extended Data should be assembled into a maximum of 10 A4 size, multi-panelled display items, submitted as individual files in .jpg, .tif or .eps format only.

We revised our Extended Data to include multi-panelled display items as suggested by the formatting guidelines as well as one of the reviewers. We also moved the legends to the end of the main text (lines 598-762).

SUPPLEMENTARY INFORMATION: ...While SI should not typically contain data figures (any figures additional to those appearing in the main text should be formatted as Extended Data),... If a manuscript has SI, each discrete item of the SI (e.g., videos, tables) must be referred to at an appropriate point in the main manuscript. We ask that you provide a word file entitled “SI Guide”, containing a cover page with manuscript title and author information; a table of contents (preferably with page numbers); and then any SI text, notes, figures, and titles and legends for any separate SI files.

Many of our Supplementary Information figures were moved to the multi-panelled Extended Data figures to reflect the guidance above. Additionally, we created a word “SI Guide” describing the included Supplementary Information.

SOURCE DATA (GRAPHS): To increase transparency, we strongly encourage you to provide, in spreadsheet form, the data underlying the graphical representations used in the figures.

We provided the source data for our figures in Supplementary Data S1.

Referee comments in italics and our responses in bold face.

Referee #1 (Remarks to the Author):

The revised manuscript is much improved, but needs some final revision as indicated below. I can't emphasize enough that all figures should be easy to interpret. This especially as Nature is not a specialists' journal, although all my Figure comments would equally apply in a journal like Journal of Human Evolution.

We would like to thank this reviewer for their careful comments and recommendations for improving the figures. We have followed all of the suggestions, and feel that the revisions to the figures and their organization have significantly enhanced them and the readability of the paper.

Line 149 "at a similar stratigraphic level". Confusing because in Line 120-121 we learn that LD 302 is 6m stratigraphically below LD 350.

This response is now in Line 133. We replaced "at similar stratigraphic level" with "in the same sedimentary package" to reduce the confusion as to where these specimens are relative to each other.

Line 181-190: as written I can't see the justification why attribution to Homo is excluded, and the conclusion is aff. Australopithecus rather than Homo or Australopithecus, but not Paranthropus. Please be clearer, or modify.

Response is in lines 178-179. We added that, specifically, LD 750 does not share any synapomorphies with *Homo*, therefore we exclude *Homo*.

*Line 229-231: "The LD 760 molars depart from the typical feature set of *Au. afarensis* in three ways: 1) the M1s are BL broad relative to their MD length...". Looking at Supplementary Figs. 8, 9 my conclusion is that the LD 760 M1s fall well within the range of variation of *A. afarensis* in this respect, but among the BL wider specimens. Just considering 'typical *afarensis* proportions' as the exact mean of the sample, as apparently done here, is biologically not realistic (majority of *afarensis* specimens would also be 'atypical'). Please moderate statement.*

We have added two moderating statements in lines 217-219 in response to this concern. We indicate that *Au. afarensis* first and second molars are widest across the mesial cusps and LD 760 is widest at midcrown. We have also adjusted the wording in the figure legends and in lines 324-328 to indicate that we are not only considering the average as the typical *afarensis* proportions and to acknowledge the range of variation.

Line 325-327: I assume the authors refer to species diversity before 3.0 Ma (i.e. A. deyiremeda, K. platyops, possibly A. Prometheus). If so, they should cite some relevant references making this clear.

The response to this is in line 301. We are not referring to hominin diversity before 3 Ma, so we changed the line to read “in the 3.0-2.0 million year interval” to make it more clear.

Line 382: Should that also include ‘southern Ethiopia (i.e. Member C, Omo Shungura Formation)?

Yes, it should, thank you. We have updated this on line 359.

As a technical comment, and the editor will correct me if I am wrong, but my reading of the Formatting Guide is that essential Methods information should be part of the article text, rather than having all methods in the Suppl Materials (“The ‘Methods’ section is in the main text file, following the figure legends”). This is important because Supplementary Materials is generally less thoroughly reviewed (cheer bulk often), not edited at all, and available separately. Of course the Methods can be expanded into the Suppl Materials.

We very much appreciate this suggestion, and reread the formatting guidelines closely. As some of our methods require figures and tables, we interpreted the guidelines to mean that our entire methods section cannot be accommodated in the main text and should be kept in the Supplementary Materials. We are certainly willing to rearrange this if the editor indicates it’s more appropriate to have a methods section in the main text.

Figures

Figure 2: it is helpful to have this overview figure (with orientation indicated). However, I would recommend to use the most conventional orientation with mesial to the top (as in some other figures). And be consistent: why is Ext Data Fig 3 oriented differently from Figure 2?

Again, thank you so much for these careful comments. We have reoriented the dentition in Figure 2 so that mesial is towards the top, and we are consistent throughout the figures.

Anatomical orientation. Is only indicated in Figure 2, and this should be done for all other figures (incl. Ext. Data Figs and Suppl Figs). This can be done in the figure itself or in the legend stating something like ‘mesial to the top, buccal to the right’.

We have added the anatomical orientation to the figure legends of Fig. 3 and the new Fig. 4.

Figure 4 (Line 275-276): “Images are oriented differently to emphasize the distinctive relevant morphology”.

Regarding the lower three images: it would be helpful if at least AL 200-1 and BOU-VP-12/130 would be oriented in the same way (and if the legend would indicate the orientation).

This figure is now Figure 5, based on the reviewer’s next comment. We have added the anatomical orientation indicators to the legend for panels C and D.

Figure 5. What is the point of when we have Figure 2 (top right) showing the same view? Supplementary Figure 12 may well be a good replacement, because the average reader may struggle to visualize ‘distal taper and bilobate contour’, whereas it is critical for identifying LD 760 as non-afarensis.

We agree, thank you. We have made the “bilobate contour” figure the new Figure 4, and replaced the previous Figure 5 with the old Figure 4, as described in the comment above.

Currently, many of the Extended Data Figures are greatly underusing the full A4 size that is available (e.g. 3, 4, 8). These can be combine with multiple images in a single Extended Data Figure, as long as they share a theme of sorts. For example, Ext Data Figs 3-5 can easily be combined. Doing so frees up space and the most important Suppl Figures can be moved to Extended Data Figs.

Again, we also agree. We have combined most of the extended and supplementary figures into multi-panelled figures so that we can keep the data figures in the Extended Data. Thank you for this suggestion.

Referee #2 (Remarks to the Author):

The authors have made a commendable effort to address the concerns raised by the reviewers. I believe that the revised version is much improved, and it can be accepted with minor revisions indicated below.

Minor comments on the R1.canine

Figure 2. LD 760 assemblage.

The authors have chosen an unusual position for the upper teeth. The I1, I2, upper canine must be rotated by 90° clockwise (or counter-clockwise, if they prefer).

Thank you for this suggestion. We rotated the anterior teeth in Figure 2, and feel that the figure is significantly improved with this change.

Figure 3. line 207. Reference to Table 1 is present. Shouldn't this be Supplementary online dental metrics ?

Yes. We corrected this in line 531 to correctly refer to the Supplementary Data S1. Thank you.

Extended Data Fig 4. Indicate mesial and distal.

We corrected this in the legend for this figure, which is now Extended Data Fig. 3A.

Supplementary Figures 4, 6, 9, 10, 11, 16, deyiremeda is incorrectly spelled "deyiremida"

This spelling is corrected in all of the figures, thank you.

Notes on the hominin dental metrics table:

We have significantly improved the legibility of this table by using these suggestions and only including data that are referenced in this paper.

Cell L1: mandibular P3 MD has no subscript in 3

We corrected this.

Cell A243 : Stw 19 is listed as A. africanus, but in cell A511 the same specimen is listed as Homo sp. Please sort this out.

We removed the incorrect taxonomic identification in what is now A415.

Cell A438 : KT 12/H40 : Guy et al. () is not in the references

We have removed the specimens that we don't reference in the paper, including this one.

Cell A 453 : KNM-ER 1813 : Zaim et al. (2011)/Wood (1991). Zaim et al is not in the references

We did not actually use data from Zaim, so we have removed it from the table.

Cell A612: Peninj 1: is not given in Moggi-Cecchi et al 2010. see Wood 1991

We updated this in cell B520, thank you.

Data for the specimen KNM-ER 5431 are not present in the table. Please add - see Wood 1991.

I hope that the data are in the plots, since this is a critical specimen.

We added these data in row 406. These data are in the plots; not including the specimen in the spreadsheet was an oversight and we very much appreciate your careful reading of these data.

Measurements of the specimens labelled Stw are indeed published in Moggi-Cecchi et al. JHE 2006, so it is more appropriate to refer to that paper. As for the other A. africanus specimens the (JMC pers. Comm.) can stay.

Thank you. We have corrected these references.

A matter of style:

Many specimens in column A, for each species, are sorted as 'text' (see specimens labelled Sts, Stw, MLD, OH, KNM-ER, DNH, KW, SK, SKW, SKX) - it is preferable having them sorted as 'number'.

We corrected this and now the table has a more straightforward sorting function.

Referee #3 (Remarks to the Author):

The authors have addressed the specific concerns I had in my initial review.

Thank you for your thoughtful review of our paper.

Referee #4 (Remarks to the Author):

since this is a review for the revision, I will keep it short. The authors have satisfied my comments and correction suggestions related to the Ar/Ar dating. If the other reviewers who evaluated the fossil material consider those revisions appropriate, then I consider this manuscript ready for publication.

We appreciate the thoughtful and careful comments on the dating portion of this paper.

Responses to formatting recommendations and referees' comments:

We have addressed all of the referee comments, as described below, as well as followed the overall formatting guidelines provided by the editor. We are very appreciative of the continued support and guidance from the reviewers and editor, and feel that the manuscript and figures have improved dramatically since the first draft we submitted. We tracked changes and have described all revisions here.

Formatting and other recommendations from the editor are in italics and our revisions are in bold face.

SOME SPECIFIC ISSUES:

Please supply the manuscript in .docx format.

Completed.

There are no methods references - please create a separate reference list for the methods with continuous numbering from the main reference list.

As recommended by a reviewer, we moved the Methods into the main text out of the Supplementary Information. The Additional References have now been included under the Methods.

Please reduce subheadings to 40 characters (with spaces) or less.

Subheadings have been shortened when necessary.

There are potential third-party rights issues in the figures - please check sources or if permissions are needed for the map, photos, schematic illustrations in the figures.

We have confirmed permission for two photographs included in our figures, and included this information on the Third-Party Rights Table.

Please ensure that the text size in all figures is at least 5 pt Arial.

We have confirmed that all text is at minimum 5 pt Arial.

Supplementary video 1 is mentioned in the Supplementary information file but has not been supplied.

We linked to a permanent online address (tinyurl.com/LediGeraru760) but have now also uploaded this file as a mov file.

Please note that the competing interest statement should be provided as a separate statement and not included in the "Ethics Declaration" section of the manuscript.

We have clearly separated these two items.

The data availability statement declares that 'All data are available in the Supplementary Data S1 online file or upon request.' Please consider making this data available in a publicly accessible repository or explain why the data can only be made available from the authors on request.

We have reworded this statement to indicate that the data are publicly accessible in the Supplementary Table S1 and Supplementary Data S1 and at the permanent online addresses [tinurl.com/LediGeraru40Ar39Ar](https://tinyurl.com/LediGeraru40Ar39Ar) and tinyurl.com/LediGeraru. We have also uploaded the spreadsheets as a Supplementary files. Readers do not need to request access from the authors.

Supplementary Figures

We added additional information in the legend and figure in Supplementary Figure S3 to confirm that all the necessary information is associated.

REPRODUCIBILITY

We have responded to comments in the Reporting Summary and the Editorial Requests document. Specifically, we confirmed that all of our figures present the data distribution clearly, that n is defined appropriately, that all error bars p values are defined, and that the legends for extended data figures are inclusive of all statistical information. Additionally, we included Supplementary Table 1, which includes all reproducibility data from the dating analysis. We also revised the Data Availability statement. For the Reporting Summary, we updated our software versions and referenced their use in the manuscript.

METHODS

As suggested by a thoughtful reviewer, we have moved our Methods into the main text after the figure legends. The associated references are now listed after the Methods.

Referee comments in italics and our responses in bold face.

Referee #1 (Remarks to the Author):

The second revision has again improved and I have just three points for consideration. I look forward to seeing this paper published. Congratulations to the authors.

‘One little ‘formatting’ comment which you could forward to the authors. Referee 2 is correct in making reference to “StW specimens”. The accession code for the Sterkfontein fossils excavated by Witwatersrand University is StW (not Stw), because it stands for ‘Sterkfontein Witwatersrand’. The earlier Transvaal Museum specimens use ‘Sts’ because it stands for ‘Sterkfontein site’

Thank you for very much for your detailed consideration of all of our paper and all of the associated data. We corrected Stw to StW in the spreadsheet, in figures, and in the manuscript.

Hence, I suggest to the editor that it is important in an article like this one that the core methods are part of the actual article rather than squirreled away in unedited Supplementary Info. Thus, summary statements about where, when and how the fossils were found, how (to what) were they compared, in what way were they dated etc. The details of all of this (comparative samples, dating and geology details etc) should obviously be in the Suppl. Info.

Thank you for following up with this concern, and we agree that our Methods should be in the main document so that they are not lost in the Supplement. We have moved all of the Methods descriptions except for the Supplementary Figures into the main text document. Again, we very much appreciate your guidance with improving the legibility of our paper.

*Line 182: “Since LD 182 750-115670 lacks any clear Homo synapomorphies”
Can we please have a reference where these synapomorphies are specified?*

We have updated this sentence to include a reference to these synapomorphies. This is in Lines 177 and 178.

Extended Data Fig. 3: please reorient the A.L. 333w-1 P3 along the correct mesiodistal axis (see Figure 6C in Delezenne & Kimbel 2011). It currently looks like a rather strange tooth.

We reoriented this tooth according to your recommendation. Thank you for this and other suggestions improving the format of our figures.

Referee #2 (Remarks to the Author):

The authors have addressed my observations and comments. The manuscript to me can now be accepted pending the very minor formatting issues indicated below.

My comment : Cell L1: mandibular P3 MD has no subscript in 3

Authors reply: We corrected this.

I still don't see the subscript in what is now cell E1. Please check

We discovered that while we had thought that Google sheets could accommodate super- and subscript, it cannot. We therefore added “man” and “max” to each column to indicate the arcade for each tooth. We thank the reviewer for these detailed comments.

My comment : A matter of style: Many specimens in column A, for each species, are sorted as ‘text’ (see specimens labelled Sts, Stw, MLD, OH, KNM-ER, DNH, KW, SK, SKW, SKX) - it is preferable having them sorted as ‘number’.

Authors reply: We corrected this and now the table has a more straightforward sorting function.

Unfortunately, this is not the case. I paste below an example for part of the StW specimens to explain what I meant:

Stw 147

Stw 179

Stw 18 - this is not in numerical order

...

I have downloaded the table and tried to sort them as numbers, but Excel does not allow to do this.

Since this just a matter of style, I leave to the Editor the decision on whether leave the list as it is now or ask the authors to reformat it (which probably implies moving manually each single row not in numerical order into the exact position, FOR EACH OF THE SITES indicated above).

As with the comment above, we thought we had solved this but agree that they were still not sorted correctly. We therefore sorted them manually so that they are in correct

numerical order for each site. Since the Google sheet is view only, it should remain in that order for all viewers until they download the data to use. Again, thank you for your close reading of the manuscript and associated files, and your willingness to review and improve this work.