Peer Review File

Manuscript Title: Dental evidence for extended growth in early Homo from Dmanisi

Redactions – Third Party Material

Parts of this Peer Review File have been redacted as indicated to remove third-party material.

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

Q1: Does the manuscript have flaws which should prohibit its publication? If so, please provide the details.

This manuscript presents a very detailed and carefully illustrated study of the dental development of an early Homo individual. The abstract concludes: “The unique combination of ape-like early maturity and human-like delayed formation of the dentition suggests that the childhood phase was prolonged in early Homo before a general slow-down of life history.” I am afraid that this interpretation is unconvincing for reasons I detail below, and thus the final speculation — “that extended childhood has evolved together with a social system that favours intergenerational information transfer, implying that gene-culture co-evolution has played a central role in the genus Homo since its beginning”— is impossible to assess from the results presented. The authors may consider familiarizing themselves with orangutans, which have a more delayed dental maturation than this early Homo fossil, yet no more “intergenerational information transfer” than other largely solitary mammals.

The manuscript begins by stating: “Humans compared to great apes show a marked slow-down of dental development – especially of the permanent molars.” This is misleading and not reflective of histological studies of great ape dental development. The speed of molar development – how fast tooth enamel is secreted – is nearly identical amongst humans and great apes (Smith, 2016: Table 9). The rate of molar crown extension varies greatly amongst apes and humans; humans tend to fall between chimpanzees at the higher end, and orangutans at the lower end (Smith, 2016: Table 11). The main difference is in the rate of root extension, but this too varies amongst apes (e.g., ref 47).

Importantly, the molar crown data presented in Figure 2 are not especially human-like. The formation times are extremely short and appear most similar to chimpanzees (Smith, 2016: Table 10). The purported initiation ages of M1 mesial cusps at ~2 – 5 months after birth are highly implausible for any human, or any great ape, which begin forming their M1 mesial cusps well before the distal ones, and nearly always a month or so prior to birth. Reported rates of dentine secretion far exceed human and chimpanzee values in ref. 47 and Smith et al. (2007). The estimated molar eruption ages are not just “more similar to those observed in wild chimpanzees than in humans,” they fall within chimpanzee ranges (Machanda et al., 2015) and entirely below normative human eruption ranges.

The first paragraph of the Discussion interpreting Figure 2 is also flawed: “crown formation periods

of the first, second and third molars of the Dmanisi individual show little to no temporal overlap, like in modern humans, whereas in chimpanzees the M1/M2/M3 crown formation periods show extensive overlap (ref. 27.)" In fact, chimpanzees show variable patterns of molar overlap (Smith et al. 2007: which also highlighted problems with ref. 27.) Claims that this fossil is modern human-like due to a lack of molar overlap also fail to consider the broader literature on primate dental development. For example, baboon molar crowns show little to no temporal overlap (Dirks et al. 2002). In short, this isn't a unique human-like characteristic, nor is the lack of molar overlap useful for inferring a prolonged life history.

The construction and interpretation of Figure 3 is problematic. The top panel contrasts histological data on this fossil with radiographic data on humans and chimpanzees – yet such comparisons are not equivalent. Beynon et al. (1998) showed how radiographic data are notoriously problematic for capturing tooth initiation and crown completion accurately, stating on p. 351 "…the human population standards in current usage may not represent true anatomical and chronological stages of crown development, and care should be taken in referring juvenile hominids to these radiological standards." This is especially evident in the excessively long chimpanzee M3 crown formation time and extremely delayed human M3 initiation age depicted, neither of which are consistent with histological studies.

The second panel of Figure 3 underpins claims about changes in "developmental rates," again based on comparisons of histological data from this fossil with radiographic data from captive chimpanzees and humans. Here "dental maturation scores" largely derive from a 50-year-old radiographic scoring system that divides crown (and root) calcification into 4 stages of unequal durations. To illustrate the problem: a human molar tooth crown that forms over 3 years would be scored as 1 (initiation), 2 (cusp coalescence), 3 (occlusal completion), and 4 (crown completion) – yet these first three stages largely occur within the first year or so, while the completion of the crown requires another two years. Similar problems exist with the 4 stages used to characterize subsequent root formation, i.e., this is a rubric developed to capture sequential changes in tooth shape rather than changes in developmental timing, and because teeth do not grow in a linear fashion, comparisons of shapes/scores cannot yield meaningful developmental rates (especially not 6-month intervals in Figure 3b). It simply isn't tenable to infer comparative maturation peaks (Figure 3c) from these data.

Q2: On a more subjective note, do you feel that the results presented are of immediate interest to many people in your own discipline, or to people from several disciplines?

The skeletal and dental similarities between this fossil and chimpanzees are broadly consistent with previous studies of the similarly-aged Nariokotome juvenile and earlier hominins; I am not sure that this is of "immediate interest." As a specialist of microscopic dental development, I would be quite interested to see the histological results situated within a more comprehensive comparative framework, but suspect that this would not be of broad interdisciplinary interest.

Beynon, A.D., Clayton, C.B., Ramirez Rozzi, F.V., Reid, D.J. (1998) Radiographic and histological methodologies in estimating the chronology of crown development in modern humans and great apes: a review, with some applications for studies on juvenile hominids. J. Hum. Evol. 35, 351–370.

Dirks, W., Reid, D. J., Jolly, C. J., Phillips-Conroy, J. E., & Brett, F. L. (2002) Out of the mouths of baboons: Stress, life history, and dental development in the Awash National Park Hybrid Zone, Ethiopia. Am. J. Phys. Anthropol., 118, 239–252.

Machanda, Z., Brazeau, N.F., Bernard, A.B., Donovan, R.M., Papakyrikos, A.M., Wrangham, R., Smith, T.M. (2015) Dental eruption in East African wild chimpanzees. J. Hum. Evol. 82:137-144.

Smith, T.M., Reid, D.J., Dean, M.C., Olejniczak, A.J., Martin, L.B. (2007) Molar development in common chimpanzees (Pan troglodytes). J. Hum. Evol. 52:201-216.

Smith, T.M. (2016) Dental development in living and fossil orangutans. J. Hum. Evol. 94:92-105.

Referee #2 (Remarks to the Author):

Thank your for the opportunity to review this exciting manuscript. The authors have performed a rigorous analysis of dental development in an important fossil specimen, providing a glimpse into growth and development at a critical stage of human evolution. The authors find that a Dmanisi individual that died at about 11.4 years of age had widely spaced molar crown formation periods as well as a relatively late dental growth spurt. Their data and interpretations are original and offer a new perspective on the evolution of extended childhood during human evolution. For these reasons, I think this MS will not only make an important contribution to paleoanthropology but will also be of general interest.

Overall, I find the data and methodology sound, but I have some suggestions, as noted below, related to treatment of uncertainties (M1 initiation) and the incorporation of data from the WITS Atlas (see below) in the authors' summary of dental growth spurt variation in humans. I also believe the authors need to define what they mean by "childhood".

To elaborate:

a) The authors use the term “childhood” but never explicitly define it. An explicit definition would help situate their findings in relation to childhood in humans, which according to some biological anthropologists is a life history stage unique to humans that is not present in other primates. So, what do the authors of this study mean, exactly, by the term “childhood”? Answering this question will improve the clarity and context of this study.

b) First molar initiation was assumed to be at birth, which is a safe bet. However, given that the authors have done such a nice job at estimating error associated with their age-at-death estimate, I

think that they should include an estimate of error associated with variation molar initiation. Two studies will be useful here: Antoine, D., & Hillson, S. (2016). Enamel structure and properties. In J. D. Irish & G. R. Scott (Eds.), A Companion to Dental Anthropology (pp. 223–244). New York: Wiley Liss, and (2) Reid, D. J., & Guatelli-Steinberg, D. (2017). Updating histological data on crown initiation and crown completion ages in southern Africans. American Journal of Physical Anthropology, 162(4), 817-829. Together these studies suggest a range of 0.14 years before birth to 0.03 years after birth for M1 initiation.

c) While I think the analyses related to the dental growth spurt are interesting and innovative, Table 1 in the Extended Data table does not include Black Southern Africans, whose dental development seems to be accelerated relative to some groups. I am unclear why the authors cite the London Atlas and use it, but not the WITS Atlas (Esan TA, Schepartz LA. The WITS Atlas: A Black Southern African dental atlas for permanent tooth formation and emergence. Am J Phys Anthropol. 2018 May;166(1):208-218. doi: 10.1002/ajpa.23424. Epub 2018 Feb 15. PMID: 29446436) and why the authors did not use the information in the WITS Atlas to estimate the dental growth spurt of Black Southern Africans.

Minor comments:
Line 50: What is this correlation based on? I think they are talking about correlations across some primates, but then instead of “correlates well with prolonged cerebral and delayed somatic maturation” they might say “correlates well with the pace of cerebral development and somatic maturation across primates.”

Line 62-64: I think it is worth noting that Dean et al., 2001 estimated M1 gingival emergence at 4.4 years of age in Sangiran S7-37, because this suggests a slight delay in M1 emergence relative to that of chimpanzees.

Line 82: Please change “exposition” to “exposure”

Line 86: Not sure why the M3 with supernumerary cusp was excluded.

Summary: This is a very interesting study that provides a new perspective on the evolution of human growth and development. I look forward to seeing it published.

Referee #3 (Remarks to the Author):

A. Summary of the key results
This manuscript presents a microstructural analysis of the dental development status of the Dmanisi cranium D2700 and mandible D2735 to draw life history inferences for early Homo. They document a pattern of delayed molar crown initiation similar to modern humans, but a short overall period of dental maturity similar to extant apes (represented here by Pan). They conclude that this reflects an extended childhood phase of growth and development, even within a shorter 'ape-like' period of dental maturity. This is regarded as a first step toward the prolonged life history of modern humans.

B. Originality and significance: if not novel, please include reference
The microstructural analysis of the complete dentition of an individual fossil specimen is a novel application of existing techniques, and the completeness of the specimens D2700 and D2735 provides an unique opportunity to document the dental development chronology of an individual representing an extinct species at an exceptional level of detail. The methods themselves are not perhaps 'unique' but the way that they are applied to analyse this specimen does represent a unique application of the existing methods. The significance of this work is very important in documenting the dental development and life history to an unprecedented level of detail for an individual fossil specimen. The use of the movie reconstructions is a novel way to visually present the estimated/ reconstructed stages and patterns of dental development through the developmental period of this individual.

C. Data & methodology: validity of approach, quality of data, quality of presentation
The methods are valid, the quality of the data and the presentation approach are excellent. The research team includes individuals who have been instrumental in the development and application of microstructural analysis and 3D reconstructions of fossil specimens. The work is excellent overall.

D. Appropriate use of statistics and treatment of uncertainties
I have no problem with the statistical approach overall. It involves a certain amount of estimation and prediction, but this is necessary given the nature of the samples available. I don't believe that anything unreasonable has been presented, but at the same time I don't know exactly how to assess the accuracy of the reconstructions (i.e. the movies, fig 3) for the full suite of crown and root formation events, or tooth eruption periods. Can the authors comment on this? Where are the potential sources of error and how much error might be involved?

I would like to see more detail on the methods to produce DGS in all samples, and also in the DMS reconstructions for the varied human samples using different systems for scoring dental maturity. The basic idea is clear enough, but this is a critical step for the comparative work and I am sure that it was a complex and challenging process given the differences in method, samples, etc among the studies cited. It is not possible to understand exactly how it was achieved with the level of detail provided - though I understand that it will be quite difficult to summarise everything succinctly.

E. Conclusions: robustness, validity, reliability
Overall, I agree that the Dmanisi specimen shows early completion of dental development similar to

Pan, and some delayed patterns of molar dental development similar to humans. See below for further comments on how this might be interpreted.

F. Suggested improvements: experiments, data for possible revision

The scenario presented is a fairly linear 'ape-like' to 'human-like' evolutionary trajectory for life history evolution - apes characterised by short periods of dental and somatic maturity, and humans by prolonged phases of growth and development including a prolonged childhood. While this linear scenario might generally characterise the overall evolution of 'human' life history, it may not represent the evolution of 'hominin' life history. Recent research on life history variation in living apes has documented a great deal of variation in dental development timing, weaning ages, and other aspects of life history. Researchers cited here such as Dean, Kelly, Schwartz, T.M. Smith and others have discussed this variation in recent papers (see examples below), and they have been reviewed by Kuykendall (2020). One additional suggestion stemming from this awareness of diversity in extant ape life history is that Pan may not be the best comparative model for reconstructing early hominin life history - though the necessary data for Gorilla and Pongo remain comparatively scarce. There are two important results to draw from this new information/ awareness: 1) the use of Pan to represent some general 'ape-like' condition is erroneous (i.e., refer to the comparisons as 'Pan-like', not 'ape-like'). Pan is not a 'typical ape', and I argue strongly against using the 'ape vs human' dichotomy at all given our current understanding; 2) In line with this, I also would not use the linear evolutionary scenario (ape-like to human-like), but suggest consideration of a model with much more diversity in life history among early hominins, including early Homo, and would seek to incorporate perspectives drawn from the range of extant ape studies. Obviously, we are limited by the available fossil record and the lack of complete dental development and life history data for all living apes, but it would still be possible to include a fuller discussion with some focus on the diversity now recognised in extant apes (and this can be extended to the diversity in modern human populations as well, which is also extensive). I think that this is relevant in discussing the Dmanisi early Homo material because it does appear to differ in morphology, geographic and environmental context, etc. from other early Homo material such as Nariokotome - and this may also have implications in reconstructions comparing life history among early Homo specimens when such data are available. Did the genus Homo really have some fundamental life history pattern 'since its beginnings' (as stated in abstract)? A fuller discussion of the potential for diversity in life history in relation to geographic, environmental and social variation among early hominins would be a very useful addition to this manuscript, and would acknowledge more fully some of the recent literature on the issue.

Finally, I think that Figure 3 outlines some very interesting differences in the dental development schedules of the Dmanisi specimen compared to the Pan and human samples used. As noted in the manuscript, both premolar and M2 crown initiation are delayed compared to both Pan and humans. Tooth eruption timing in P4 and M2 are delayed as well. This is very interesting, and some consideration of factors such as delay or variation in weaning might be involved. Comparison with Gorilla and Pongo dental development schedules, weaning process and other life history factors would thus be useful, as they differ substantially from Pan. Tanya Smith has done some work on this, and other references in the primate literature are also relevant.

Overall, the Dmanisi dental development pattern is unique, and if the previous work (Dean, etc) on

early Homo life history schedules is correct, it may also be different from other early Homo populations. As with my comments above, I would consider this as possible evidence of diversity in early hominin life history schedules, not a 'first step' toward modern human delays. The Dmanisi pattern shows variation in molar and other dental development events (relative delay) but the overall timing of the growth and development period is not extended. It is thus not clear how the pattern difference relates to the timing of life history. None of this precludes the observation that the delayed modern human dental development and life history schedule must eventually have evolved from this diversity.

References to consider:

Dean, M. C. (2010). Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 365, Issue 1556, pp. 3397–3410). Royal Society. https://doi.org/10.1098/rstb.2010.0052

Kuykendall, K.L., (2020). Approved by volume editors: Paranthropus life history: toward a primate perspective. In Paleobiology of Paranthropus: The Forgotten Lineage(s). (P.J. Constantino, K.E. Reed, B.A. Wood, eds.). Springer, Cham, Switzerland. Published online here: https://www.smcvt.edu/pages/the-forgotten-lineages-paleobiology-of-paranthropus/

Kelley, J., & Schwartz, G. T. (2012). Life-history inference in the early hominins Australopithecus and Paranthropus. International Journal of Primatology, 33(6), 1332–1363. https://doi.org/10.1007/s10764-012-9607-2

Lockwood, C. A., Menter, C. G., Moggi-Cecchi, J., & Keyser, A. W. (2007). Extended male growth in a fossil hominin species. Science, 318(5855), 1443–1446. https://doi.org/10.1126/science.1149211

Smith, T. M., Austin, C., Hinde, K., Vogel, E. R., & Arora, M. (2017). Cyclical nursing patterns in wild orangutans. Science Advances, 3(5), e1601517. https://doi.org/10.1126/sciadv.1601517

Smith, Tanya M., Machanda, Z., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Muller, M. N., & Wrangham, R. (2013). First molar eruption, weaning, and life history in living wild chimpanzees. Proceedings of the National Academy of Sciences of the United States of America, 110(8), 2787–2791. https://doi.org/10.1073/pnas.1218746110

G. References: appropriate credit to previous work?

No issues, aside from those listed above.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

Very clearly presented. Any issues are covered above.

Author Rebuttals to Initial Comments:

Response to points raised by all referees:

We would like to thank the referees for their critical and constructive comments on our manuscript, which prompted us to review all our previous analyses and inspired us to undertake a number of new analyses. Here we summarize the key points raised by all the referees and provide an overview of how we have addressed them.

1. *Methodology*:
    a. Validity and consistency of the dental maturity scoring (DMS) approach used to compare dental ontogenies in great apes, humans and Dmanisi?
    b. Comparability across different data acquisition techniques (radiography, CT/histology) and scoring systems (Demirjian etc.)?

→ To address these points, we performed a series of consistency checks, which are presented in the Appendix of this document (see **Studies 1-4**) and summarized in a new Methods section ("Consistency checks") and Extended Data Figure 8. We show that, with appropriate calibration procedures, the DMS approach is consistent across a wide range of methodologies.

2. *Comparative sample, variation*:
    a. Documentation of intra- and inter-taxon variation?
    b. Comparative data on other great ape taxa, in addition to chimpanzees?
    c. Comparative data on fossil hominin specimens?

→ To address these points, we performed new analyses, using the multivariate approach introduced by Boughner, Der and Kuykendall 2015 [1] (see new **Fig. 3b** in the revised manuscript, and **Studies 3, 5** in the Appendix of this document). The basic idea is to perform a principal components analysis (PCA) on the dental maturation scores (DMS) of all teeth (the variables DMS_{I1} … DMS_{M3}) for a sample of specimens (the observations). The "DMS-PCA" approach makes it possible to document variation along and across ontogenetic trajectories, and to identify taxon-specific differences [1]. A major advantage is that specimens of unknown individual age can also be included in the analyses. This has allowed us to greatly expand the comparative sample, which now includes bonobos, gorillas and orangutans, as well as various fossil hominin specimens (data from the literature and from medical CT scans, as specified in the revised Methods section). In the revised manuscript, we now differentiate between *pattern* and *rate* of a dentition's ontogeny, where *pattern* denotes relative timing (DMS of an individual's teeth relative to each other, **Fig. 3**), and *rate* denotes absolute timing (total DMS versus age in years, **Fig. 4**). Using this approach, we can now characterize various aspects of dental ontogeny with greater clarity:

i. While there is overlap between taxa with regard to almost all single variables measuring dental maturation (crown/root initiation, formation, completion; gaps between successive molar crown formation periods), the DMS-PCA method permits to distinguish between intra-taxon and inter-taxon variation. It shows that humans clearly differ from all great ape taxa in both rate and pattern of their dentition's ontogeny. It is therefore sensible to discriminate between "human-like" and "great ape-like" dental ontogenies, which we use as basic concepts to discuss dental ontogenetic diversity in living and fossil taxa.
ii. Importantly, Dmanisi followed a human-like pattern of ontogeny, but at a higher rate after the eruption of M1.
iii. Other early *Homo* specimens such as Nariokotome are also associated with a human-like pattern.
iv. Ontogenies of *Australopithecus* dentitions most likely were ape-like regarding rate and pattern, while *Paranthropus* seems to have followed its own trajectory (as suggested earlier, see ref. [2]).

3. *Evolutionary interpretation of the Dmanisi dental ontogeny in comparative context*:
In the previous version of the manuscript, we assumed a human-vs-ape dichotomy in ontogenetic rate, and we used (captive) chimpanzees as a model for the "typical ape" to draw inferences on the evolutionary significance of Dmanisi's dental ontogeny. The reviewers asked for a more nuanced interpretation of evolutionary diversification of hominin dental ontogenies and the links that can be established to the evolution of their life histories.

→ The new DMS-PCA results and the expanded comparative sample provide a broader perspective on the past and present diversity of modes of dental ontogeny. In the revised discussion, we provide a deeper and more critical interpretation of Dmanisi's dental ontogeny in terms of intra-/intertaxon variation, primitive versus derived features, possible evolutionary scenarios, and links to life history evolution. We clearly mark our proposed evolutionary scenarios as hypotheses that require further testing.

Additional text and materials:

- We have expanded the Methods section on synchrotron tomography with details on the two scanning methods used (monochromatic versus polychromatic beams).
- We have added source files containing the data used to produce Figures 3 and 4.

Response to referee #1

Referee #1 (Remarks to the Author):

Q1: Does the manuscript have flaws which should prohibit its publication? If so, please provide the details.

This manuscript presents a very detailed and carefully illustrated study of the dental development of an early Homo individual. The abstract concludes: "The unique combination of ape-like early maturity and human-like delayed formation of the dentition suggests that the childhood phase was prolonged in early Homo before a general slow-down of life history." I am afraid that this interpretation is unconvincing for reasons I detail below, and thus the final speculation — "that extended childhood has evolved together with a social system that favours intergenerational information transfer, implying that gene-culture co-evolution has played a central role in the genus Homo since its beginning"— is impossible to assess from the results presented. The authors may consider familiarizing themselves with orangutans, which have a more delayed dental maturation than this early Homo fossil, yet no more "intergenerational information transfer" than other largely solitary mammals.

We thank the reviewer for drawing our attention to various "loose ends" in our manuscript. This helped us correct various inconsistencies and clarify our arguments. The reviewer's comments also inspired us to carry out additional analyses using a broad comparative sample. Our point-by-point responses (also regarding orangutans) are given below.

The manuscript begins by stating: "Humans compared to great apes show a marked slow-down of dental development – especially of the permanent molars." This is misleading and not reflective of histological studies of great ape dental development. The speed of molar development – how fast tooth enamel is secreted – is nearly identical amongst humans and great apes (Smith, 2016: Table 9).

We realized that we had not explicitly defined what we mean with "dental development". We checked the literature, and it appears that terms such as dental development, formation, growth, maturation and ontogeny tend to be used interchangeably, and at different levels of organization such as tooth crowns and roots, individual teeth, and the entire dentition. Following the reviewer's suggestion, we have revised the entire text to be consistent in terminology. We use "dental ontogeny" (as in Smith et al. 2015; [3]) to denote the maturation of the entire dentition. Using the DMS-PCA approach described above (see response to all referees), we distinguish between the pattern and rate of dental ontogeny.

The rate of molar crown extension varies greatly amongst apes and humans; humans tend to fall between chimpanzees at the higher end, and orangutans at the lower end (Smith, 2016: Table 11). The main difference is in the rate of root extension, but this too varies amongst apes (e.g., ref 47). Importantly, the molar crown data presented in Figure 2 are not especially human-like. The formation times are extremely short and appear most similar to chimpanzees (Smith, 2016: Table 10).

The molar crown formation times in Dmanisi are indeed short (as mentioned in the first paragraph of the discussion: "…rates are exceptionally high") and more similar to values reported for chimpanzees than humans. However, as we explain in the response to all reviewers, and in detail below, we do not base our evolutionary interpretation of Dmanisi's dental ontogeny on a feature-by-feature comparison; rather, we use the multivariate DMS-PCA approach to simultaneously account for variation in all features, both within and between groups.

The purported initiation ages of M1 mesial cusps at ~2 – 5 months after birth are highly implausible for any human, or any great ape, which begin forming their M1 mesial cusps well before the distal ones, and nearly always a month or so prior to birth.

Thank you for pointing out this inconsistency, which was due to a mislabeling of mesial versus distal cusps in the analysis sheets. We corrected the respective data and figure (SI Data1, Fig. 2).

Reported rates of dentine secretion far exceed human and chimpanzee values in ref. 47 and Smith et al. (2007).

We cross-validated these rates and the resulting root formation times (see SI Data 1) and added a sentence to the Methods section mentioning the fast dentine secretion rate.

The estimated molar eruption ages are not just "more similar to those observed in wild chimpanzees than in humans," they fall within chimpanzee ranges (Machanda et al., 2015) and entirely below normative human eruption ranges.

Indeed, in this context, "more similar to chimps than humans" sounds like an understatement (probably not for the inferred M2 eruption time). We therefore adjusted the phrasing as suggested.

The first paragraph of the Discussion interpreting Figure 2 is also flawed: "crown formation periods of the first, second and third molars of the Dmanisi individual show little to no temporal overlap, like in modern humans, whereas in chimpanzees the M1/M2/M3 crown formation periods show extensive overlap (ref. 27.)" In fact, chimpanzees show variable patterns of molar overlap (Smith et al. 2007: which also highlighted problems with ref. 27.) Claims that this fossil is modern human-like due to a lack of molar overlap also fail to consider the broader literature on primate dental development. For example, baboon molar crowns show little to no temporal overlap (Dirks et al. 2002). In short, this isn't a unique human-like characteristic, nor is the lack of molar overlap useful for inferring a prolonged life history.

We agree with the reviewer that gaps between molar crown formation periods cannot be used alone for inferring a human-like life history. More generally speaking, this is likely the case for any dental developmental feature when considered alone (e.g. crown and root formation times, enamel and dentin secretion rates, eruption times, etc.). Importantly, we did not claim that "this fossil is modern human-like due to a lack of molar overlap". The respective paragraph of the Discussion is not aimed at inferring a human-like life history from single human-like aspects of Dmanisi's dental ontogeny. Rather, in the Discussion, we take the opposite approach, decomposing the multivariate DMS signal back into its component features and asking whether these features evolved as a package or as a mosaic.

The DMS-PCA approach used in the revised manuscript is best suited to systematically address these issues in a broad comparative context. In the revised Discussion, we combine the comparative information on living species (dental ontogeny and life history) with the information on Dmanisi (dental ontogeny only) and other fossil hominin specimens ("snapshots" of the dental ontogeny at the time of death) to propose hypotheses about how evolutionary changes in dental ontogeny might provide information about the evolution of human life history.

Chimpanzee molar crown formation timing: We have changed the respective statement. Also, based on the reviewer's comments, we have updated Figure 3a with standard deviation bars to show intra-group variation of crown and root formation characteristics in chimpanzees and humans. Also, we have added comparative fossil hominin and extant great ape data on M1 eruption.

Side note: the new standard deviation bars around crown initiation (Ci) and completion (Cc) times illustrate why chimpanzees also have gaps between successive molar crown formation periods, but at a lower frequency than humans: in humans, the means of Cc and successive Ci time points are more widely spaced than in chimps, while sdevs are similar. Therefore – statistically speaking – the "gap probability" is higher in humans than in chimps.

Baboon molar crown formation non-overlap: Baboons represent a different primate clade; therefore, in the sense of phylogenetic contrasts, we cannot directly compare baboons, great apes and humans with regard to this feature. See below for further comments on baboons.

The construction and interpretation of Figure 3 is problematic. The top panel contrasts histological data on this fossil with radiographic data on humans and chimpanzees – yet such comparisons are not equivalent. Beynon et al. (1998) showed how radiographic data are notoriously problematic for capturing tooth initiation and crown completion accurately, stating on p. 351 "…the human population standards in current usage may not represent true anatomical and chronological stages of crown development, and care should be taken in referring juvenile hominids to these radiological standards." This is especially evident in the excessively long chimpanzee M3 crown formation time and extremely delayed human M3 initiation age depicted, neither of which are consistent with histological studies.

The Dmanisi DMS data presented in Fig. 3 had been recalibrated to match radiological standards, using the methodology presented in ref. [4]. While we had briefly mentioned this in the Methods section, the revised text gives more emphasis to this point. For a detailed analysis of potential methodological bias see Study 3 in this document's Appendix.

We agree with the reviewer that Fig. 3a provided an overly schematic view of taxon-specific differences. We now show standard deviation bars for the group-specific average values of crown initiation/completion (Ci, Cc), emergence (E) and root completion (Rc). It remains to be noted that, in this graph, average crown formation times (CFTs) are represented as the difference between average Cc and Ci values. We observe that these CFT values tend to be somewhat larger than CFTs directly determined on individual teeth.

Please see below for detailed comments.

The second panel of Figure 3 underpins claims about changes in "developmental rates," again based on comparisons of histological data from this fossil with radiographic data from captive chimpanzees and humans. Here "dental maturation scores" largely derive from a 50-year-old radiographic scoring system that divides crown (and root) calcification into 4 stages of unequal durations. To illustrate the problem: a human molar tooth crown that forms over 3 years would be scored as 1 (initiation), 2 (cusp coalescence), 3 (occlusal completion), and 4 (crown completion) – yet these first three stages largely occur within the first year or so, while the completion of the crown requires another two years. Similar problems exist with the 4 stages used to characterize subsequent root formation, i.e., this is a rubric developed to capture sequential changes in tooth shape rather than changes in developmental timing, and because teeth do not grow in a linear fashion, comparisons of shapes/scores cannot yield meaningful developmental rates (especially not 6-month intervals in Figure 3b). It simply isn't tenable to infer comparative maturation peaks (Figure 3c) from these data.

We thank the reviewer for her critical comments on all these issues, which have prompted us to check the consistency of all our analyses in great detail. We address the specific points as follows:

Point 1: Scoring schemes used to track dental maturation; DMS curves and DMS rate peaks.

Reviewer #1 raises several caveats regarding the use of dental maturation scores (DMS) in comparative studies, notably because tooth development itself is non-linear in time, various imaging methods and scoring/staging systems are used, successive score stages tend to have different durations in different systems, and therefore DMS curves and rate peaks are difficult to compare between groups.

First, we would like to point out that the unequal temporal distribution of successive dental maturation stages in the scoring systems does not *per se* prevent comparisons between groups; the only requirement for such comparisons is that the same dental scoring scheme be used for the entire sample. Nevertheless, the reviewer rightly asks whether DMS can serve as a biologically relevant measure to quantify dental maturation characteristics. To address this question, we analyzed in greater detail how the DMS-based ontogenetic characterization of

individual teeth and of the dentition as a whole is influenced by each of the factors mentioned by the reviewer.

Study 1 (see Appendix of this document) shows that DMS systems capture the non-linear growth characteristics of individual teeth fairly well (Graph 1.1). Graph 1.2 shows that, even if only limited information about tooth development is available (e.g. only ages at crown initiation and root completion) and linear growth is assumed, the resulting total DMS curves of the entire dentition still show the characteristic differences between Dmanisi, humans and chimpanzees.

Study 2 explores the influence of different scoring schemes on the resulting DMS curves and on the evaluation of DMS rate peaks. We used data from three independent studies on the dental development of Finnish children. While different scoring schemes yield different DMS vs. age curves, the age at the DMS rate peak is similar in all studies. This indicates that the evaluation of DMS rate peaks is robust to differences in DMS scoring schemes.

Study 3 further assesses how differences in methodology influence the DMS-vs-age curves, and the dental ontogenetic trajectories through multivariate DMS-PCA space (details explained in Study 5). Methodological differences influence the DMS-vs-age profiles (Graph 3A). However, the resulting ontogenetic trajectories through multivariate space are largely similar besides temporal shifts along the trajectory. Standardization through re-coding the different scoring systems yields largely coincident data.

Together, Studies 1-3 show that the dental maturation scoring approach is robust, and that the potentially confounding factors discussed here do not bias the basic findings of our study. In the revised methods section, we now provide detailed information on the respective procedures.

Point 2: radiology-based vs. histology/tomography-based studies

As noted by the reviewer, measuring dental maturation is potentially sensitive to the imaging methods used.

As we briefly stated in the Methods section, the Dmanisi synchrotron-based dental maturity scores (DMS) were corrected toward the radiographic standards that are used in dental maturation studies of living subjects, using the method described in [4]. In the revised text, we give more emphasis to this point.

In addition to the effects of different scoring systems, **Study 3** also examines the effects of different imaging modalities on the resulting dental ontogenetic data. Tomography-based scoring compared to radiology-based scoring yields more advanced DMS-vs-age profiles (Graph 3A), but the ontogenetic trajectories largely coincide in multivariate space, besides showing an "age shift" of about 1 year (Graph 3B). Re-calibrating the tomography data to radiological standards yields a close match. Overall, this study underlines the effectiveness of re-calibration and standardization across imaging modalities.

To further check whether there are systematic differences between radiology-based and histology-based measurements, **Study 4** uses data on molar crown initiation/completion and root completion (Ci, Cc and Rc) from the literature, comprising a wide range of taxa (humans, great apes, hylobatids and cercopithecids) and methodological approaches. This study shows that methodology does not significantly bias the results.

Point 3: Within-group and between-group variation in dental developmental features:

The reviewer notes that features once thought to be uniquely human are also found in other primate taxa. For example, baboons in general, as well as at least some chimpanzee individuals (discussed above), show temporal gaps between consecutive molar crown formation periods, as humans do. Also, within each taxon, there is substantial variation in the timing of Ci, Cc and Rc of any tooth. These effects potentially blur the differentiation between groups.

Study 4 on molar crown formation characteristics shows that within-group variation is substantial, but that humans are distinct from all other primates, with Dmanisi being closer

to humans than non-human primates. Chimpanzees with and without molar crown formation overlap are within the same taxon-specific cluster. On the other hand, *Papio* (showing temporal gaps between crown formation periods) is grouped with the other non-human primates. These results demonstrate that a multivariate approach permits an integrative view on dental developmental features, and a quantitative assessment of within-group versus between-group variation. As noted by reviewer #1, *Pongo* as well as *Papio* share several dental developmental features with humans, but when viewed in multivariate context, these "human-like" features are best interpreted as examples of convergent evolution [5].

Study 5 examines variation along ontogenetic trajectories. In both humans and chimpanzees, there is substantial natural variation at any given age in dental maturation patterns. Importantly, the range of natural variation (Graph 5) tends to exceed method-related variation (Graph 3).

Q2: On a more subjective note, do you feel that the results presented are of immediate interest to many people in your own discipline, or to people from several disciplines?

The skeletal and dental similarities between this fossil and chimpanzees are broadly consistent with previous studies of the similarly-aged Nariokotome juvenile and earlier hominins; I am not sure that this is of "immediate interest." As a specialist of microscopic dental development, I would be quite interested to see the histological results situated within a more comprehensive comparative framework, but suspect that this would not be of broad interdisciplinary interest.

Our DMS-PCA analysis now provides the comprehensive comparative framework requested by the reviewer. Indeed, as shown in previous studies, at an estimated age at death of ~8 years [6], Nariokotome exhibited a "chimpanzee-like" total dental maturation score, similar to that of Dmanisi at 8 years of age (Fig. 4a). However, the *pattern* of dental ontogeny in Nariokotome was within the range of human variation, close to the reconstructed pattern of Dmanisi, and clearly outside the range of great ape variation (new Fig. 3b). Overall, our study thus provides new evidence for a derived pattern of dental ontogeny in early *Homo*.

Beynon, A.D., Clayton, C.B., Ramirez Rozzi, F.V., Reid, D.J. (1998) Radiographic and histological methodologies in estimating the chronology of crown development in modern humans and great apes: a review, with some applications for studies on juvenile hominids. J. Hum. Evol. 35, 351–370.

Dirks, W., Reid, D. J., Jolly, C. J., Phillips-Conroy, J. E., & Brett, F. L. (2002) Out of the mouths of baboons: Stress, life history, and dental development in the Awash National Park Hybrid Zone, Ethiopia. Am. J. Phys. Anthropol., 118, 239–252.

Machanda, Z., Brazeau, N.F., Bernard, A.B., Donovan, R.M., Papakyrikos, A.M., Wrangham, R., Smith, T.M. (2015) Dental eruption in East African wild chimpanzees. J. Hum. Evol. 82:137-144.

Smith, T.M., Reid, D.J., Dean, M.C., Olejniczak, A.J., Martin, L.B. (2007) Molar development in common chimpanzees (Pan troglodytes). J. Hum. Evol. 52:201-216.

Smith, T.M. (2016) Dental development in living and fossil orangutans. J. Hum. Evol. 94:92-105.

We have included most of these references in the revised manuscript.

Response to referee # 2

Referee #2 (Remarks to the Author):

Thank your for the opportunity to review this exciting manuscript. The authors have performed a rigorous analysis of dental development in an important fossil specimen, providing a glimpse into growth and development at a critical stage of human evolution. The authors find that a Dmanisi individual that died at about 11.4 years of age had widely spaced molar crown formation periods as well as a relatively late dental growth spurt. Their data and interpretations are original and offer a new perspective on the evolution of extended childhood during human evolution. For these reasons, I think this MS will not only make an important contribution to paleoanthropology but will also be of general interest.

Overall, I find the data and methodology sound, but I have some suggestions, as noted below, related to treatment of uncertainties (M1 initiation) and the incorporation of data from the WITS Atlas (see below) in the authors' summary of dental growth spurt variation in humans. I also believe the authors need to define what they mean by "childhood".

To elaborate:

a) The authors use the term “childhood” but never explicitly define it. An explicit definition would help situate their findings in relation to childhood in humans, which according to some biological anthropologists is a life history stage unique to humans that is not present in other primates. So, what do the authors of this study mean, exactly, by the term “childhood”? Answering this question will improve the clarity and context of this study.

> Thank you for pointing out this omission. We have updated the introduction, using the childhood definition of ref. [7]

b) First molar initiation was assumed to be at birth, which is a safe bet. However, given that the authors have done such a nice job at estimating error associated with their age-at-death estimate, I think that they should include an estimate of error associated with variation molar initiation. Two studies will be useful here: Antoine, D., & Hillson, S. (2016). Enamel structure and properties. In J. D. Irish & G. R. Scott (Eds.), A Companion to Dental Anthropology (pp. 223–244). New York: Wiley Liss, and (2) Reid, D. J., & Guatelli-Steinberg, D. (2017). Updating histological data on crown initiation and crown completion ages in southern Africans. American Journal of Physical Anthropology, 162(4), 817-829. Together these studies suggest a range of 0.14 years before birth to 0.03 years after birth for M1 initiation.

> Thank you for this suggestion. We revised the respective text and data to account for variation in M1 initiation, integrating the data of the studies indicated by the reviewer. This is also reflected in the sdev bars that we introduced in Fig. 3a.

c) While I think the analyses related to the dental growth spurt are interesting and innovative, Table 1 in the Extended Data table does not include Black Southern Africans, whose dental development seems to be accelerated relative to some groups. I am unclear why the authors cite the London Atlas and use it, but not the WITS Atlas (Esan TA, Schepartz LA. The WITS Atlas: A Black Southern African dental atlas for permanent tooth formation and emergence. Am J Phys Anthropol. 2018 May;166(1):208-218. doi: 10.1002/ajpa.23424. Epub 2018 Feb 15. PMID: 29446436) and why the authors did not use the information in the WITS Atlas to estimate the dental growth spurt of Black Southern Africans.

> We used the London Atlas data because the sample spans the entire ontogenetic trajectory from birth to adulthood, while the WITS Atlas sample starts at 5 years, thus probably missing an early dentition growth spurt. Nevertheless, following the reviewer’s suggestion, we

included the WITS Atlas data in our analyses and updated the SI Data 1 file, the graphs in Fig. 3, and Extended Table 1 accordingly. Interestingly, the growth spurt in the WITS sample is not earlier than in other populations.

Minor comments:
Line 50: What is this correlation based on? I think they are talking about correlations across some primates, but then instead of “correlates well with prolonged cerebral and delayed somatic maturation” they might say “correlates well with the pace of cerebral development and somatic maturation across primates.”

Thank you for pointing out this inconsistency; we revised the text accordingly.

Line 62-64: I think it is worth noting that Dean et al., 2001 estimated M1 gingival emergence at 4.4 years of age in Sangiran S7-37, because this suggests a slight delay in M1 emergence relative to that of chimpanzees.

We included these data in Fig. 3a; see symbols beneath age axis, indicating taxon-specific mean ages at M1 eruption.

Line 82: Please change “exposition” to “exposure”

done

Line 86: Not sure why the M3 with supernumerary cusp was excluded.

We excluded this tooth to be "on the safe side" for comparability. The supernumerary cusp may have had an effect on the timing of the development of the other cusps that are comparable across teeth. See updated Extended Data Fig. 1.

Summary: This is a very interesting study that provides a new perspective on the evolution of human growth and development. I look forward to seeing it published.

Response to referee #3

Referee #3 (Remarks to the Author):

A. Summary of the key results
This manuscript presents a microstructural analysis of the dental development status of the Dmanisi cranium D2700 and mandible D2735 to draw life history inferences for early Homo. They document a pattern of delayed molar crown initiation similar to modern humans, but a short overall period of dental maturity similar to extant apes (represented here by Pan). They conclude that this reflects an extended childhood phase of growth and development, even within a shorter 'ape-like' period of dental maturity. This is regarded as a first step toward the prolonged life history of modern humans.

B. Originality and significance: if not novel, please include reference
The microstructural analysis of the complete dentition of an individual fossil specimen is a novel application of existing techniques, and the completeness of the specimens D2700 and D2735 provides an unique opportunity to document the dental development chronology of an individual representing an extinct species at an exceptional level of detail. The methods themselves are not perhaps 'unique' but the way that they are applied to analyse this specimen does represent a unique application of the existing methods. The significance of this work is very important in documenting the dental development and life history to an unprecedented level of detail for an individual fossil specimen. The use of the movie reconstructions is a novel way to visually present the estimated/ reconstructed stages and patterns of dental development through the developmental period of this individual.

C. Data & methodology: validity of approach, quality of data, quality of presentation
The methods are valid, the quality of the data and the presentation approach are excellent. The research team includes individuals who have been instrumental in the development and application of microstructural analysis and 3D reconstructions of fossil specimens. The work is excellent overall.

D. Appropriate use of statistics and treatment of uncertainties
I have no problem with the statistical approach overall. It involves a certain amount of estimation and prediction, but this is necessary given the nature of the samples available. I don't believe that anything unreasonable has been presented, but at the same time I don't know exactly how to assess the accuracy of the reconstructions (i.e. the movies, fig 3) for the full suite of crown and root formation events, or tooth eruption periods. Can the authors comment on this? Where are the potential sources of error and how much error might be involved?

> The movies have been designed as a visual complement to the data presented in SI Data 1. We added a new paragraph to the Methods section describing in detail how the movies were created.

I would like to see more detail on the methods to produce DGS in all samples, and also in the DMS reconstructions for the varied human samples using different systems for scoring dental maturity. The basic idea is clear enough, but this is a critical step for the comparative work and I am sure that it was a complex and challenging process given the differences in method, samples, etc among the studies cited. It is not possible to understand exactly how it was achieved with the level of detail provided - though I understand that it will be quite difficult to summarise everything succinctly.

> We added a Methods section that provides detailed information on how we converted the published raw data into a common DMS scoring framework. Basically, the challenge was to deal with differences in a variety of factors: data acquisition methods (radiographic, CT, histology), age range of the sample, temporal resolution, dental subsamples used (e.g. with/without M3), dental maturation scoring systems used, statistical modalities to summarize the data, and natural variation within/between samples. We performed extensive validation tests to ascertain that our method of data standardization is consistent across studies. These

tests are described in detail in the Appendix of this document (see Studies 1-3 and 5) and are included in the revised Methods.
SI Data 4 contains the source data, the DMS standardization schemes and the Excel functions used to obtain the final DMS data for Figures 3 and 4.
Please also see our response to reviewer #1 regarding similar topics.

E. Conclusions: robustness, validity, reliability
Overall, I agree that the Dmanisi specimen shows early completion of dental development similar to Pan, and some delayed patterns of molar dental development similar to humans. See below for further comments on how this might be interpreted.

F. Suggested improvements: experiments, data for possible revision
The scenario presented is a fairly linear 'ape-like' to 'human-like' evolutionary trajectory for life history evolution - apes characterised by short periods of dental and somatic maturity, and humans by prolonged phases of growth and development including a prolonged childhood. While this linear scenario might generally characterise the overall evolution of 'human' life history, it may not represent the evolution of 'hominin' life history. Recent research on life history variation in living apes has documented a great deal of variation in dental development timing, weaning ages, and other aspects of life history. Researchers cited here such as Dean, Kelly, Schwartz, T.M. Smith and others have discussed this variation in recent papers (see examples below), and they have been reviewed by Kuykendall (2020). One additional suggestion stemming from this awareness of diversity in extant ape life history is that Pan may not be the best comparative model for reconstructing early hominin life history - though the necessary data for Gorilla and Pongo remain comparatively scarce.

We agree with the reviewer that comparative data on intra- and intertaxon variation are essential, and that *Pan* is not the best model for reconstructing hominin life history evolution. The new DMS-PCA approach has allowed us to include a significant amount of data on other great ape taxa (bonobos, gorillas, orangutans) and fossil hominins in our comparative analyses. We provide detailed comments in the next paragraph.

There are two important results to draw from this new information/ awareness: 1) the use of Pan to represent some general 'ape-like' condition is erroneous (i.e., refer to the comparisons as 'Pan-like', not 'ape-like'). Pan is not a 'typical ape', and I argue strongly against using the 'ape vs human' dichotomy at all given our current understanding; 2) In line with this, I also would not use the linear evolutionary scenario (ape-like to human-like), but suggest consideration of a model with much more diversity in life history among early hominins, including early Homo, and would seek to incorporate perspectives drawn from the range of extant ape studies. Obviously, we are limited by the available fossil record and the lack of complete dental development and life history data for all living apes, but it would still be possible to include a fuller discussion with some focus on the diversity now recognised in extant apes (and this can be extended to the diversity in modern human populations as well, which is also extensive). I think that this is relevant in discussing the Dmanisi early Homo material because it does appear to differ in morphology, geographic and environmental context, etc. from other early Homo material such as Nariokotome - and this may also have implications in reconstructions comparing life history among early Homo specimens when such data are available. Did the genus Homo really have some fundamental life history pattern 'since its beginnings' (as stated in abstract)? A fuller discussion of the potential for diversity in life history in relation to geographic, environmental and social variation among early hominins would be a very useful addition to this manuscript, and would acknowledge more fully some of the recent literature on the issue.

We agree with the reviewer that chimpanzees are not "typical apes" and that they do not necessarily represent good models for the human-chimp last common ancestor (HC-LCA). In the previous version of the manuscript, we made a virtue out of necessity by contrasting chimpanzee and human modes of dental ontogeny, simply because the most comprehensive great ape data available are those of chimpanzees. The reviewer's comments inspired us to look for ways to incorporate the comparatively less complete information from other great ape taxa. The DMS-PCA approach has

permitted us to expand the comparative sample, which now includes bonobos, gorillas, orangutans and immature hominin fossils representing *Australopithecus*, *Paranthropus* and early *Homo*. As noted above (response to all reviewers), distinguishing between pattern and rate of dental ontogeny provides a clearer picture of commonalities and differences between taxa. With regard to the HC-LCA question, we can now state that all great ape taxa studied here follow a shared (likely ancestral) pattern of dental ontogeny, but at different rates. Thus, the pattern of dental ontogeny in chimpanzees is likely to be characteristic of great apes in general, while their rate is not.

These new insights are summarized above (responses to all referees), and have been integrated in the Results and Discussion sections.

Finally, I think that Figure 3 outlines some very interesting differences in the dental development schedules of the Dmanisi specimen compared to the Pan and human samples used. As noted in the manuscript, both premolar and M2 crown initiation are delayed compared to both Pan and humans. Tooth eruption timing in P4 and M2 are delayed as well. This is very interesting, and some consideration of factors such as delay or variation in weaning might be involved. Comparison with Gorilla and Pongo dental development schedules, weaning process and other life history factors would thus be useful, as they differ substantially from Pan. Tanya Smith has done some work on this, and other references in the primate literature are also relevant.

Our updated Fig. 3a now includes error bars for the major tooth formation events, and the new DMS-PCA analysis presented in Fig. 3b gives a better sense of ontogenetic variation within and between taxa. The DMS vs. age graph (Fig. 4a) now provides comparative data of known-age great apes and fossil hominins, and the revised discussion includes the suggestions of the reviewer regarding diversity in dental ontogenies and life histories.

Overall, the Dmanisi dental development pattern is unique, and if the previous work (Dean, etc) on early Homo life history schedules is correct, it may also be different from other early Homo populations. As with my comments above, I would consider this as possible evidence of diversity in early hominin life history schedules, not a 'first step' toward modern human delays. The Dmanisi pattern shows variation in molar and other dental development events (relative delay) but the overall timing of the growth and development period is not extended. It is thus not clear how the pattern difference relates to the timing of life history. None of this precludes the observation that the delayed modern human dental development and life history schedule must eventually have evolved from this diversity.

The DMS-PCA approach and its differentiation between pattern and rate has been crucial to resolve the apparent paradox of Dmanisi showing a "human-like" relative delay (mostly of posterior tooth formation) within a conserved "ape-like" absolute time frame. Given the new comparative data, it appears that there was indeed diversity in both the pattern and rate of fossil hominin dental ontogenies. Interestingly, all specimens attributed to early *Homo* are similar in ontogenetic pattern to Dmanisi, while rates might have been more diverse. As suggested by the reviewer, this indicates evolutionary diversity rather than a single-lineage process of life history evolution.

References to consider:
Dean, M. C. (2010). Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 365, Issue 1556, pp. 3397–3410). Royal Society. https://doi.org/10.1098/rstb.2010.0052
Kuykendall, K.L., (2020). Approved by volume editors: Paranthropus life history: toward a primate perspective. In Paleobiology of Paranthropus: The Forgotten Lineage(s). (P.J. Constantino, K.E. Reed, B.A. Wood, eds.). Springer, Cham, Switzerland. Published online here: https://www.smcvt.edu/pages/the-forgotten-lineages-paleobiology-of-paranthropus/

Kelley, J., & Schwartz, G. T. (2012). Life-history inference in the early hominins Australopithecus and Paranthropus. International Journal of Primatology, 33(6), 1332–1363. https://doi.org/10.1007/s10764-012-9607-2
Lockwood, C. A., Menter, C. G., Moggi-Cecchi, J., & Keyser, A. W. (2007). Extended male growth in a fossil hominin species. Science, 318(5855), 1443–1446. https://doi.org/10.1126/science.1149211
Smith, T. M., Austin, C., Hinde, K., Vogel, E. R., & Arora, M. (2017). Cyclical nursing patterns in wild orangutans. Science Advances, 3(5), e1601517. https://doi.org/10.1126/sciadv.1601517
Smith, Tanya M., Machanda, Z., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Muller, M. N., & Wrangham, R. (2013). First molar eruption, weaning, and life history in living wild chimpanzees. Proceedings of the National Academy of Sciences of the United States of America, 110(8), 2787–2791. https://doi.org/10.1073/pnas.1218746110

We have included most of these references in the revised manuscript.

G. References: appropriate credit to previous work?
No issues, aside from those listed above.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions
Very clearly presented. Any issues are covered above.

Appendix: validation studies 1-5

Study 1: Comparing dental maturation scores with dental growth characteristics

Reviewer #1 raised the question of whether DMS scores are a realistic and reliable measure of actual dental growth characteristics. Graph 1.1A visualizes crown and root extension profiles in human canine teeth (data from [8]). Broadly speaking, crown extension follows an "exponential-like" trajectory (fast-to-slow saturation function), while root extension follows a "logistic-like" trajectory (slow-fast-slow sigmoid saturation function). Graph 1.1B visualizes the unequal temporal spacing of the stages in a 10-stage dental maturation scoring (DMS) system (M2 data from [9]). Interestingly, the non-linear growth characteristics in Graph 1.1A are fairly well reflected by the non-linearities of the DMS system in Graph 1.1B. This indicates that DMS does not just measure dental shape change, but tracks crown and root extension characteristics fairly well.

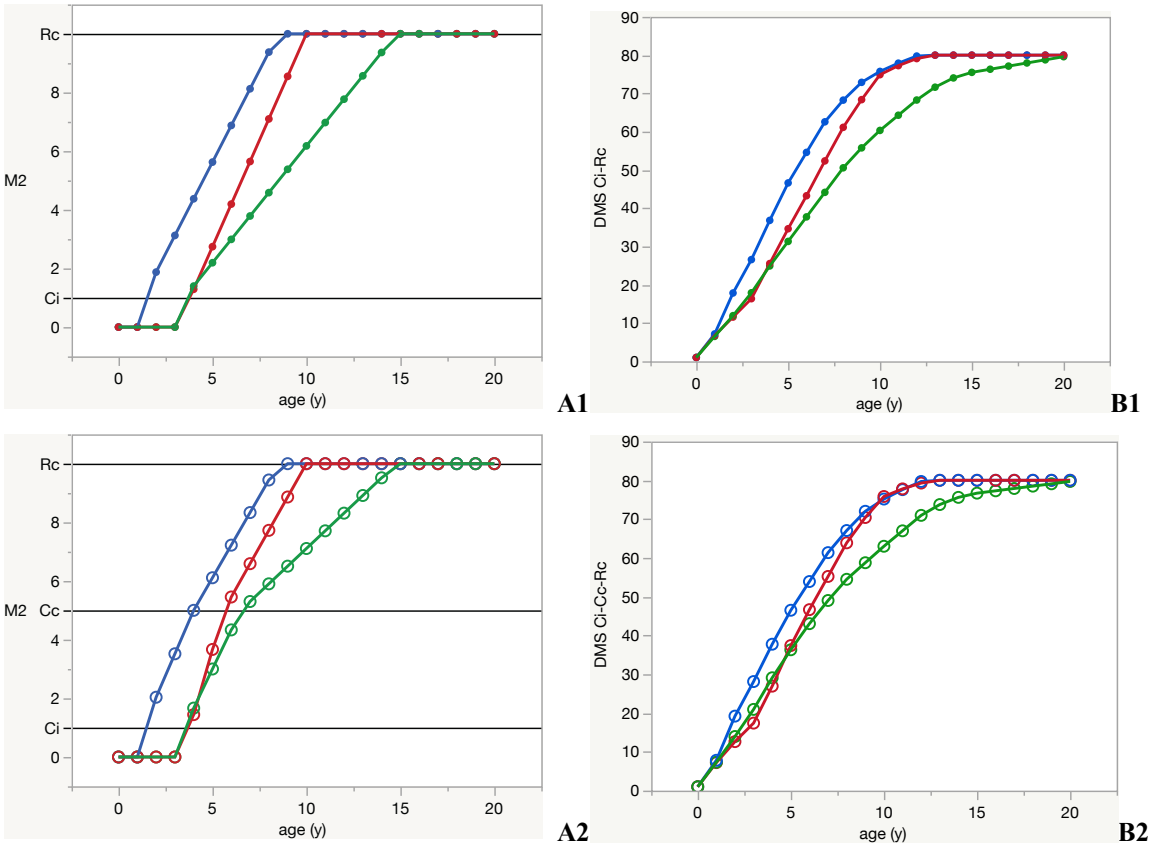
[REDACTED]

Graph 1.1. **[REDACTED]**

The analyses presented in Graph 1.2 (see below) address the question whether different assumptions about individual dental growth characteristics influence the DMS profile of the dentition as a whole. We used ages at Ci, Cc, Rc for chimpanzees, humans and Dmanisi to model two types of dental growth trajectories:

- Model 1: In this model, only the time points of Ci and Rc are known. Each tooth grows linearly from crown initiation (Ci, score=1) to root completion (Rc, score=10).
- Model 2: In this model, the time points of Ci, Cc and Rc are known. Each tooth grows according to a two-piece linear function: from Ci (score=1) to Cc (crown completion, score=5), and from Cc to Rc (score=10).

In both models, the DMS profiles of the entire dentition show the same characteristics as in Figure 3b (main text). This demonstrates that even quite limited data about tooth formation (e.g. onset/offset ages) yield reliable information about taxon-specific maturation rates of the dentition as a whole.

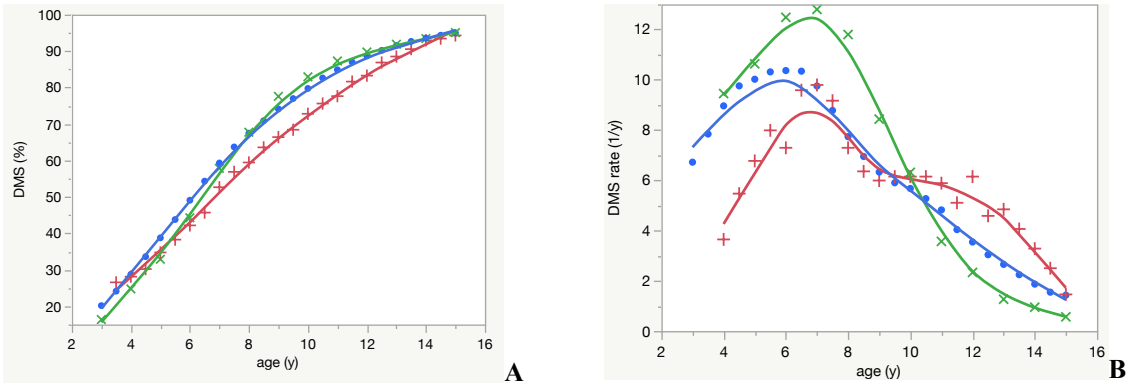


Graph 1.2. Tooth growth models and resulting DMS profiles of the dentition of humans (green), Dmanisi (red) and chimpanzees (blue). **A1:** Linear tooth growth function from age at crown initiation (Ci, score = 1) to age at root completion (Rc, score = 10); data for M2. **A2:** Piecewise linear tooth growth function with two segments: from Ci to crown completion (Cc, score = 5), and from Cc to Rc; data for M2. Note that non-linearities around start and end points (Ci and Rc) are due to roundoff errors of the 0.5-year interpolation function. **B1** and **B2**: DMS profile resulting from the summation of the DMS profiles of all teeth (I1 to M3) in **A1** and **A2**.

Study 2: Dental maturation profiles and DMS rate peak evaluation.

Reviewer #1 stated that "comparisons of shapes/scores cannot yield meaningful developmental rates" and that "it simply isn't tenable to infer comparative maturation peaks (Figure 3c)…" from the DMS data.

To assess the influence of different scoring schemes on the evaluation of the DMS rate peak (i.e., the "dentition growth spurt", DGS), we compared dental maturation data from three independent studies on Finnish children [9-11]. These studies use different scoring schemes, and different tooth arrays (including/excluding M3). Graph 2A shows the resulting DMS profiles, Graph 2B shows that the DMS rate peaks are at similar locations along the age axis. This indicates that the DMS rate peak is a stable property of a population's dental maturation profile and robust to differences in scoring schemes.



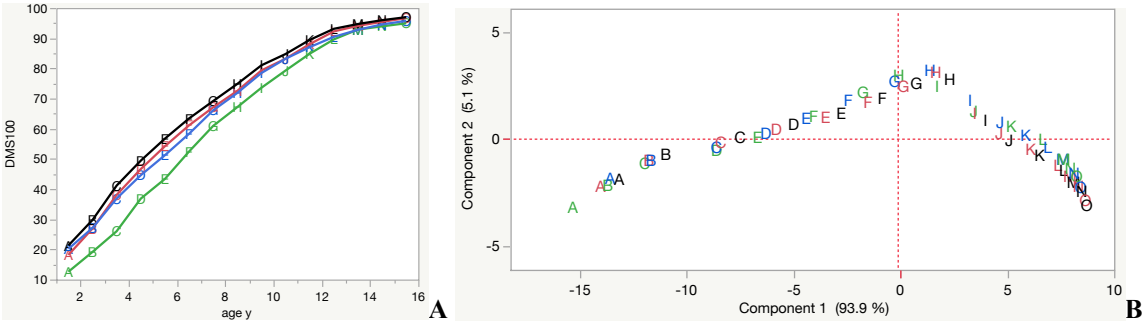
Graph 2. Dental maturation profiles of three different samples of Finnish children. **A**: total DMS vs. age. **B**: DMS instantaneous rate vs. age. Red: data from Haavikko (1970) [9], 10-stage DMS system, 8 teeth. Green: data from Nyström et al. (1986) [11], Demirjian 8-stage DMS system, 7 teeth (I1-M2). Blue: data from Nyström et al. (2007) [10], Demirjian system, only stages 1-7, 8 teeth. Although DMS-vs-age profiles differ between analyses, the timing of the rate peaks is similar: at ~6 years in the most recent sample (Nyström et al., 2007 [10]) and at ~7 years in the earlier samples (Haavikko, 1970 [10] and Nyström et al., 1986 [11]).

Study 3: Influence of scoring schemes and imaging methods on dental ontogenetic trajectories

As a complement to Study 2, we investigated how different scoring schemes and different imaging methods influence the dental maturation paths. We used data from two independent studies on Finnish children also used in Study 2 [9,10] to evaluate DMS-vs-age profiles (Graph 3A). Also, we performed a PCA on the dental maturation data of all individual teeth (I1-M3) at any given age (Graph 3B). Results show that different scoring schemes yield different DMS-vs-age profiles, and that standardization leads to good correspondence between different data sets.

We also assessed the influence of imaging methods (clinical/dental radiography versus slice-based tomography). To this end, we recoded the Haavikko 1970 data [9] from radiographic to histological scores, using the conversion scheme presented in [4]. Results confirm earlier findings that slice-based DMS-vs-age profiles are consistently more advanced than radiography-based profiles [4]. However, the dental maturation trajectories through PCA space largely coincide, despite differences in imaging and scoring systems.

Regarding Dmanisi, we can learn the following: Even if we had not recalibrated the DMS data from tomography to radiography standards, we would still have been able to observe the "human-like" pattern in the DMS-PCA space. On the other hand, the recalibration yields a DMS-vs-age profile of Dmanisi that is directly comparable to the radiography-based profiles of humans and chimpanzees.

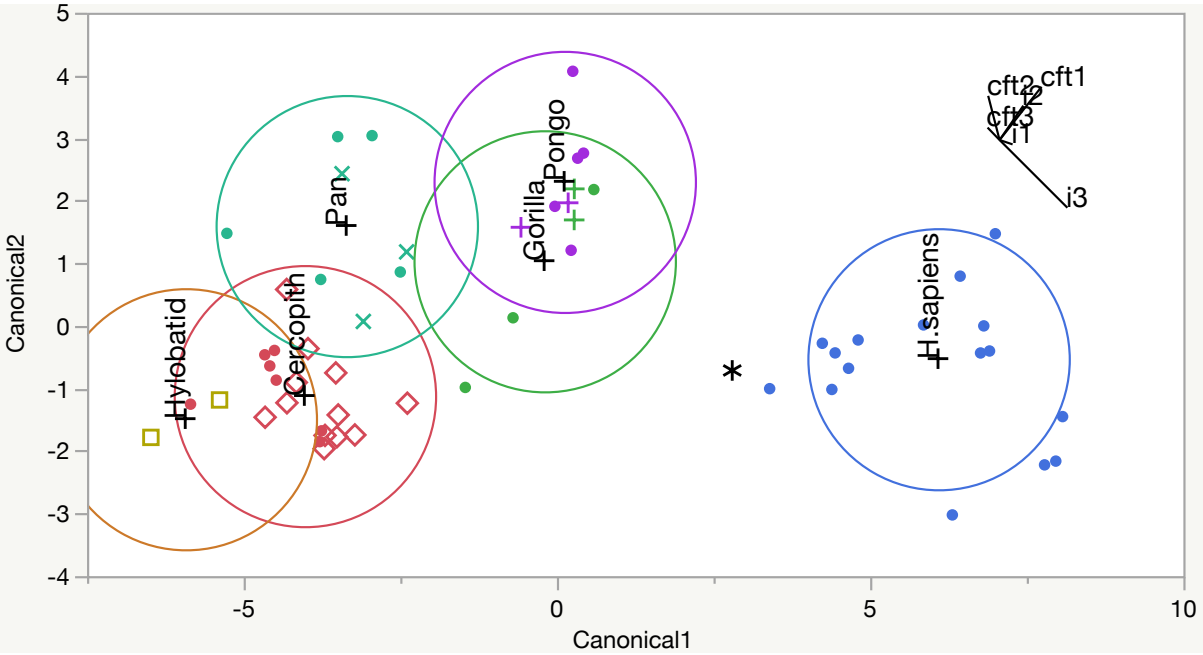


Graph 3. Influence of scoring schemes and imaging modalities on the dental maturation trajectories of Finnish children. **A**: DMS of the total dentition versus age in years. **B**: DMS-PCA of the maturation data of all teeth (I1-M3) at given ages (A-O denote 1-year groups from 1.5 to 15.5 years). Blue: 8-stage (Demirjian) radiography-based DMS data from Nyström et al. (2007) [10]. Green: 10-stage radiography-based DMS data from Haavikko 1970 [9]. Red: Haavikko 1970 radiography-based data recoded to 8-stage system. Black: Haavikko 1970 data recoded to (simulated) histological 8-stage scores (using the conversion tables provided in Gunz et al. 2020 [4], SI). Graph **A** shows that recoding of the original Haavikko 1970 data (green → red) results in good correspondence with the Nyström data [10] (blue). Tomography-based DMS scores (black) are consistently more advanced than radiography-based scores (red). Graph **B** shows that all trajectories through PC space largely coincide, but differ in advancement along the trajectory for any given age.

Study 4: Identification of taxon-specific characteristics of molar crown development

Reviewer #1 mentioned various factors that potentially hamper the identification of taxon-specific dental maturation characteristics: methodology (e.g. radiography versus histology), wide intraspecific variability of developmental traits that blurs between-group differences (e.g. in crown formation times), features thought to be typical for humans but also present in other taxa (e.g. gaps between successive molar crown formation periods).

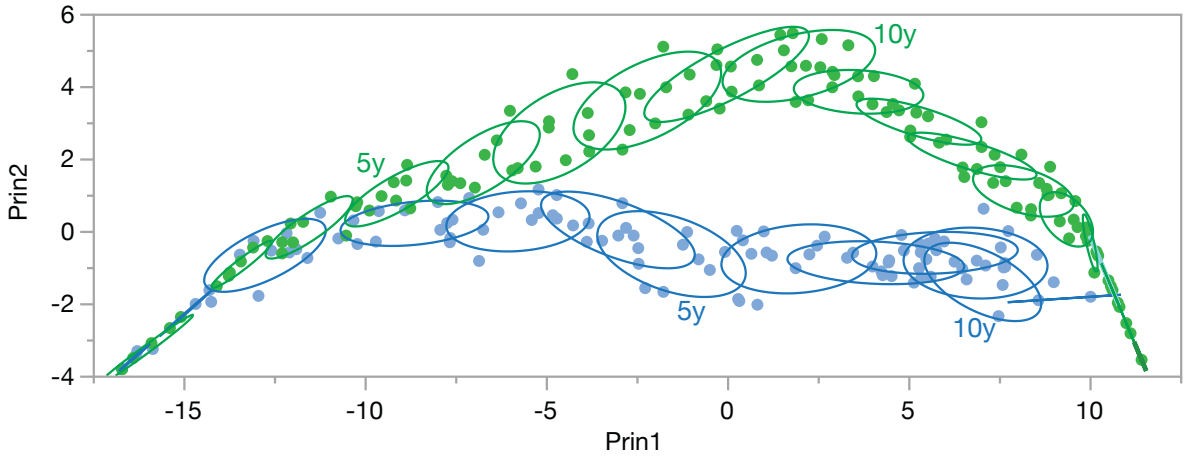
To assess the magnitude of these effects, we collected data on molar crown initiation/completion and root completion (Ci, Cc and Rc) from the literature, for humans and non-human primates (great apes, hylobatids and cercopithecids). Graph 3 shows the results of a canonical variate analysis (CVA) on these variables. CVA clearly separates humans from non-human primates, while potential methodological biases do not blur group differences. Dmanisi (star in Graph 3) is more closely associated with humans than with great apes and other non-human primates. Radiographic and histological data for chimpanzees form a single cluster. Gorillas/orangutans are closer to humans than are chimpanzees, reflecting the more delayed molar maturation schedule compared to chimpanzees, as mentioned by reviewer #1. We agree with reviewer #1 that "*several of these [dental maturation] variables are similar to modern humans, representing examples of convergent evolution"* (ref. [5], abstract). The additional benefit of the analysis presented here is that it reveals the convergence effects but also confirms the general great-ape pattern of orangutan molar maturation.



Graph 4. Canonical variate analysis of molar crown formation characteristics in humans, great apes, hylobatids and cercopithecoids. The 6 variables used in this analysis are the crown initiation and formation times of the three molars: i1, cft1, i2, cft2, i3, cft3. Canonical components 1 and 2 account for 90.2% and 7.4% of the total variation in the sample, respectively. Circles represent 50% density distributions of the 6 pre-defined groups. Diamonds: baboons; ×: chimpanzees with temporal gaps between successive molar crown formation periods. +: Gorilla and orangutan data based on histological studies. Star: Dmanisi (no pre-defined group affiliation). The loading plot in the upper-right corner visualizes the orientation of the original variables in canonical space, indicating that canonical components 1 and 2 mostly account for variation in i1, and in cft1/cft2. Data are from [5,10,12-23].

Study 5: Intragroup variation along dental maturation trajectories.

This study investigates the variation in dental maturation patterns along taxon-specific ontogenetic trajectories. DMS-PCA was performed on known-age humans and chimpanzees (same methodology as in Study 3). Results are visualized in Graph 5, which shows overlap between 1sdev-density ellipses around consecutive age classes. The variation within 1-year age groups along trajectories tends to be larger than the potential age bias introduced by different DMS methods (see Graph 3).



Graph 5. DMS-PCA on I1-M3 dental maturation data of known-age humans (green) and known-age chimpanzees (blue). Density ellipses (1 sdev) are drawn around 1-year age classes.

References

1 Boughner, J. C., Der, J. & Kuykendall, K. L. A multivariate approach to assess variation in tooth mineralization using free-lived and captive-raised chimpanzees (*P. troglodytes*). *Am J Phys Anthropol* **158**, 452-462 doi:10.1002/ajpa.22800 (2015).

2 Kuykendall, K. L. in *The Forgotten Lineage(s): Paleobiology of Paranthropus* (eds P.J. Constantino, K.E. Reed, & B.A. Wood) 1-52 (Springer Nature, 2020).

3 Smith, T. M. *et al*. Dental ontogeny in Pliocene and Early Pleistocene hominins. *PLoS One* **10**, e0118118 doi:10.1371/journal.pone.0118118 (2015).

4 Gunz, P. *et al*. *Australopithecus afarensis* endocasts suggest ape-like brain organization and prolonged brain growth. *Sci Adv* **6**, eaaz4729 doi:10.1126/sciadv.aaz4729 (2020).

5 Smith, T. M. Dental development in living and fossil orangutans. *Journal of Human Evolution* **94**, 92-105 doi:10.1016/j.jhevol.2016.02.008 (2016).

6 Dean, M. C. & Liversidge, H. M. Age estimation in fossil hominins: comparing dental development in early *Homo* with modern humans. *Ann Hum Biol* **42**, 415-429 doi:10.3109/03014460.2015.1046488 (2015).

7 Bogin, B. Evolutionary hypotheses for human childhood. *Am J Phys Anthropol* **104**, 63-89 (1998).

8 Dean, M. C., Liversidge, H. M. & Elamin, F. Combining radiographic and histological data for dental development to compare growth in the past and the present. *Annals of Human Biology* **41**, 336-347 doi:10.3109/03014460.2014.922614 (2014).

9 Haavikko, K. The formation and the alveolar and clinical eruption of the permanent teeth. An orthopantomographic study. *Proc Finn Dent Soc* **66**, 103-170 (1970).

10 Nyström, E. M., Ranta, M. H., Peltola, S. J. & Kataja, M. J. Timing of developmental stages in permanent mandibular teeth of Finns from birth to age 25. *Acta odontologica Scandinavica* **65**, 36-43 doi:10.1080/00016350600965900 (2007).

11 Nyström, M. *et al*. Dental maturity in Finnish children, estimated from the development of seven permanent mandibular teeth. *Acta Odontol Scand*. **44**, 193-198 doi:10.3109/00016358608997720 (1986).

12 Beynon, A. D., Dean, M. C. & Reid, D. J. Histological study on the chronology of the developing dentition in gorilla and orangutan. *American Journal of Physical Anthropology* **86**, 189-203 doi:DOI 10.1002/ajpa.1330860208 (1991).

13 Anemone, R. L., Mooney, M. P. & Siegel, M. I. Longitudinal study of dental development in chimpanzees of known chronological age: Implications for understanding the age at death of Plio-Pleistocene hominids. *Am J Phys Anthropol* **99**, 119-133 (1996).

14 Kuykendall, K. L. Dental development in chimpanzees (*Pan troglodytes*): The timing of tooth calcification stages. *Am J Phys Anthropol* **99**, 135-157 (1996).

15 Dirks, W., Reid, D. J., Jolly, C. J., Phillips-Conroy, J. E. & Brett, F. L. Out of the mouths of baboons: Stress, life history, and dental development in the Awash National Park hybrid zone, Ethiopia. *American Journal of Physical Anthropology* **118**, 239-252 doi:https://doi.org/10.1002/ajpa.10089 (2002).

16 Swindler, D. R. *Primate dentition: an introduction to the teeth of non-human primates*. Vol. 32 (Cambridge University Press, 2002).

17 Reid, D. J. & Dean, M. C. Variation in modern human enamel formation times. *Journal of Human Evolution* **50**, 329-346 doi:https://doi.org/10.1016/j.jhevol.2005.09.003 (2006).

18 Dirks, W. & Bowman, J. E. Life history theory and dental development in four species of catarrhine primates. *Journal of Human Evolution* **53**, 309-320 (2007).

19 Blenkin, M. & Taylor, J. Age estimation charts for a modern Australian population. *Forensic science international* **221**, 106-112 doi:https://doi.org/10.1016/j.forsciint.2012.04.013 (2012).

20 Esan, T. A., Yengopal, V. & Schepartz, L. A. The Demirjian versus the Willems method for dental age estimation in different populations: A meta-analysis of published studies. *PLoS One* **12**, e0186682 doi:10.1371/journal.pone.0186682 (2017).

21 Kralick, A. E. *et al*. A radiographic study of permanent molar development in wild Virunga mountain gorillas of known chronological age from R wanda. *American Journal of Physical Anthropology* **163**, 129-147 (2017).
22 Lemmers, S. A. M. *Stress, life history and dental development: a histological study of mandrills (Mandrillus sphinx)*, Durham University, (2017).
23 Hu, R. & Zhao, L. Molar crown formation times of fossil orangutan molars from Guangxi, China. *American Journal of Physical Anthropology* **174**, 315-326 doi:https://doi.org/10.1002/ajpa.24183 (2021).

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

The experimental design of this study is founded on previous reported associations between dental development and life history, yet none of these approaches support the authors' interpretation of an 'extended childhood' in this fossil.

The seminal paper by Holly Smith (1989) (ref 3) found strong associations between first molar tooth (M1) eruption, age at the completion of the dentition, and several life history variables across a wide sample of primates. Here the estimated age of M1 eruption of the Dmanisi individual is reported to be "more similar to that observed in wild chimpanzees than in humans (p. 6 line 185)." The estimated age at the completion of the dentition is also reported to be "more similar to chimpanzees and other great apes than to modern humans (p. 6 line 187)." Thus, by Holly Smith's logic (which Chris Dean employs in refs 4 and 10), *this fossil is not human-like in its early or late tooth formation, nor its life history.*

Gabriele Macho (2001: American Journal of Primatology 55:189–201) reported an association between molar crown formation and primate life history, building on Smith's work in her abstract: "It seems counterintuitive that one aspect of dental development should be correlated with life-history variables, whereas the other should not." An extrapolation of Dmanisi molar crown formation times (from Figure 2b) are approximately 1/2 to 2/3 of the duration of modern human times. Here again Dmanisi is more similar to chimpanzees than to modern humans, and this holds for all molars. By Macho's (2001) logic, *this fossil is not human-like in its early or late molar crown formation, nor its life history.*

Tanya Smith and colleagues (refs 5, 11, 29, 54) employed tooth calcification standards to compare chimpanzees, australopiths, Neanderthals, and modern humans, finding differences amongst all groups. The Dmanisi M3s are the only teeth that can be scored in such a manner, matching the M3 calcification stage of a 11.4 year-old Taï Forest chimpanzee—which had yet to complete formation of several of its anterior and posterior teeth. *In this regard, Dmanisi shows more rapid development than a wild chimpanzee*, whilst modern humans typically attain these M3 calcification stages between ~15-17 years of age.

Most recently Hogg and colleagues (ref 26) conducted a comparative study of dental long-period line periodicities as a theoretical reflection of the process that "regulates metabolic output, growth rates, and lifespan among other life history characteristics" (p. 2). Here Dmanisi's periodicity falls at the low end of all hominin (and hominoid) values, and by the logic of this paper, *its' life history is more akin to Australopithecus and Paranthropus, as well as fossil members of the genus Homo, than to modern humans*.

These aspects of dental development uniformly support a more primitive interpretation consistent with its small brain size—*an even more robust life history proxy* (ref 2; also see Isler & van Schaik, 2009). The authors instead emphasize comparisons of sequential anatomical growth stages termed dental maturity scores (DMS). Critically, they do not establish how such scores actually reflect aspects of childhood development or life history more broadly. Others have shown that these

scores are only moderately correlated with skeletal development, peak height velocity, and age at menarche amongst living humans (Demirjian et al. 1985; Lewis 1991; Seselj 2013), and the PCA analysis of DMS in Figure 3b does not distinguish great ape genera *despite their well-documented life history variation* (ref 1), undermining inferences about Dmanisi's life history from these same patterns.

Ontogenetic transitions among members of the same genus may resemble one another due to close phylogenetic relationships, and Dmanisi's tooth sizes and shapes are more similar to living humans than to great apes—meaning that they would be expected to pass through similar stages to reach a similar end point. In other words, the developmental patterns of hominins with small canines and non-sectorial premolars should differ from great apes with different dental anatomy. These differences are not due to life history variation.

In summary, without a comparative basis establishing that dental maturity scores/patterns are actually predictive of life history variation in great apes and humans, and an explanation for why other dental and cranial life history proxies are contradictory, this study does not establish that Dmanisi had an 'extended childhood,' nor that "The derived mode of dental ontogeny in early *Homo* (represented by Dmanisi and Nariokotome) probably indicates a further prolongation of brain growth and maturation but only little delay in reaching dental/somatic maturity (p. 8 lines 231-234)."

Demirjian A, Buschang PH, Tanguay R, Patterson DK. 1985. Interrelationships among measures of somatic, skeletal, dental and sexual maturity. Am. J. Orthod. 88:433–38

Isler, K., van Schaik, C.P. 2009. The Expensive Brain: A framework for explaining evolutionary changes in brain size. J. Hum. Evol. 57: 392–400

Lewis AB. 1991. Comparisons between dental and skeletal ages. Angle Orthod. 61:87–92

Seselj M. 2013. Relationship between dental development and skeletal growth in modern humans and its implications for interpreting ontogeny in fossil hominins. Am. J. Phys. Anthropol. 150:38–47

Referee #2 (Remarks to the Author):

As this is a re-review, I will not comment on A-H, but only on some additional points because I feel this is a thoughtful and thorough revision. So, here are my few comments:

Abstract:
First line: "Human life history is characterized by an extended period of immaturity in which prolonged cerebral maturation contrasts with delayed somatic maturation 1."

This sentence is unclear to me. Perhaps something like this better captures the idea? “Human life history is characterized by an extended period of immaturity during which there is a disjunction between cerebral and somatic growth rates.”

Manuscript Line 55
Change “permitting to temporally….” to “permitting researchers to use dental growth chronologies to calibrate…”

Manuscript Lines 240-242. The authors speculate that the *Homo* pattern of dental ontogeny might reflect a dietary shift to omnivory. Do they specifically mean the inclusion of more meat in the diet, because omnivory can mean a lot of things. If so, then exactly why do they think that the inclusion of more meat in the diet would have this selective effect?

The entire last paragraph of the discussion is speculative. I’d like to see clearer acknowledgement of the speculative nature of these ideas, which at the moment build a complex scenario (three generations, alloparenting, increase in reproductive success) based on little direct evidence.

The statistical analysis seems fine.

Referee #3 (Remarks to the Author):

In my view, the authors have made a concerted, objective and fair effort to address the comments of all three reviewers, some of which overlap in topic or content. They have re-worked extensive sections of the analysis and of the text in order to address those comments. Their exemplary attitude in addressing the comments is very open, objective and gracious toward the reviewers, which is fantastic to see.

I appreciate the revision of the discussion in particular, which takes into account comments and suggestions of the different reviewers, and presents an alternative to the linear 'ape to human' dental ontogeny evolutionary scenario involving more diversity in life history schedules among both extinct and extant species.

A couple of minor wording changes that I would suggest if they are in line with the authors' intended message:

line 195 - suggest change to: Paranthropus demonstrates a mode of dental ontogeny 'not found' ... (vs. 'no longer found')? - i.e., Paranthropus may have followed a unique dental ontogenetic pattern, unlike modern apes.

line 229 - a prolonged phase of postnatal brain growth and maturation... suggest adding 'compared to extant apes'??

All in all, I am satisfied that the authors have taken in to account the reviewers comments, and recommend that the revised manuscript be accepted for publication in Nature.

Author Rebuttals to First Revision:

Response to all referees:

We would like to thank the referees for the second round of comments on our manuscript. Referees #1 and #2 raised concerns about the speculative nature of the last paragraph of the discussion. We have revised the discussion accordingly, placing more emphasis on the diversity of fossil hominin life histories and highlighting the great ape-like versus human-like aspects of Dmanisi's dental ontogeny and inferred life history. We refrain from proposing scenarios of life history evolution from Dmanisi to modern humans. Rather, we conclude the discussion by suggesting that the extended childhood of early *Homo* evolved before a substantial increase in brain size and a general slow-down of life history.

In our responses below, we have taken particular care to highlight the differences between referee #1's views and our own, and have therefore gone into detail on each point raised. The basic question that has arisen repeatedly is whether lists of ontogenetic traits should be compared item by item, or all traits together in comparative multivariate analyses of ontogenetic trajectories. In our opinion, the latter approach provides a more comprehensive comparative picture of the dental ontogenies of fossil and extant taxa.

All changes made to the previous version of the manuscript are marked with the track function.

Response to referee #1

Referee #1 (Remarks to the Author):

Authors' note: For the sake of clarity, we have numberws each of the points raised by the referee.

(1) The experimental design of this study is founded on previous reported associations between dental development and life history, yet none of these approaches support the authors' interpretation of an 'extended childhood' in this fossil.

We agree with the referee that none of the traditional, typically univariate, approaches to establishing links between fossil hominin dental development and life history provides evidence for an extended childhood phase in the Dmanisi fossil. For this reason, we attempted to go one step further and use multivariate techniques (DMS-PCA and total DMS vs. age trajectories) to search for integrated patterns of dental ontogeny that have not been previously described and to explore their relationships with life history. Using this approach, our study is the first to reconstruct the full DMS vs. age profile for an individual fossil hominin (Fig. 4) and to show a clear difference between *Homo* and great ape patterns of dental ontogeny (Fig. 3b).

The difference between referee #1's perspective and ours is best illustrated by the following thought experiment: Suppose that the Dmanisi individual had already died at the age of 4 years. The dental record up to that age would suggest that its dentition had developed like that of a modern human, both in terms of pattern (Fig. 3) and rate (Fig. 4). On the other hand, if we only had the snapshot of dental ontogeny at Dmanisi's actual age at death of 11.4 years, both the pattern (Fig. 3) and the rate (Fig. 4) would be interpreted as virtually indistinguishable from those of great apes, which is referee #1's perspective. Our perspective is that we need the full ontogenetic trajectory and the full multivariate data on dental ontogeny to obtain the complete picture.

(2) The seminal paper by Holly Smith (1989) (ref 3) found strong associations between first molar tooth (M1) eruption, age at the completion of the dentition, and several life history variables across a wide sample of primates. Here the estimated age of M1 eruption of the Dmanisi individual is reported to be "more similar to that observed in wild chimpanzees than in humans (p. 6 line 185)." The estimated age at the completion of the dentition is also reported to be "more similar to chimpanzees and other great apes than to modern humans (p. 6 line 187)." Thus, by Holly Smith's logic (which Chris Dean employs in refs 4 and 10), *this fossil is not human-like in its early or late tooth formation, nor its life history.*

Indeed, when comparing selected single variables such as age at M1 eruption or age at completion of the dentition, Dmanisi appears more similar to chimpanzees than to humans. However, as mentioned in point 1 and illustrated in the thought experiment, the entire dental ontogenetic record must be considered in order to draw comparative inferences. Our analyses show that - within an ape-like time frame for the formation of the entire dentition - there appear to be shifts in the maturation trajectories of the different tooth types relative to each other. Our argument is that these evolutionary changes in dental ontogeny indicate changes in dietary ontogeny and life history.

(3) Gabriele Macho (2001: American Journal of Primatology 55:189–201) reported an association between molar crown formation and primate life history, building on Smith's work in her abstract: "It seems counterintuitive that one aspect of dental development should be correlated with life-history variables, whereas the other should not." An extrapolation of Dmanisi molar crown formation times

(from Figure 2b) are approximately 1/2 to 2/3 of the duration of modern human times. Here again Dmanisi is more similar to chimpanzees than to modern humans, and this holds for all molars. By Macho's (2001) logic, *this fossil is not human-like in its early or late molar crown formation, nor its life history.*

Similar arguments apply here as for points 1 and 2: indeed, crown formation times in Dmanisi are short, even shorter than in typical chimpanzees, but focusing on selected univariate features does not reveal the relevant patterns. For example, one could argue with equal reason that the long gaps between M1-M2 and M2-M3 crown formation times indicate a human-like pattern of molar crown formation. The key point is that all these univariate features must be considered in relation to each other, as mentioned by Dean (2010). Also see our Study 4 in the previous round of reviews (multivariate analysis of molar crown initiation and formation times), which shows that Dmanisi has closer affinities to humans than to great apes.

(4) Tanya Smith and colleagues (refs 5, 11, 29, 54) employed tooth calcification standards to compare chimpanzees, australopiths, Neanderthals, and modern humans, finding differences amongst all groups. The Dmanisi M3s are the only teeth that can be scored in such a manner, matching the M3 calcification stage of a 11.4 year-old Taï Forest chimpanzee—which had yet to complete formation of several of its anterior and posterior teeth. *In this regard, Dmanisi shows more rapid development than a wild chimpanzee*, whilst modern humans typically attain these M3 calcification stages between ~15-17 years of age.

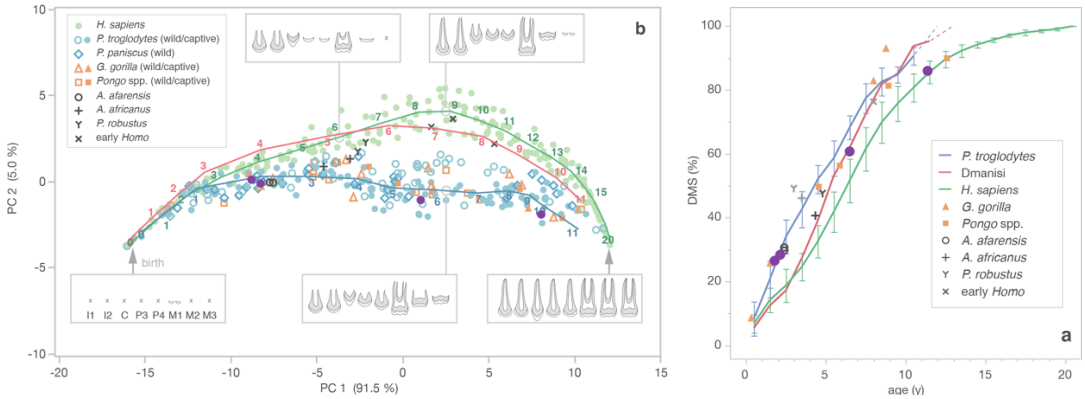
The Taï chimpanzees provide an interesting test case to illustrate the differences between the approaches of referee #1 and ours. In the analyses presented below, we consider all the available information on the dental ontogeny in the Taï chimpanzees and in Dmanisi: for the Taï population, all the DMS data for each individual at its age at death, and for Dmanisi all the reconstructed DMS data from birth to death (not just for M3 at the age at death, as suggested by referee #1).

To do so we include the DMS data published in Smith et al. (2010; Table 3, immature individuals with complete dentition) in our comparative analyses of Fig. 3b and Fig. 4a (see graphs below). The DMS-PCA plot shows that all these Taï individuals exhibit a typical great ape pattern of dental ontogeny. The DMS-vs-age plot shows that the two younger individuals follow the fast rate trajectory characteristic of young chimpanzees, while the two older individuals suggest a slow rate of late maturation in the Taï chimpanzees (>1 sdev below the chimpanzee mean). The significant deviation from the mean trajectory during the late maturation phase could be further investigated: does it reflect wild-vs-captive differences and/or population-specific differences? This is in line with Smith et al.'s (2010: p. 372) conclusion: "Parallels between environmental variation, hormonal variation, and tooth development represent an interesting area worthy of further study".

Regarding direct comparisons between Dmanisi and the 11.4 year-old Taï chimpanzee (called "Kana"), we can state the following: As noted by referee #1 (and indicated by the DMS-vs-age plot), "Dmanisi shows more rapid development" than Kana. This is true as long as we compare the two at the age of 11.4 years. However, the comparative data from the ~2 year-old Taï individuals suggest that Kana at ~2 years of age would have shown more rapid development than Dmanisi. Furthermore, the referee states above that Kana "had yet to complete formation of several of its anterior and posterior teeth". DMS-PCA shows that this pattern is not unusual, but a characteristic of chimpanzees with incomplete M3 formation.

These analyses show that, on the one hand, comparisons of M3 calcification in Dmanisi and chimpanzee individuals appear to be straightforward because the same variable is being measured. On the other, however, a closer look reveals that this is like comparing apples and oranges, given the significant *Homo-Pan* differences in ontogenetic patterns of the dentition.

Overall, and as already outlined in our responses to points 1 - 3, focusing on a single trait does not tell the whole story.



DMS data of Taï chimpanzees, included in Figures 3b (left) and 4a (right). The Taï individuals are represented by purple dots (from left to right: Leonardo, age at death 1.77 years; Bambou, 2.13 y; Goshu, 6.54 y; Kana, 11.39 y). Data from Smith et al. 2010, Table 3.

(5) Most recently Hogg and colleagues (ref 26) conducted a comparative study of dental long-period line periodicities as a theoretical reflection of the process that "regulates metabolic output, growth rates, and lifespan among other life history characteristics" (p. 2). Here Dmanisi's periodicity falls at the low end of all hominin (and hominoid) values, and by the logic of this paper, *its' life history is more akin to Australopithecus and Paranthropus, as well as fossil members of the genus Homo, than to modern humans*.

Statistically speaking, the referee's logic is flawed: comparing the long-periodicity (LP) value of the Dmanisi specimen with the taxon-specific LP mean values of Hogg et al. confuses individual-level and population-level inferences. As shown by Hogg et al., there is substantial within-taxon variation in LP values (with a concentration on the range of 6 to 9 days for fossil hominins and living humans). The fact that the LP of Dmanisi (6 days) is at the lower end of the total variation does not mean that it represents a population with a low long-periodicity mean value.

(6) These aspects of dental development uniformly support a more primitive interpretation consistent with its small brain size—*an even more robust life history proxy* (ref 2; also see Isler & van Schaik, 2009). The authors instead emphasize comparisons of sequential anatomical growth stages termed dental maturity scores (DMS). Critically, they do not establish how such scores actually reflect aspects of childhood development or life history more broadly. Others have shown that these scores are only moderately correlated with skeletal development, peak height velocity, and age at menarche amongst living humans (Demirjian et al. 1985; Lewis 1991; Seselj 2013), and the PCA analysis of DMS in Figure 3b does not distinguish great ape genera *despite their well-documented life history variation* (ref 1), undermining inferences about Dmanisi's life history from these same patterns.

Brain size as a life history proxy: Absolute brain size is indeed a good predictor of the overall pace of life history. However, adult absolute brain size does not tell anything about potential shifts of life history phases within the more general framework of slow versus fast life histories. Brain growth trajectories are more informative in this respect (see e.g. Gunz et al. 2020).

Use of DMS data: Contrary to the perception of referee #1, DMS data are widely used in comparative studies of dental ontogeny and life history, because they capture key ontogenetic stages such as crown and root initiation and completion. Referee #1 actually makes extensive use of DMS data in point 3 (crown formation time = crown completion - crown initiation) and

point 4 (M3 stages). We agree with referee #1 that single DMS variables are unlikely to reflect aspects of life history. However, as we outline in the discussion section, the ensemble of all DMS data is informative about life history-related shifts in dental maturation, which are likely related to changes in masticatory function during an individual's development. These, in turn, reflect changes in the duration of life history phases.

Correlation between DMS data and variables measuring skeletal and sexual maturity: In modern humans, the moderate correlation of total DMS with skeletal ontogeny and reproductive maturation is basically not surprising for several reasons.

1) The studies cited here (Demirjian et al. 1985; Lewis 1991; Seselj 2013) are on humans alone, while the studies cited further above (H. Smith, Hogg, etc.) look at correlations between dental ontogeny and life history above the species level, not within species. As shown by Klingenberg (2014), correlations evaluated at different taxonomic levels typically yield different results regarding integration (high correlation) versus modularity (low correlation). The dentition, cranium, postcranial skeleton, reproductive system etc. represent fairly independent developmental modules. Current research on this topic indicates that intraspecific developmental modularity is more expressed in humans than in great apes, which is typically interpreted as enhanced developmental and life history plasticity that allows human populations to cope with a large variety of environmental conditions (see e.g. Dean & Cole 2013, Gómez-Robles et al. 2017).
2) A closer look at the three studies cited by referee #1 shows a complex picture of correlations between dental and other developmental markers that does not support the arguments of referee #1.
    a. Demirjian et al. (1985) compare individual attainment ages (ages at attaining specific dental, skeletal and sexual maturation stages). The study concludes that "temporary disharmonies between dental and somatic/skeletal development might be expected". This is consistent with the above observations on modularity in humans (Klingenberg 2014). Also, the low correlation between dental and somatic/skeletal attainment ages may reflect a limitation of the study design: as a dental developmental marker, the study used "age at 90% dental maturity", which captures only the last stage of total dental developmental variation.
    b. Lewis (1991) uses an alternative approach, comparing estimates of dental and skeletal age in individuals of known chronological age. The author states that *estimated* ages (i.e., proxies of dental and skeletal maturation) differ from *chronological* age by up to three years. However, the correlation between dental and skeletal age estimates is still between R^2=0.67 (boys) and R^2=0.79 (girls). Given the large error introduced by the estimation procedures themselves (which the author himself considers suboptimal), the reported R^2 values are quite high.
    c. Seselj (2013; p. 43) concludes that "the relationship between dental development and skeletal growth *when controlling for age* appears at most to be moderate, … Therefore, in modern humans it may be misleading to use one developmental system (either dental or skeletal) as a proxy for the other." However, this inferential logic confuses population-level and individual-level inferences (also see our response to point 5): At the individual level (i.e., controlling for age; see the partial correlation analysis of Seselj's Fig. 1B on p. 42) it is indeed not possible to accurately predict dental from skeletal markers or vice versa. However, at the population level (see standard correlation analysis of Seselj's Fig. 1A on p. 42), dental and skeletal developmental markers are closely correlated (R^2~0.9, our estimate from re-digitized data of Seselj's Fig. 1A). These are the data that are relevant for interspecific comparative analyses and life history inferences, and they contradict the conclusions of reviewer #1.

DMS-PCA and discrimination between great ape genera: We agree with referee #1 that the DMS-PCA study does not distinguish between great ape genera despite well-documented life history variation. However, this seemingly "negative" result is an important positive one:

it shows that there is a common pattern of tooth development in great apes that can serve as a reference for characterizing the derived *Homo* pattern in our Fig. 3b. The differentiation between great ape genera (along the lines of the studies cited by referee #1) is evident in our Fig. 4a, with orangutans (and the Taï chimps; see above) on the slow side.

(7) Ontogenetic transitions among members of the same genus may resemble one another due to close phylogenetic relationships, and Dmanisi's tooth sizes and shapes are more similar to living humans than to great apes—meaning that they would be expected to pass through similar stages to reach a similar end point. In other words, the developmental patterns of hominins with small canines and non-sectorial premolars should differ from great apes with different dental anatomy. These differences are not due to life history variation.

We agree with referee #1 that similar ontogenetic transitions may reflect close phylogenetic relationships. However, three points need to be considered:

1) Technically speaking, all possible DMS-PCA (not just the Dmanisi and human trajectories) trajectories converge to one and the same endpoint (i.e., 100% maturity of all tooth types).
2) Our data effectively falsify the referee's hypothesis: *Australopithecus africanus*, which has small canines and non-sectorial premolars shows a great ape-like pattern of dental ontogeny.
3) The derived *Homo* pattern of dental ontogeny is unlikely to be a neutral phylogenetic marker; it is more likely to reflect adaptive functional changes (mastication, timing of deciduous tooth replacement, reduced secondary sexual dimorphism, etc.), which in turn are related to changes in diet and life history.

(8) In summary, without a comparative basis establishing that dental maturity scores/patterns are actually predictive of life history variation in great apes and humans, and an explanation for why other dental and cranial life history proxies are contradictory, this study does not establish that Dmanisi had an 'extended childhood,' nor that "The derived mode of dental ontogeny in early Homo (represented by Dmanisi and Nariokotome) probably indicates a further prolongation of brain growth and maturation but only little delay in reaching dental/somatic maturity (p. 8 lines 231-234)."

Technically speaking, none of the studies of dental ontogeny in living species published to date have been predictive of life history variation, but rather correlative. In fact, as we argued in our reply to point 6, DMS data and DMS patterns are regularly used in the literature to explore correlations between dental ontogeny and life history, and these correlations are then used to infer life history traits of fossil species. Therefore, contrary to the referee's view, our DMS pattern and rate data are indeed consistent with published data on correlations between dental ontogeny and life history in great apes and humans. We believe that seemingly contradictory life history proxies actually indicate that the complex pattern of correlation between life history-related variables and life history variables is not yet fully understood. As one example, consider the development of the anterior permanent dentition (I1, I2, C) in great apes and humans: on an absolute time scale, there is large overlap between the great ape and human maturation trajectories of each of these teeth (see our Fig. 3a), especially when body size differences are accounted for (Zollikofer & Ponce de León 2010), such that correlations with the pace of life history cannot be established from these data alone. However, on a relative time scale (anterior versus posterior dentition), significant differences in dental maturation trajectories are revealed between great apes and humans (see our Fig. 3b) that correlate with life history differences.

Of course, it would be ideal to have a broader comparative basis, but it will take at least another decade or more to collect and analyze the respective data. The Dmanisi specimen is currently the only subadult individual for which a complete dental ontogenetic trajectory from

birth to death has been reconstructed. Such data do not yet exist for other fossil hominin specimens, nor for great ape and human individuals. In this sense, our study is typical of the way in which palaeoanthropology proceeds: Based on limited new evidence, new hypotheses are proposed, which are then tested with additional new data.

We agree with referee #1 (and with referee #2, who had similar reservations; see below) that inferences about the evolution of an extended childhood in fossil *Homo* remain ultimately hypothetical. We have therefore substantially revised our text to address this criticism. In the discussion section, we no longer propose a hypothetical evolutionary scenario leading from the life history of early *Homo* to that of living humans, but focus on possible evolutionary explanations of the differences between life history characteristics then and now.

In summary, our univariate analyses show that Dmanisi is more similar to great apes in some aspects of dental ontogeny, and more similar to humans in others. Our multivariate analysis of the combined dental ontogenetic data indicates that Dmanisi had a derived pattern and rate trajectory of dental ontogeny compared to great apes and earlier hominins. Based on this evidence, we hypothesize that early *Homo* at Dmanisi had an extended childhood phase. We need more fossil evidence to support this hypothesis, but the hypothesis cannot be falsified by advocating only those of our results that reflect the great ape-like dental ontogenetic features of Dmanisi.

Demirjian A, Buschang PH, Tanguay R, Patterson DK. 1985. Interrelationships among measures of somatic, skeletal, dental and sexual maturity. Am. J. Orthod. 88:433–38
Isler, K., van Schaik, C.P. 2009. The Expensive Brain: A framework for explaining evolutionary changes in brain size. J. Hum. Evol. 57: 392–400
Lewis AB. 1991. Comparisons between dental and skeletal ages. Angle Orthod. 61:87–92
Seselj M. 2013. Relationship between dental development and skeletal growth in modern humans and its implications for interpreting ontogeny in fossil hominins. Am. J. Phys. Anthropol. 150:38–47

Literature cited:

Dean MC (2010) Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. Phil Trans Roy Soc B, 365(1556), 3397-3410.

Dean MC, Cole J (2013) Human life history evolution explains dissociation between the timing of tooth eruption and peak rates of root growth. PLOS ONE 8(1): e54534

Gómez-Robles A, Smaers JB, Holloway RL, Polly PD, & Wood BA (2017). Brain enlargement and dental reduction were not linked in hominin evolution. PNAS 114(3), 468-473.

Gunz P, Neubauer S, Falk D, Tafforeau P, Le Cabec A, Smith TM, Kimbel WH, Spoor F, Alemseged Z. (2020) *Australopithecus afarensis* endocasts suggest ape-like brain organization and prolonged brain growth. Sci Adv 6(14):eaaz4729. doi: 10.1126/sciadv.aaz4729

Klingenberg, Ch P (2014) Studying morphological integration and modularity at multiple levels: concepts and analysis. Phil Trans R Soc B 36920130249

Smith TM, Smith BH, Reid DJ, Siedel H, Vigilant L, Hublin JJ & Boesch C (2010) Dental development of the Taï Forest chimpanzees revisited. J Hum Evol, 58(5), 363-373.

Zollikofer CPE, Ponce de León, MS (2010). The evolution of hominin ontogenies. In *Seminars in cell & developmental biology* (Vol. 21, No. 4, pp. 441-452). Academic Press.

Response to referee #2

Referee #2 (Remarks to the Author):

As this is a re-review, I will not comment on A-H, but only on some additional points because I feel this is a thoughtful and thorough revision. So, here are my few comments:

Abstract:
First line: "Human life history is characterized by an extended period of immaturity in which prolonged cerebral maturation contrasts with delayed somatic maturation 1."

This sentence is unclear to me. Perhaps something like this better captures the idea? “Human life history is characterized by an extended period of immaturity during which there is a disjunction between cerebral and somatic growth rates.”

Thank you for your suggestion, which we have included in the abstract

Manuscript Line 55
Change “permitting to temporally….” to “permitting researchers to use dental growth chronologies to calibrate…”

Reworded as suggested.

Manuscript Lines 240-242. The authors speculate that the *Homo* pattern of dental ontogeny might reflect a dietary shift to omnivory. Do they specifically mean the inclusion of more meat in the diet, because omnivory can mean a lot of things. If so, then exactly why do they think that the inclusion of more meat in the diet would have this selective effect?

We have tried to clarify this point as good as possible, recognising its hypothetical nature.

The entire last paragraph of the discussion is speculative. I’d like to see clearer acknowledgement of the speculative nature of these ideas, which at the moment build a complex scenario (three generations, alloparenting, increase in reproductive success) based on little direct evidence.

We have revised the abstract and the final paragraph of the discussion to reflect this. In the discussion section, we no longer propose an evolutionary scenario from the life history characteristics of early *Homo* to those of living humans. Rather, we focus on the diversity of fossil hominin life histories and ask which evolutionary implications can be drawn from the life history differences between early *Homo* and living humans.
Also see our response to referee #1, point 6.

The statistical analysis seems fine.

Response to referee #3

Referee #3 (Remarks to the Author):

In my view, the authors have made a concerted, objective and fair effort to address the comments of all three reviewers, some of which overlap in topic or content. They have re-worked extensive sections of the analysis and of the text in order to address those comments. Their exemplary attitude in addressing the comments is very open, objective and gracious toward the reviewers, which is fantastic to see.

I appreciate the revision of the discussion in particular, which takes into account comments and suggestions of the different reviewers, and presents an alternative to the linear 'ape to human' dental ontogeny evolutionary scenario involving more diversity in life history schedules among both extinct and extant species.

A couple of minor wording changes that I would suggest if they are in line with the authors' intended message:

line 195 - suggest change to: Paranthropus demonstrates a mode of dental ontogeny 'not found' ... (vs. 'no longer found')? - i.e., Paranthropus may have followed a unique dental ontogenetic pattern, unlike modern apes.

Changed as suggested (this is what we wanted to express).

line 229 - a prolonged phase of postnatal brain growth and maturation... suggest adding 'compared to extant apes'??

Changed as suggested.

All in all, I am satisfied that the authors have taken in to account the reviewers comments, and recommend that the revised manuscript be accepted for publication in Nature.

(Apologies, intended to identify myself in the first review cycle

Reviewer Reports on the Second Revision:

Referees' comments:

Referee #2 (Remarks to the Author):

As before, I have only a few comments on this revision. The authors responded thoughtfully to my remaining comments, though I still find the discussion to be overly speculative in part because it is a long way from "a delay in posterior relative to anterior dental development" and a "delayed dental growth spurt" to "extended childhood" with its implication of an extended period of time after weaning and before nutritional independence.

I feel that "extended growth" is a more justifiable phrase to use throughout the MS in light of the evidence from the authors analysis, specifying that there is evidence for an extended phase of growth prior to the dental growth spurt in Dmanisi. Calling it evidence of "extended childhood" over-reaches a bit. The significance of what the authors have found about Dmanisi's dental maturation profile, to my thinking, lies in revealing that not all aspects of dental growth prolongation in modern humans may have evolved in lockstep.

The other issue I have with the remaining speculation in the discussion is that given that a species' life history profile is the result of multiple selection pressures, its phylogenetic history, and developmental constraints, it is not possible to pinpoint the reasons for Dmanisi's unique combination of dental developmental features. Its uniqueness may suggest that the path toward a modern human pattern and rate of dental growth and development was more complex than previously realized (assuming Dmanisi is ancestral to modern humans and not an offshoot). It is this complexity that is, in my view, the paper's fundamental and significant finding. A better title for this paper might be then be something along the lines of: "Dmanisi dental remains demonstrate human-like developmental shift at 1.77 MYA"

I have two additional suggestions:

1. Last line of abstract: I would prefer to see this read "…possibly related to biocultural reproduction…" rather than "probably related to biocultural reproduction." I don't see the evidence for this being the "probable" reason.

2. In the discussion… lines 228-230, the authors state: "This pattern is typically thought to have evolved because the large human brain requires a longer period of time to grow to adult size." I should have mentioned this before, but Steve Leigh has argued that it is not a matter of extended time for brain growth but a question of energy allocation. Please take a look at Leigh (2004) Brain Growth, Life History, and Cognition in Primate and Human Evolution (Am J Primatol 62:139-164), where Leigh concludes (pg 162): "The human case merits special consideration, particularly given the cognitive distinctions between humans and other taxa. The present results suggest that marked extensions of brain growth periods are not crucial to the evolution of human cognitive skills [Leigh, 1996]. Specifically, although humans have a much larger adult brain size compared to chimpanzees, human brains do not increase in size for much longer periods of time than chimpanzee brains.

However, the rate of brain growth in humans greatly exceeds that in chimpanzees–at least in absolute terms." Essentially Leigh suggests that energy is being allocated to rapid brain growth and that this is the cause of the somatic slow down. Kuzawa's work is consistent with this explanation. So, it would be nice to at least acknowledge that one explanation for what is driving the slow-down in somatic (and presumably also dental) growth in modern humans relative to chimpanzees is the shift in energy allocation away from somatic growth to support a rapidly-growing brain, rather than an extension of the period of brain growth.

Overall, this is a very interesting paper and I support its publication, though, as I say, I would prefer the interpretation to be further qualified so that is more congruent with the authors' findings.

Referee #3 (Remarks to the Author):

As indicated in my previous comments, the authors have addressed the concerns of all reviewers to a degree that I find acceptable. In particular, they have now revised the discussion so that it is less speculative, and addressed the comments of reviewers in great detail in their response - and reflected in the revisions made.

This is an interesting and comprehensive analysis of an important fossil specimen in an appropriate comparative context, concluding with the authors' own interpretation of the evidence presented. I am sure that there will be replies, disagreements and probably debates about some aspects of the paper - but this is why we publish research results and it should be expected. Thus, I recommend that this paper can now be accepted for publication in Nature.

Author Rebuttals to Second Revision:

Response to referees

We would like to thank the referees for the third round of comments on our manuscript and their positive feedback.

Referee #2 (Remarks to the Author):

As before, I have only a few comments on this revision. The authors responded thoughtfully to my remaining comments, though I still find the discussion to be overly speculative in part because it is a long way from "a delay in posterior relative to anterior dental development" and a "delayed dental growth spurt" to "extended childhood" with its implication of an extended period of time after weaning and before nutritional independence.

I feel that "extended growth" is a more justifiable phrase to use throughout the MS in light of the evidence from the authors analysis, specifying that there is evidence for an extended phase of growth prior to the dental growth spurt in Dmanisi. Calling it evidence of "extended childhood" over-reaches a bit. The significance of what the authors have found about Dmanisi's dental maturation profile, to my thinking, lies in revealing that not all aspects of dental growth prolongation in modern humans may have evolved in lockstep.

The other issue I have with the remaining speculation in the discussion is that given that a species' life history profile is the result of multiple selection pressures, its phylogenetic history, and developmental constraints, it is not possible to pinpoint the reasons for Dmanisi's unique combination of dental developmental features. Its uniqueness may suggest that the path toward a modern human pattern and rate of dental growth and development was more complex than previously realized (assuming Dmanisi is ancestral to modern humans and not an offshoot). It is this complexity that is, in my view, the paper's fundamental and significant finding. A better title for this paper might be then be something along the lines of: "Dmanisi dental remains demonstrate human-like developmental shift at 1.77 MYA"

> Indeed, as a scientific term, "childhood" is used almost exclusively in the context of modern human life history. We have therefore included the suggested changes in the wording. As a title, we propose "Dental evidence for extended growth in early *Homo* from Dmanisi". We have also added a concluding sentence to emphasise the complex and ramified process of hominin life history evolution.

I have two additional suggestions:

1. Last line of abstract: I would prefer to see this read "…possibly related to biocultural reproduction…" rather than "probably related to biocultural reproduction." I don't see the evidence for this being the "probable" reason.

2. In the discussion… lines 228-230, the authors state: "This pattern is typically thought to have evolved because the large human brain requires a longer period of time to grow to adult size." I should have mentioned this before, but Steve Leigh has argued that it is not a matter of extended time for brain growth but a question of energy allocation. Please take a look at Leigh (2004) Brain Growth, Life History, and Cognition in Primate and Human Evolution (Am J Primatol 62:139-164), where Leigh concludes (pg 162): "The human case merits special consideration, particularly given the cognitive distinctions between humans and other taxa. The present results suggest that marked extensions of brain growth periods are not crucial to the evolution of human cognitive skills [Leigh, 1996]. Specifically, although humans have a much larger adult brain size compared to chimpanzees, human brains do not increase in size for much longer periods of time than chimpanzee brains. However, the rate of brain growth in humans greatly exceeds that in chimpanzees–at least in absolute terms." Essentially Leigh suggests that energy is being allocated to rapid brain growth and that this is the cause of the somatic slow down. Kuzawa's work is consistent with this explanation. So, it would be

nice to at least acknowledge that one explanation for what is driving the slow-down in somatic (and presumably also dental) growth in modern humans relative to chimpanzees is the shift in energy allocation away from somatic growth to support a rapidly-growing brain, rather than an extension of the period of brain growth.

Overall, this is a very interesting paper and I support its publication, though, as I say, I would prefer the interpretation to be further qualified so that is more congruent with the authors' findings.

We have incorporated the suggested changes, emphasising the role of energetic trade-offs (body, brain, reproduction). In addition, we have clearly marked our interpretations as hypotheses that need to be tested in more detail.

Referee #3 (Remarks to the Author):

As indicated in my previous comments, the authors have addressed the concerns of all reviewers to a degree that I find acceptable. In particular, they have now revised the discussion so that it is less speculative, and addressed the comments of reviewers in great detail in their response - and reflected in the revisions made.

This is an interesting and comprehensive analysis of an important fossil specimen in an appropriate comparative context, concluding with the authors' own interpretation of the evidence presented. I am sure that there will be replies, disagreements and probably debates about some aspects of the paper - but this is why we publish research results and it should be expected. Thus, I recommend that this paper can now be accepted for publication in Nature.