

New finds shed light on diet and locomotion of *Australopithecus deyiremeda*

Corresponding Author: Professor Yohannes Haile-Selassie

Any redactions in this file are there to maintain patient confidentiality, the confidentiality of unpublished data, or to remove third-party material.

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)

"New fossils from Woranso-Mille (Ethiopia) reveal the taxonomic affinity of the Burtele foot" by Haile-Selassie et al. describes 13 new hominin fossils attributed to *Australopithecus deyiremeda*. Of significance, these fossils were found in close enough proximity to the perplexing Burtele foot to now definitively assign that fossil to *Au. deyiremeda*, supporting the hypothesis for both taxonomic and locomotor diversity in Pliocene australopiths. Furthermore, stable carbon isotope analysis reveals that in contrast to *Au. afarensis* and fossils attributed to *Kenyanthropus platyops*, *Au. deyiremeda* had a more restricted, C3 diet, indicating that it fed in more wooded environments as did *Ardipithecus* and *Au. anamensis*.

These are important new fossils and should be the final word on the question of whether *Au. deyiremeda* is a legit taxon. Given the dietary and locomotor differences between this taxon and *Au. afarensis*, it clearly is distinct. In fact, given how distinct it is, I would have liked to have seen more justification for why *deyiremeda* is in the genus *Australopithecus* and not in *Ardipithecus*. To that end, what I feel the paper is missing and what would give this study the impact generally expected from a Nature publication are some hypothesized phylogenetic relationships between *Ar. ramidus*, *Au. anamensis*, *Au. deyiremeda*, *Au. afarensis*, and *K. platyops*. In some ways, this paper vaguely reminded me of the 2006 Nature paper on the Asa Issie, Aramis fossils. But what made that paper memorable were the phylogenetic hypotheses for the origin of *Australopithecus*. I believe something similar is required here. It could be in the form of a detailed cladistic analysis. Or it could be as simple as a table that lists salient features of the craniodental and pedal anatomy that are shared, primitive, or derived in each of these taxa. A preferred middle ground might be some hypothesized relationships between these different taxa based on the preserved anatomy, recalling perhaps the diagrams (Figure 5) in the 1999 Asfaw Science paper announcing the existence of *Au. garhi*. For example, do you hypothesize *Au. anamensis* evolved into *Au. afarensis* and *Au. deyiremeda* via cladogenesis? This would be a fascinating finding, given previous arguments for anagenesis between *Au. anamensis* and *Au. afarensis*. Or is *Au. deyiremeda* more likely to be a sister taxon of *Au. anamensis* which might lead to an evolutionary scenario of an *Ardipithecus*-like foot evolving into a Hadar-like one via the morphology of Burtele.

Additional, minor suggestions:

Abstract: lines 29, 35, 37. Can simplify *Australopithecus* to *Au.*

Abstract: line 43. Change "component of australopith..." to "component of this australopiths positional..."

Main: line 69. Comparative description: line 77. And again line 186. Please make clear that this juvenile mandible is not from the same individual at the adult Burtele Foot. Some of this text could be misread as indicating these are from one individual which I do not think is the intention.

Comparative description: line 93. Here and throughout the "W" of StW catalogue numbers should be capitalized since it refers to Witwatersrand.

Molars: lines 173-177. Given these comparisons (and given the foot), why is this not *Ardipithecus deyiremeda*? Here is where a cladogram might help convince readers.

Postcranial comparative description: lines 192-194. I read this over and over again and don't understand what you mean here. Many authors have described differences between the foot fossils of *Ardipithecus* and *Australopithecus*, most notably the convex Mt1 facet on the medial cuneiform, but also anatomies of the talar body, and length of the phalanges. Please clarify what you mean here.

Figure 3. Please make clear what you mean by “megadontia” (line 339, for example) given what appear to be quite small, Ardipithecus-sized UM1s in *Au. deyiremeda*.

Table 1. Any details to share about the cranial fragments (BRT-VP-2/150 & 2/200)?

Referee #2

(Remarks to the Author)

This is an interesting manuscript which (a) reports new hominin fossils from Burtele and (b) comes to the conclusion that the foot BRT-VP-2/73 can be attributed to *A. deyiremeda*.

If various practical issues outlined below can be addressed satisfactorily I would certainly recommend publication. I will outline two main points first, followed by line-by-line comments.

a) New fossils

These finds contribute to an improved diagnosis of the species *A. deyiremeda*, and form the basis for the attribution of BRT-VP-2/73. It is great to see Table 1 with new discoveries, but unfortunately this material is not adequately reported here.

Various BRT specimens are discussed in the text and used as evidence, but not shown and/or described (apart from some narrow comments). This also applies to two specimens that were already listed by this team in 2015 (ref 1), but not shown or described at the time. I think it is essential that any specimens used as evidence should be shown in an Ext Data Fig, and a short description should be given in the Suppl Info.

In addition there are specimens that are just listed but neither discussed nor shown, for example partial mandibles BRT-VP-1/271, BRT-VP-1/345 and BRT-VP-1/363. Each of these should be described in a few lines in the Suppl Info, and preferably shown as well. Otherwise, what is the point of presenting a list (Table 1) but otherwise leaving the reader wondering why the specimens are not considered at all. Typical example: mandibular corpus morphology is important in the present context and I wonder if any of those three partial mandibles shows evidence of a lateral corpus hollow?

Extended Data Figure 3 is important and all relevant lower premolar specimens from BRT should be included here, not just BRT-VP-2/135.

The authors have plenty of unused space left of their 10 allowed Extended Data Figures/Tables (noting that current Ext Data Figs 4 and 5 can easily fit on one page as a single Ext. Data Fig). Hence, lack of space is not an argument not to show us what they found.

b) Attribution of BRT-VP-2/73

The key arguments for the attribution of the foot to *A. deyiremeda* can found here:

Line 30-32, summary paragraph: “Based on its spatial and temporal proximity, and the absence of other hominin species at the Burtele localities, we find it parsimonious to also attribute the Burtele foot (BRT-VP-2/73) to this species” [i.e. *deyiremeda*].

Line 320-322, conclusions: “The assignment of the BRT partial foot (BRT-VP-2/73) to *Au. deyiremeda* is based on its temporal and spatial proximity to the dentognathic specimens that are assigned to the species.”

However, these three crucial aspects, (1) temporal proximity, (2) spatial proximity and (3) no evidence for other species, are not properly discussed in either the main text or Suppl Info.

- Regarding temporal proximity it would be important to see in Figure 1d where the key specimens are positioned in the stratigraphy. Where does BRT-VP-2/73 fit among diagnostic *A. deyiremeda* specimens; right in the middle or marginal?

- Regarding the spatial proximity it would be good to get some actual distances between BRT-VP-2/73 and diagnostic *A. deyiremeda* specimens. And although BRT-VP-2/73 is obviously not *A. afarensis*, it would still be good to get the wider perspective of how far the nearest non-BRT hominin localities are located, which represent the same temporal slice 3.3 – 3.6 Ma.

- The absence of evidence for other species argument makes me wonder why the authors do not equally apply this to all the other unattributed fossils from BRT. Or do they still consider the option that *A. afarensis* was present as well (with the foot not being *A. afarensis* on morphological grounds)? And what are the chances that in other localities everything is simply assumed to be *A. afarensis*, because that has been the default for that time period in the Afar ever since the first fossils were found.

I think it is probably reasonable to assume that BRT-VP-2/73 is *A. deyiremeda*, but this needs some thoughtful discussion rather than a ‘just so’ approach.

Individual comments (these partly replicate the issues raised above, now specifically linked to specific text).

Line 28: you mean “..these dental specimens”?

Line 64: for those not intimately familiar with the Woranso-Mille area, could the sentence include an indication what “close spatial ...proximity” means? Is that 2 m, 10 m, 100 m, 500 m?

Line 74: is reference to article ‘2’ missing at the end of the line?

Line 77: “due to its provenience relative to the Burtele foot”; this is meaningless unless the nature of the provenience is mentioned. Presumably this intended as ‘close’ or ‘similar’ provenience, but this can be stratigraphic (vertical) or geographic (horizontal). Please specify.

Line 77-78: “whose taxonomic attribution has been indeterminate thus far” seems unnecessary repeat of earlier statements.

Line 83: Why ‘partially erupted’ when the next sentence indicates that the crowns were in occlusion mesially and distally?

Line 97-99: can the presence of a lateral corpus hollow be seen in BRT-VP-1/271, BRT-VP-1/345 or BRT-VP-1/363?

Line 99 and 440-442: reference 28 seems incomplete, assuming this is not a regular journal.

Line 114: “Au. deyiremeda dm2s”, do you mean those of BRT-VP-2/135? In the logical order of the text you have not yet demonstrated that that specimen is Au. deyiremeda.

Line 121- 124: can this be illustrated somewhere, please.

Line 128: Should that be BRT-VP-1/380 in the caption of Ext Data Fig 2 (instead of BRT-VP-1/13b)?

Line 126: “is also similar to Au. anamensis canines”. Does that ‘also’ mean that BRT-VP-2/135 is similar to anamensis in this respect?

Line 133-134 “generated from high-resolution micro-computerized tomography (micro-CT) visualization”. Why add this here, given that the Cs were obtained the same way.

Line 134 and 136: Add BRT-VP-1/363 and BRT-VP-1/324 to Ext Data Fig 3.

Line 135: does that ‘absent’ refer to the left side? Not overly clear from figures.

Line 139-142: Ext Data Fig 3 shows that the angle is 91-93 degrees (right, left) in BRT-VP-2/135 and 88 degrees in AL 288-1. That 3 degrees difference (88 to 91) seems marginal. Are there stats on the full afarensis sample that are more convincing? If so report.

Line 142: can we see that mesial view? Would also show the metaconid development.

Line 145-149: this is important, and BRT-VP-3/14 should therefore be shown in Ext Data Fig 3.

Line 161, 163: Add BRT-VP-2/120, BRT-VP-1/2 and BRT-VP-3/14 to Ext Data Fig 3. And should that be BRT-VP-1/120, as published in 2015, instead of 2/120?

Line 167-168: this suggests that BRT-VP-2/89 is newly found (as opposed to BRT-VP-3/37), but it was already reported in 2015 (Ref 1). Show both specimens in an Ext Data Fig.

Line 174: what are those “two measurable M1s”? BRT-VP-2/135 and BRT-VP-1/365?

Line 177: show BRT-VP-1/365 in an Ext Data Fig.

Line 186: “spatially close” see comment Line 64.

Line 186-189: not clear what to make of these two sentences. What time span is represented by those 20 m? Is the difference between VP-1 and VP-2 important or not? Presumably not, but say so.

Line 201: please translate “habitual frontal plane rotation of the MT1” to something meaningful for the more general reader. Does presence reflect arboreal behavior?

Line 209-214: the actual substance seems to start here. Should this statement be made first before outlining the comparative differences/similarities with various species? Especially lines 190 – 202 seem out of place without any reference to BRT-VP-2/73.

Line 290: reference 29 correct?

Line 305-306: "It remains unclear whether any of the australopiths actually had the whole suite of morphological traits....". This is suddenly a broad 'on the fence' statement, having just advocated that there is locomotor diversity. A statement such as "It seems increasingly likely that most or all australopiths lacked the full suite...." seems more appropriate. Yes, we don't know about anamensis, garhi and aethiopicus, but still...

Line 313-314: instead of "e.g." I suggest you mention all conclusive diagnostic features (including premolars) since this is the key issue of this paper. Tight editing of other parts of the manuscript can easily reduce the word count if required.

Line 329: 'Some species...' instead of "Some of them..."

Line 332-333: and so? This seems an open statement after the conclusion of the previous sentence.

Line 333: Year of reference 55?

Line 336-337: "it is now clear". This seems to suggest that these new finding open our eyes and we finally see that postcanine tooth size and locomotor behavior did not evolve concurrently. I think that "the new results confirm that..." would be a better representation because the notion has been widely recognized for decades.

Line 337 – 339: "appears to correlate with the beginning of an increase in craniodental size resulting in a stronger selection for postcanine megadontia". An increase in craniodental size resulting in stronger selection for megadontia? Perhaps the other way round?

Figure 1b: mark Waytaleyta (WYT)

Figure 1d:

- mark the range of BRT-VP-3 in colour like the others, even if it is only a single horizon.
- mark the position of the relevant fossils so that it can be seen how BRT-VP-2/73 fits among the others.
- Are the dates provided in Haile-Selassie (2015) still correct?

Referee #3

(Remarks to the Author)

I am commenting only on the stable isotope aspect of this study, as requested by the editor. The $\delta^{13}\text{C}$ results are brief, with several additional values being added to the original database. However, the number of analyses now in hand (8) is sufficient to confirm the earlier suggestion that *Au. deyiremeda* had a diet dominated by C_3 resources, similar to (and not distinguishable from) the early hominids *A. ramidus* and *Au. anamensis*. However, this diet is different than the *Au. afarensis* and *K. platyops*. This finding alone is significant because it demonstrably shows the presence of multiple hominin species at 3.5 Myr with differing diets, which likely had minor dietary competition. It also may bring into question the identification of some hominin specimens, previously assigned to *Au. afarensis* or *K. platyops*, that are only partial isolated teeth and whose $\delta^{13}\text{C}$ values are at the negative end of the spectrum of carbon isotope values.

As an aside, it would be useful to include at least one latitude and one longitude mark on the map in Figure 1B.

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The authors have adequately addressed my first-round suggestions in either manuscript revisions or in detailed explanations in their response letter. The paper is publication ready. I have some very minor suggestions listed below which are optional.

Title. I might recommend a title that includes *Australopithecus deyiremeda*

Line 107. Developmental incongruity would also preclude the foot and the mandible from belonging to the same individual, yes?

Line 257. I might insert "presumed" between "another" and "*Au. africanus*" given the possibility of taxonomic diversity in the Sterkfontein sample

Line 322-323. A line about the timing of faunal exchange between East and South Africa prior to 4 Ma would enhance this section.

Referee #2

(Remarks to the Author)

The authors have done an admirable job addressing my concerns, especially by providing more information regarding

various specimens. Below I have provided some suggestions for consideration.

My only substantial comment is the question whether any *A. africanus* specimens can be added to Extended Data Figure 7 and, if possible, the linear discriminant analysis. StW 595 has likely been CT scanned and Wits tends to be accommodating when it comes to providing comparative digital data. One of the important findings highlighted in this paper is the relationship between the *Australopithecus* species, and especially between *A. deyiremeda* and *A. africanus*. Hence, including the latter as suggested would certainly be insightful.

Lines 22-47: What seems to be the 'Summary paragraph' is substantially over the 200 word limit. That is an editorial decision, but if scaling back to 200 words is required the major shortening will impact how the paper is introduced (also including the first 'Main' paragraph).

Line 105: "more likely" than what? Perhaps "most likely"?

Line 107-108: I realize that another reviewer asked to add that the mandible and foot are not from the same individual. Given that you clearly indicate that it concerns a juvenile mandible and the foot is adult this seems the obvious argument, rather than that the distance 'suggests' this. Perhaps something like "...and the difference in developmental age and distance between the two specimens shows that....".

Line 222: "One of these is...."

Line 221: "Postcranial comparative description".

This heading does not cover the contents. This sections is mostly a review and discussion of previously published BRT-VP-2/73, and the description of the one new specimen (BRT-VP-2/87) is not given here but in the Suppl Info. Perhaps call this e.g. 'Postcranial evidence'.

Line 225: Extended Data Figs 8 and 9 are cited before Extended Data Fig. 7 (Line 250). Reorder.

Lines 232-233: this statement has been made once or twice before and feels repetitive.

Line 256 (and Ext Data Fig 7). Would it not be possible to add StW 595 to the comparative figure? This would strengthen the discussion of phylogenetic relationships.

Line 258: "A multivariate analysis..." because this analysis has not been mentioned previously in the text.

Line 297: Reference 44 has been updated with better samples etc to:

Hanegraef H, Leakey MG, Leakey LN and Spoor F. (2024) Mid-Pliocene hominin diversity revisited. *C.R. Paleovol.* 23, 453-464. doi.org/10.5852/cr-palevol2024v23a29

It does not change the conclusion mentioned here, with the BRT-VP 3/1 maxilla being statistically significantly different from *A. afarensis* but not from *A. africanus*.

Line 420: delete "now". This statement applied ever since the publication of the foot in 2012 (independent of attribution to *A. deyiremeda*).

Line 460: Could these variables be obtained for any *A. africanus* specimen (perhaps not)? That would make an important addition, given the *A. deyiremeda* – *A. africanus* similarities mentioned in the paper.

Supplementary Information

p.10 (BRT-VP-1/345): check format of dental abbreviation C(=> C1) and P3.

Version 2:

Reviewer comments:

Referee #2

(Remarks to the Author)

n/a

Open Access This Peer Review File is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

In cases where reviewers are anonymous, credit should be given to 'Anonymous Referee' and the source.

The images or other third party material in this Peer Review File are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

To view a copy of this license, visit <https://creativecommons.org/licenses/by/4.0/>