

Nanotyrannus and Tyrannosaurus coexisted at the close of the Cretaceous

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

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

I have read the manuscript by Zanno and Napoli. The study describes a new specimen of tyrannosauroid dinosaur from the Late Cretaceous Hell Creek Formation, which is directly relevant to the debated taxonomy of Tyrannosaurus/Nanotyrannus. In my opinion, the paper is comprehensive, strongly argued, and about as decisive on the issue as the fossil record can be.

I feel that it is important to contextualize some of the philosophical issues at play in the Nanotyrannus/Tyrannosaurus debate. This, at its core, is a lumpers/splitters debate. That is, it centres around how different scientists interpret the same data, and whether, when presented with variation in the fossil record, our default assumption should be that it represents a taxonomic difference (splitters) or simply intraspecific variation (lumpers). There is no correct answer, and the problem is impossible to escape. Through self reflection, I have identified that my philosophy is that of a lumper: I treat species as alternative hypotheses, meaning that we must falsify the default assumption of shared taxonomy. This will necessarily impart a bias in my review, and other reviewers and scientists will have different perspectives that impart their own biases.

However, despite my initial perspective, the information that the authors present in this manuscript is, in my eyes, incontrovertible evidence that Nanotyrannus and Tyrannosaurus are two different taxa. The new specimen shows a suite of differences across the skeleton that cannot be explained by ontogenetic transformation, and the authors demonstrate that they are outside of the range of intraspecific variation. Even if several of the characters are likely controlled by allometry, the histological evidence of skeletal maturity (or nearly so) in this specimen confirms that these differences remain useful diagnostic characters. As the authors outline, this is the key point: establishing skeletal maturity for a Nanotyrannus-morph individual is the 'smoking gun' that has been sought in this debate.

I was initially a little more hesitant to accept that the magnitude of differences between BMRP 2002.4.1 and NCSM 40000 are sufficient to establish a new species, but I will concede that this may simply be my human reaction to rejecting too much change when it comes all at once. Upon reflection, I have no arguments against any of the characters listed, and I agree with the authors that they are substantial differences unlikely to be attributable to ontogeny. Indeed, some of my own work shows that characters like 2nd dentary tooth reduction are established prenatally, so I can't really argue that they're not valid.

There are two main emphases in the manuscript: tyrannosaur anatomy, and palaeohistology. I am familiar with both fields but I am not as well versed in tyrannosaur anatomy as the authors, nor, likely, some of the other reviewers (although if you feel you need suggestions for experts in this field, I can recommend some). Accordingly, my focus will be on the palaeohistology, as I feel that I can comment more authoritatively, but I have a few comments about the anatomy as well.

Anatomy:

- In my reading through the main text and supplementary information, I cannot identify any major anatomical inconsistencies, although others may have a better knowledge (or stronger opinions) of the details of tyrannosaur anatomy and the referenced specimens in particular.

- To me, the differences noted between Nanotyrannus and Tyrannosaurus are substantial, and characters like the opposite

locations of cornual processes, presence/absence of foramina in the quadratojugal, and especially highly divergent forelimbs, are highly unlikely to be intraspecifically or ontogenetically variable. Therefore, they support the taxonomic distinction of these specimens.

- I am unclear on one of the autapomorphic features the authors identify: the lack of a subnarial foramen. To my eyes, there is a gap between the maxilla and premaxilla on both sides of NCSM 40000, which is similar in expanse to the subnarial foramen described in 'Sue' by Brochu (2003). Indeed, the pointers on Extended Data Fig. 1i seem to point to such a foramen. [[Note, I cannot seem to find captions for the Extended Data Figures, so it could be that this panel is intended to show the presence of the feature, and has been mis-annotated. In any case, it would be useful to have Extended Data captions somewhere in the manuscript.]] In any case, it would be useful if the authors could provide a more detailed comparison figure showing what this feature looks like when it's present, compared to what exists in NCSM 40000, especially because it is a key trait in the manuscript.

Palaeohistology:

- Overall, the palaeohistological analysis is done well. Based on the images and data provided, I come to the same conclusion as the authors, that the new specimen represents an individual in the asymptotic growth phase, which corresponds with skeletal maturity. This is an animal that is highly unlikely to grow to the size of an adult *T. rex*, or indeed, much more at all. The authors emphasize that their approach underestimates age and maturity, and I agree that they have been maximally conservative.

- I think the authors' reinterpretation of Woodward et al.'s (2020) data is reasonable, and in comparison with the new data the other specimen provides, the patterns make more sense.

- I was able to replicate the growth curve analysis using the script provided, and I cannot identify any errors in the code, underlying data, or resulting analyses.

- The authors comprehensively outline the terminology they follow, which is important because histological terminology is a mess, and these thin sections are quite complex. While the authors choose to follow Woodward et al.'s (2013) definition of LAG as an annual CGM, they should be aware that some other groups have essentially equated LAGs with rest lines, as component parts of CGMs, which may or may not be annual (e.g., Ch. 31 in de Buffrénil et al. 2021). If the authors wish to avoid this discrepancy, they could use the term "Annual mark" in place of LAG in their figures, which would make clearer to readers the interpretations of these structures. If they do choose to retain their terminological scheme, I would recommend that they outline this in the main text methods, so that readers familiar with the term LAG don't have to go too far to determine which definition is being used.

- The authors outline their logic for selecting which CGMs within CGM complexes they select as annual bands in NCSM 40000, used for calculating body mass for the growth curve. If they want to fully dispel any uncertainty, they could present a sensitivity analysis that shows growth curves for the alternative interpretations of the CGMs that they consider. Essentially, this would further demonstrate that there's no way to interpret the observed marks as indicating an individual in the exponential phase of growth. This is optional in my eyes, but wouldn't be very difficult to implement, seeing as their data analysis pipeline is automated.

I have not attempted to reproduce the phylogenetic analyses because of the computational power required, but I have taken a look at the priors for the Bayesian analysis and they seem appropriate. There are no aberrant results that would cause me to suspect an error in the analyses, and the authors do a good job of addressing unexpected findings and urging caution where necessary.

I don't think it's reasonable to expect the authors to incorporate the recently-named *Khankhuuluu* into their phylogenetic dataset, even if it might have an impact on the evolutionary and biogeographic scenarios they discuss. This would require a considerable amount of extra work in scoring the taxon, as well as non-negligible computing time re-running the analyses. Instead, I think this recent study is better dealt with via discussion of the implications of the Voris et al. (2025) paper in the last paragraph of the Discussion. The authors may also wish to emphasize some of the anatomical comparisons they draw, for example in the pectoral girdle. These provide stronger evidence for a non-tyrannosaurid affinity of *Nanotyrannus* now that MPC-D 100/50 is understood as a stem eutyranosaurian itself.

In addition to these comments, I have made some minor suggestions to the text and corrections to typographical errors in the attached documents, using the "Track changes" features of Microsoft Word. I realize that Nature prefers all edits spelled out, but this would be very difficult to do because the document provided does not have page or line numbers.

As there is identifying information in my review and annotated files, I am willing to waive anonymity.

Sincerely,

Gregory F. Funston, PhD
Visiting Assistant Professor
University of California, Davis

(Remarks on code availability)

I have reviewed all of the code provided by the authors. I have reviewed all of the data I am able to, particularly the histological data, but I have not attempted to verify the scorings of the phylogenetic matrix -- this is a major undertaking and I do not have access to the specimens required to accomplish this task.

I was able to replicate the growth curve analysis using the script provided, and I cannot identify any errors in the code, underlying data, or resulting analyses.

I have not attempted to reproduce the phylogenetic analyses because of the computational power required, but I have taken a look at the priors for the Bayesian analysis and they seem appropriate. There are no aberrant results that would cause me to suspect an error in the analyses, and the authors do a good job of addressing unexpected findings and urging caution where necessary.

Referee #2

(Remarks to the Author)

This manuscript is very much anticipated, to say the least. The discovery of the "Dueling Dinosaurs" reached the attention of the public about 15 years ago, and then in 2013 Peter Larson presented a poster on the tyrannosaur at the Society of Vertebrate Paleontology meeting in LA. As the specimen was still in private hands it remained in purgatory until the North Carolina Museum of Natural Sciences purchased it in 2021. At that point the game was on, leading up to this manuscript. This manuscript is very compelling, presenting diverse lines of evidence that show conclusively that *Nanotyrannus* is not only a valid genus but holds two species, findings that have more implications than this manuscript can really address (as the authors state), although they touch on a few. I won't go over the osteohistology and phylogenetics in any detail but both were particularly innovative and well done, perhaps even a quantum advance in both arenas. The biogeography was also really interesting (the idea that nanotyrannosaurids may have had their roots in Appalachia is fascinating!).

A key strength of this manuscript is that it's a dispassionate exposition of scientific reasoning leading to its conclusions rather than an advocacy piece, which is refreshing. The "Nanotyrannus debate" has had some solid scientific discourse but has also sometimes degenerated into an eye-rolling weariness of back-and-forth vitriol, often involving whispers about a passel of annoyingly nicknamed specimens in private collections. The fact that the authors here are not among the "usual suspects" in this debate, with little to no prior investment or axes to grind, immediately presents the opportunity for a fresh look, which this manuscript offers—along with a boatload of brand-new analyses. It's important to emphasize that there is much more at stake here than declaring a victor in a pissing match, as there are literally decades of research and dozens (probably hundreds) of publications based on a premise that this manuscript overturns. *Tyrannosaurus rex* has emerged as something of a model species given its great fossil record and has been a centerpiece in evolutionary analyses of functional morphology, ecology, biogeography, and phylogenetics, but these analyses will all need revision. So, yes, this manuscript is very effective. However, it still needs some work to be ready. The authors are permitted to know that this review is by Larry Witmer (Ohio University), in case they want to reach out to me for clarification on any of the points that I raise.

I'll present some general issues and then follow up with a bunch of small things, typos, etc.

1. First, a bookkeeping thing... If there were captions for the Extended Data figures, I couldn't find them. I could kind of figure it out, but captions would be helpful.
2. Line 1: The title ("*Nanotyrannus* and *T. rex* cohabited at the close of the Cretaceous") is okay, but "co-occurred" or "were contemporaneous" might be better. "Cohabit" has more of a "shacking up" vibe, and Webster's defines it as "to share a home and have a sexual relationship." Lol.
3. New-ish works that should be considered for incorporation.
 - a. Longrich & Saitta (2024) is indeed cited but only twice (that I counted) in the main text and just in the context of being an advocate for *Nanotyrannus* being valid. Obviously L&S 2024 present lots of analyses and characters that merit citation and discussion.
 - b. Voris et al. (2025) just published a major article here in *Nature* about a new tyrannosauroid. *Khankhuuluu* itself may not be all that relevant but their SI has relevant discussions of numerous tyrannosauroids, including *Nanotyrannus*, which they regard as a juvenile *T. rex*. Their section on *Nanotyrannus* has relevant discussions of some of the key characters discussed here (e.g., tooth counts, QJ pneumatic foramen).
 - c. Witton (2025) just published a book titled "King Tyrant." Although it's a "popular book," it's well referenced and has a lot of interesting discussions, including a presentation of *Nanotyrannus* (which he regards as a juvvy rex).
 - d. Paul (2025: <https://doi.org/10.11646/mesozoic.2.2.1>) came out so recently (last night, as I write this) that I haven't had a chance to do much more than buzz through it, but there are lots of citable and discussable points. For example, he also thinks Jane might be a different species of *Nanotyrannus* and tentatively refers NCSM 40000 to *Stygivenator*.
- In general, all these recent publications reflect how hot this topic is right now. They also highlight how important and timely the Zanno & Napoli manuscript is, given the detailed careful analyses and their unique access to perhaps the most relevant specimen (NCSM 40000). I regard the scholarship in the above four works as worthy of attention. This debate has sometimes had a somewhat disturbing tendency to hinge on elite academics versus non-degreed, non-party-line outsiders... which kinda ain't right.
4. Thoughts on basic organization. I struggled with the organization when I hit the sections "Ontogenetic Assessment" (starting on line 196) and "Differential description" (starting on line 225). The headers don't say it, but I eventually figured out that these were basically dedicated to NCSM 40000.
 - a. As I'll advocate below, there might be a better way to organize the main text, but first a couple comments on the "Differential description" section as it stands now. The section headers don't indicate that the focus is on NCSM 40000. And, given its position under the *Nanotyrannus* section, shouldn't it also be focusing on CMNH 7541 and Jane? It's hard to tell

which specimens/species the description pertains to. Also, there's no clear organization to these sentences or their sequence. Sometimes sequential sentences pertain to the same character, but then it can be hard to know whether the subsequent sentences pertain to the previous one or is a new character. Maybe this needs to be broken into a series of numbered items. It's also pretty detailed "inside baseball" stuff, which I'm loving but may be too much for the general readership of *Nature*. The SI also has a lot of description of NCSM 40000 (and a separate monographic treatment is promised), so there's some redundancy. The description here in the main text runs on for almost four pages and maybe should be more focused.

b. I'll pull this out as a separate point... In truth, the manuscript isn't (or shouldn't be, in my view) *about* NCSM 40000 but rather about establishing the validity of *Nanotyrannus*. Obviously the new specimen is a key document in this argument, but the distinction is important. It shouldn't be "hey, look at this new specimen which has implications" but rather, "hey, look at this important scientific hypothesis, which now has an important new test based on the new specimen." The authors may disagree with my assessment because they have this sweet new specimen, but I'm positive that the rest of the world will see this publication as being *about* the validity of *Nanotyrannus* and how decades of research on the most famous dinosaur may be wrong. So please don't bury the lede. :)

c. The authors actually present the following summary statement in the Discussion (lines 467–471), which is super important as a summary statement, but it may also suggest a new and better outline for presentation of the argument: "In combination, four independent lines of evidence—osteohistological indicators of somatic maturity, shared autapomorphies between CMNH 7541 and NCSM 40000, absence of synapomorphies exclusive to *Nanotyrannus* and *Tyrannosaurus*, and ontogenetically invariant characters differentiating *Nanotyrannus* from *Tyrannosaurus*—demonstrate beyond reasonable doubt that *Nanotyrannus* is a valid taxon." These four "independent lines of evidence" could be four sections, probably in that order. In other words, hit the main points hard—so that they can't be missed—in the main text. You can fold in a pile of anatomy/description as you go, but it'll be just the anatomy that is central to the main point; the rest will be in the SI. Yes, this may require a rethink and a rewrite, but it may make the manuscript that much more compelling.

5. As for the ontogenetic assessment ("osteohistological indicators of somatic maturity"), this probably should indeed be the first topic to take on. It might be beneficial to state at the outset of the section that it's particularly important to establish the ontogenetic status of NCSM 40000 given that so many attributes of putative *Nanotyrannus* specimens have been regarded (even dismissed) as early stages of the ontogeny of *T. rex*.

a. In truth, the osteohistology/skeletochronology here will be the target of those likely to be resistant to the validity of *Nanotyrannus*. I'm no expert on osteohistology, but I'm pretty well acquainted with the issues involved, and I have to say that I'm very impressed with how the authors carried out this component. Still, the fact that NCSM 40000 is almost at somatic maturity is so important to the argument that critics will be looking very closely at all the skeletochronology. Longrich & Saitta (2024) and Paul (2025) also discuss histology (based mostly on literature reports in both cases), and their discussions are relevant.

b. Carr (1999) made a big deal about "immature bone grain" in CMNH 7541—it was the first piece of evidence that he listed in the abstract—and it was influential for years (it was all the rage in the late '90s, with Scott Sampson's team also using it as supposedly a size-independent indicator of age). That line of argumentation seems to have faded but was mentioned in Mark Witton's recent book (*King Tyrant*) and by Longrich & Saitta. It'd be useful to discuss that here. Does NCSM 40000 have surface bone textures that shed any light?

6. "Shared autapomorphies between CMNH 7541 and NCSM 40000" also needs to be prominent. Another (maybe a better) way to put it would be "basis for referral of NCSM 40000 to *Nanotyrannus lancensis*." This basis was frankly a little hard to extract from the current text. In terms of the logical flow of ideas, the two key elements are (1) NCSM 40000 is not a juvenile but rather is close to somatic maturity and (2) it has unique features that resemble CMNH 7541 and dictate referral to the same species.

a. The holotype CMNH 7541 is only cited a few times in the main text outside of introductory material; same with the SI. There's maybe just a single image of the holotype skull and it's just a single CT slice (Extended Data Fig. 1n). If anything at all is *Nanotyrannus*, it's the holotype, CMNH 7541. Thus, it seems that a more formal accounting of why NCSM 40000 can be referred to *N. lancensis* is in order, probably with illustrations, and in the main text. The SI (lines 97–109) has a "Differential Diagnosis [of?] *Nanotyrannus* and *Tyrannosaurus*" but again there's no means of easily checking what features of the skull of NCSM 40000 justify referral to the same species as the holotype.

b. My team has some of the bony elements of CMNH 7541 segmented, including the braincase with columella, and would be happy to provide them to the authors, if that would help.

7. The last two remaining sections—"absence of synapomorphies exclusive to *Nanotyrannus* and *Tyrannosaurus*, and ontogenetically invariant characters differentiating *Nanotyrannus* from *Tyrannosaurus*"—also would merit their own sections. My intent here is to suggest an organization that would help convey the compelling nature of the evidence the authors have amassed, which will help convince the readers that the conclusions are inescapable. If you can't convince the readers of the validity of *Nanotyrannus*, then the phylogenetics, biogeography, etc. won't have much impact.

More minor points, typos, etc...

8. Lines 48–51: The second sentence of the opening paragraph ("As one of the last surviving non-avian dinosaurs, a crucial datum for assessing terrestrial biodiversity, ecosystem structure and stability, and biogeographic exchange immediately preceding the end-Cretaceous mass extinction event—one of Earth's greatest biological catastrophes.") is not a complete sentence.

9. Line 54: The term "hypodigm" may be too jargony for the opening paragraph. It's not all that widely used in paleontology, and its meaning is not apparent from the roots of the word.

10. Lines 60–61: Regarding "ontogenetic invariance in extant archosaurs" doesn't really seem to factor in here in this manuscript, at least not enough to merit mention in the opening paragraph.

11. Lines 110–111: Regarding listing BMRP 2006.4.4 as referred material directly under *Nanotyrannus* seems a little weird here. I get that you're not referring this specimen to either species (it's *Nanotyrannus* sp.), but it seems odd, if only because it

seems like the only specimen referred to the genus. Maybe there's a different way to notate this sense.

12. Line 133: "absolutely larger forelimb elements." This could be interpreted as ALL forelimb elements are absolutely larger. Figure 6 indicates that the humerus is absolutely shorter. Is it just the hand that's absolutely longer than in *T. rex*. If so, say that.

13. Line 142: *N. lethaeus* sp. nov. is presented first. Shouldn't the existing species, *N. lancensis*, be presented before the new species?

14. Line 157: "was" should be "were."

15. Line 172: For the name *Nanotyrannus lancensis*, shouldn't Bakker et al. 1988 be listed?

16. Line 227: Are you trying to reference the skull figure? Seems like it might be Ext Data Fig. 7, not 6.

17. Line 251: missing words. It should be "between *Nanotyrannus* and *Tyrannosaurus*"

18. Lines 257–258: Regarding "*Tyrannosaurus* entirely lacks a lacrimal cornual process," *T. rex* has lacrimal osteoderms, so does the attachment area on the lacrimal count as a cornual process?

19. Line 263: "marred" probably isn't the best word here. Maybe "Instead, it has rugose striations...." would be adequate.

20. Line 273: Probably should be "most other tyrannosaurines"

21. Lines 277–279: Regarding "The lateral surface of the quadratojugal is pierced by a small pneumatic foramen, a trait also present in the mid-Cretaceous tyrannosauroid MPC-D 100/50..." Voris et al. 2025 talk about this character and these specimens and should be minimally cited or even discussed. Also, should this be MPC-D 100/05 rather than 100/50? Voris et al. (2025) make reference to MPC-D 107/5 having a QJ pneumatic foramen. Whether people use the leading 0 (05 vs. 5) seems variable.

22. Lines 284–285: Regarding "The braincase of *N. lancensis* is only preserved in articulated specimens, where it is difficult to visualize..." We segmented the braincase out of CMNH 7541 (W&R 2010) and illustrated it with labeled stereopairs in multiple views. I can provide an STL, if needed.

23. Lines 309–311: Tooth counts were already discussed earlier in this section, so this might be a bit redundant.

24. Line 355: Regarding "of one of the largest known *T. rex* individuals", state which individual (presumably FMNH PR 2081).

25. Line 358: Did you want "is" italicized (e.g., for emphasis) or is it left over from the taxon name?

26. Lines 394–400: The manuscript needs more passages like this that really distinguish *Nanotyrannus* from *T. rex* and why they can't be the same species. Also, "precipice" is spelled incorrectly.

27. Lines 448–450: Regarding tooth count reductions, Voris et al. 2025 (the Khankhuuluu article) says in the SI that "tooth count reduction in *Tyrannosaurus* is present in the CT scans of the adult specimen FMNH PR 2081 where a resorbed 13th alveolus is present at the posterior end of the left maxillary tooth row." Also, what about mysticetes that kinda develop teeth as fetuses but then switch over to baleen? <https://doi.org/10.1111/joa.12579> Is that tooth count reduction that's known in amniotes?

28. Line 460: Should be MPC-D 107/7

29. Line 495–497: I understand use of "failure" here but pitching it differently may raise fewer hackles...and I think most workers who accepted *Jane* as a juvv *rex* were honest and thought they were following consensus thought. Also, saying "did not mirror the spatial niche partitioning of their prey" is a little convoluted and obscures the point you're trying to make.

30. Line 506: Should be "*Tyrannosaurus*"

31. Line 512: There is no Fig. 5e

32. Line 523: There is no Fig. 5f

33. Line 582: You could mention that CMNH 7541 was also scanned on that Philips scanner in June 2023. Maybe not a transformative scan but still another attempt.

34. Line 631: Should be "constrained"

35. Line 654: What do you mean about "our" specimens? Better to state specimen numbers.

36. SI.1.1 Table of specimens: Under CM 9380, it should be "Firsthand" not "Firsthead" (although that's kinda true, too!). Also, I'm virtually positive that RTMP uses "TMP" as the museum prefix in catalog numbers. That is, they drop the "R". (I guess they're not fans of the Royal Family...which is on-brand for Alberta.)

37. SI Line 100: Should be "absolutely"

38. SI Line 102: As noted in #21 above, the SI for Voris et al. (2025, Khankhuuluu) has a discussion of this character and *Nanotyrannus* in general that will need to be incorporated.

39. SI Line 111: As noted above, how the description of NCSM 40000 is handled may need a bit of an overhaul, particularly if my suggestions for the reorganization of the main text are accepted.

40. SI Line 117: I think it'd be legit and helpful to remind the reader that the histology of NCSM 40000 suggests somatic maturity. As I was reading the descriptions I couldn't help thinking of the authors who have regarded the attributes as juvenile or "ontogenetic characters" and had to remind myself that you're arguing for somatic maturity. Thus, maybe it'd be beneficial to the argumentation to remind the reader from time to time, or at least with some of the more "classic" characters.

41. SI Line 162: The "A" in "as" should be capitalized.

42. SI Line 208: My point #21 above pertains here, too. Should this be MPC-D 100/05? Voris et al. (2025) make reference to MPC-D 107/5 having a QJ pneumatic foramen.

43. SI Line 239: Italicize the "T." in *T. rex*

44. SI Line 276: Should be "pneumatopores"

45. SI Lines 313–314: Regarding "We also take a conservative approach by not adding conditions observed to the species-level diagnoses for these taxa." Not sure what you mean by this statement. Reword?

46. SI Line 528: Do you mean "cortex" here...or "cortical"? "Cortice" seems like an improperly constructed singular of "cortices" which should be "cortex."

47. SI Line 533: "redacted" doesn't seem like the right word here.

48. SI Lines 562–564: Regarding "A more stringent 1:1 interpretation of CGM to growth cycle count, as employed in other studies of tyrannosauroid growth (e.g., Woodward et al.), would only strengthen the argument for a growth trajectory in NCSM 40000 distinct from that of FMNH PR 2081." Can you provide an age estimate using the criteria of Woodward et al.?

49. SI Line 644: Should be "CGMs"
50. SI Line 966: Should be "permitted"
51. SI Line 1027: As you start to present the different topologies, it would be super helpful if you could relate these different topologies to the figures in the Extended Data and main text. Also, the character list in the "Parsimony Matrix" file is not particularly readable and looks like program output rather a more readable formatted document.
52. SI Line 1080: Should be "Supplementary"
53. SI Line 1094: Regarding Stygivenator, both Longrich and Saitta (2024) and Paul (2025) raise the question of whether NCSM 40000 could be Stygivenator. Paul even illustrates NCSM 40000 and labels it as "Stygivenator? incertae sedis".
- Respectfully submitted by Larry Witmer (Ohio University)

(Remarks on code availability)

Referee #3

(Remarks to the Author)

Before diving into assorted minutiae relevant to this manuscript, I have two main points that I would like the authors and editors to consider.

Point 1. This is a fascinating, well-crafted and surprising manuscript, but also a troubling one since it indicates that mistakes in interpretation made by a previous set of authors misled an entire generation of dinosaur workers (maybe more than one generation) into making arguments (pertaining to histology and ontogeny, anatomical character states, and phylogeny) that are here stated to be erroneous, and based on misinterpretation.

The current ms does emphasize this point (lines 663-678 in particular; the Introduction – lines 76-81 in particular – does too) but this is such an important point that I wonder if it should be flagged more than it is, especially seeing as Carr et al. are accused of making “pervasive errors in character construction and definition” (lines 676-7) – ouch! What we’re saying is that social inertia – and/or ‘in-group’ membership – led to mass adoption of an incorrect conclusion. That’s a non-trivial issue that should have everyone more worried than they already are. Needless to say, further discussion of this issue would be scope for a social science study, not appropriate for the current ms, but I wonder if it might be appropriate to emphasize this even further. I seriously wonder if words to the effect of ‘Reversing an erroneous consensus’ or such should be worked into the abstract or even the title. I personally find the title lacklustre given the massive interest there will be in this paper, and in the fallout and subsequent discussion... though I also recognise that the authors are being good, conservative scientists in using understated language.

Point 2. Given the heated nature of discussions on Nanotyrannus, the authors need to be as clear as possible in stating that there is no ‘massaging’ of the data in order to win the incredibly gratifying conclusions they report. While I congratulate the authors in being as transparent and forthright as possible in stating the work that was done and what conclusions were reached, I see points in which the wording implies data massaging. My suggestion is that the wording is changed such that things are better explained, or that extra text is added to precisely explain the relevant text segments. Consider the following...

In line 381, it is stated that inferred hatching age and growth rates are estimated by “[applying] an isometric allometric scaling mass adjustment”. The growth trajectory here is based on patterns presented in Erickson & Tumanova’s 2000 Psittacosaurus analysis. Rather than refer obliquely to an “isometric allometric scaling mass adjustment”, I recommend that the authors instead describe that a growth model was inferred based on a standardized or averaged (non-bird) dinosaurian pattern established for the ornithischian Psittacosaurus. I would also like the authors to state why a growth model for Psittacosaurus was used and not one incorporating data from multiple dinosaurian taxa – is this really because that for Psittacosaurus is the only one available?

In line 395, it’s stated that published models positing an ontogenetic transition from Nanotyrannus into Tyrannosaurus present a “biologically implausible bimodal life history”. A typical response to assertions like this is that implausibility is not the same as impossibility, and the authors who’ve argued for this transition of course already regard Tyrannosaurus as an unusual, possibly unique, animal. It might be more appropriate to refer instead to a ‘bimodal life history that would be wholly unique within reported archosaur diversity’ or such. In addition, while I accept and agree with the authors’ assertion that the aforementioned ‘bimodal life history’ would indeed be ‘wholly unique’, the authors would better demonstrate this assertion if they listed appropriate citations: space is an issue, of course, but there are select good studies that make this point, and I see a dearth of citations in this section.

Finally, lines 403-4 refer to a “new protocol for handling logical character inapplicability”. This sounds scarier than it is (the authors are referring to the moderately familiar Goloboff et al. 2021). I would reword the text here, something along the lines of ‘following accepted protocols of rejecting inapplicable phylogenetic characters’, since otherwise the text reads as if the authors have devised and are implementing a new way of excluding characters they don’t like.

Taxonomy and phylogenetic definition. Any ‘family-level’ group anchored on Nanotyrannus cannot be ‘Nanotyrannosauridae’ because there is no ‘Nanotyrannosaurus’: it must instead be Nanotyrannidae. As precedent, the authors may not be aware that there is an extant dinosaur family based on Tyrannus (kingbirds), namely Tyrannidae. Use of ‘Nanotyrannosauridae’ and ‘nanotyrannosaurids’ later in the ms (lines 516-531, Fig. 5) needs to be changed in view of this.

The phylogenetic definition is noted as being 'stem'. That looks dated given that workers now mostly prefer to refer to 'node-based' vs 'branch-based' definitions, and this is a branch-based definition. This issue may be redundant anyway, as a 'family-level' term is itself redundant (in terms of phylogenetic nomenclature) with respect to *Nanotyrannus*... viz, there's no need for a *Nanotyrannidae* in a system where we employ phylogenetic nomenclature. On the use of 'stem', line 511 (which refers to 'stemward outgroups') should be tweaked such that the lineages concerned are described as 'early-diverging' or such.

Minor final observations...

Line 120: I'm of the unpopular (but anatomically correct according to *Nomina Anatomica* works) opinion that a bone like the quadrate does not and cannot have a 'proximal' end because proximal-distal terminology applies only to appendages. A quadrate has a ventral end and a dorsal end. 'Proximal' makes no sense when applied to this element.

Line 215: typo for 'osteohistological'

Lines 219 and 222: 'cranialmost caudals' should be 'proximalmost caudals' as per anatomical convention otherwise mostly used throughout ms

Line 303: 'bounded caudally' should be 'bound caudally' I think

Line 330: vertebral variation is not unique to the groups listed; some cetacean species are variable in vertebral count too.

Lines 343 and 344: are 'supraradiocondylar' and 'ectepicondylar' correctly formulated? I would think that they should be 'supraradiocondylar' and 'ectepicondylar'.

Line 364: double use of 'is'

Line 431: 'lacking exclusive synapomorphies with *T. rex*' should be "lacking exclusive synapomorphies shared with *T. rex*", though I appreciate the redundancy given the meaning of the word 'synapomorphies'.

Line 675: space missing in '*N. lethaeus*'.

Darren Naish

(Remarks on code availability)

Referee #4

(Remarks to the Author)

This paper presents a comprehensive re-evaluation of the debate surrounding whether the theropod dinosaur *Nanotyrannus* is a juvenile of *Tyrannosaurus rex* or a distinct smaller-bodied species. The manuscript presents a stunning new fossil specimen of *Nanotyrannus*, along with a host of new gross anatomical, histological, and phylogenetic data. The authors have provided a comprehensive and incredibly convincing case that not only is *Nanotyrannus* a distinct and valid species separate from *T. rex*, but that there are actually two different species of *Nanotyrannus* from the Hell Creek/Lance Formation assemblage. As *T. rex* is the most iconic non-avian dinosaur species with a worldwide cultural saturation, there is no doubt this paper will appeal to the broad scientific readership of *Nature* (and when published, will certainly receive worldwide coverage from news media). More importantly though, it is an exemplary case study of how one should approach questions about the interplay of variation, growth, speciation, and phylogenetic evolution in the fossil record, where the fourth dimension of deep time can muddy the waters that are artificially clear for neontologists. Further, the results of this paper have important implications for the paleoecology of latest Cretaceous ecosystems. Nearly all Jurassic and Cretaceous non-marine ecosystems have a diversity of predatory dinosaurs occupying a wide variety of body sizes and ecological roles. The Hell Creek/Lance ecosystem has always appeared aberrant in lacking medium-sized theropod dinosaurs that would fill the 'mesopredator' role. Now we know that these dinosaurs were present - they had just been confused for juveniles of the giant *T. rex*!

The science presented in this manuscript is of the highest quality. Below, I note some issues with overall organization and the figures that should be rectified in revision. However, after these changes are made, the MS is certainly worthy of publication in *Nature*.

- Right now, the paper is couched in the context of the taxonomy debate about *T. rex*. The MS should be written for the broad readership of *Nature*, so should introduce the topic with questions that will interest those readers. Alpha taxonomy is boring for the non-theropod specialist. What is interesting is the implications of this taxonomic debate for how we interpret species in the fossil record, and what it tells us about the paleoecology of latest Cretaceous ecosystems. So that is what I would stress in the first two paragraphs, rather than the taxonomic debate itself.

- The diagnosis of *Nanotyrannus* should be differential (i.e., with some comparisons to other taxa) - if the debate has centered on whether it's synonymous with *T. rex*, then the authors need to emphasize in the main text diagnosis how it is different rather than referring reader to Supplementary Info.

- Flip the order of *N. lancensis* & *N. lethaeus* in the Systematic Paleontology section. Now that *Nanotyrannos* is no longer

monotypic, its important to give a revised diagnosis of the existing species *N. lancensis* *before* you introduce the new species (*N. lethaeus*)

- Radioisotopic dating is cited as "submitted". What is the guarantee that this will be accepted or published by the time this Nature paper is published? As a reviewer, I can't evaluate stratigraphic arguments because I have no access to this submitted geochron manuscript and none of the details are presented here. If for some reason the geochron MS is delayed or rejected, the reader has to take it on faith that the geochron data are correct and interpreted correctly. I don't know if this was submitted as a companion MS to Nature (much like is done with fossil hominids), or to another journal within NPG that will coordinate publication timing?

- The 'differential description' is difficult to read for anyone except a tyrannosaurid specialist. I suggest that it be re-written a bit so it has a stronger, easier-to-read, narrative. It can remain organized in anatomical order, but should basically center around three things: 1) how *Nanno* differs from *T. rex* but there are shared apomorphic similarities the two *Nannotyrannus* species; 2) differences between the two *Nanno* species; and 3) character states that support the placement of *Nannotyrannosauridae* outside of *Tyrannosauridae*. In a Nature paper, the osteological description should focus on the anatomical highlights that support the main arguments of the paper, rather than trying to touch on every possible character state.

- There's no transition between the description, CGM, phylogeny, etc sections - the text just abruptly changes topic. Tell the reader a story, and provide some sort of bridge between these sections so they understand where you are going.

- lines 450-451: you could also emphasize here that *Limusaurus* is not closely related to tyrannosaurs

- Figure 1: The 'strat column' isn't really helpful because there's no detail here - its just a box with dates at top and bottom. Also, the radioisotopic date for NCSM 40000 has uncertainty/error associated with it and should always be reported as such; stripping the uncertainty is misleading.

- Figure 1: the photo of the snout of NCSM 40000 is really dark - could be lightened slightly (similar to Figure 2)

- Figure 1: Each element should have its own letter - its hard for the reader to interpret when three bones each are grouped under (b) and (c). Further, I would find it more helpful if the two palatines were next to each other and the two postorbitals were next to each other. Finally, the figure caption is incomplete - it doesn't actually say what bones are figured.

- Figure 3: the lambda filtered image for (i) is really dark and hard to see much detail - could be helpful to brighten just a touch.

- Figure 3: this figure takes up alot of space. I think with just one histological transect of the femur you can make your point convincingly and use less space. The rest can go in an extended data figure.

- Figure 4: Graph (a) to me is difficult to interpret, because you're comparing the growth curve of a single species (*T. rex*) to a composite growth curve of a genus (two species of *Nannotyrannus*). Similar to (b), the two *Nannotyrannus* species should be plotted separately (or only plot one species).

- Figure 5: This is a really confusing figure. Its trying to communicate too many different things to the reader. Please simplify. Pick one phylogenetic topology and put the other in extended data. The implied weighting results, while interesting, are not important for your main conclusions, and can also be put in extended data or supplementary info.

- Figure 6: This figure is not that important to the main points of the paper and can be moved to the extended data section.

(Remarks on code availability)

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The authors have satisfied my suggestions on the previous draft, and have also undertaken extra work that further improves the manuscript. I am satisfied with the content of the manuscript, and have noted only a few small typos here and there, outlined below. I have one optional suggestion for moving a paragraph between sections, which I will leave to the authors.

Lines 205–213, beginning with “over the past two decades, consensus [...]” and ending “*Nanotyrannus* is a valid taxon.” : I see why this short paragraph is located here, as a segue from the systematic palaeontology section to the remainder of the manuscript, but because it doesn't have its own header, it's easily missed if readers jump around the manuscript. Optionally, the authors could move it to the introduction, somewhere towards the end before setting up the stinger about describing NCSM 40000, or they could add a “Results and Discussion” header before this paragraph, making the following headings (NCSM 40000 is skeletally mature, etc.) into subheadings of that broader section. Realistically, this is a very minor issue and does not need to be fixed, but could help with the ‘polish’ of the manuscript.

Line 229: This is the first appearance of the abbreviation EFS in the text, so it should be defined here.

Line 239: “caudals” should be “caudal vertebrae”

Line 274: “this proposed character transformations” should be “these proposed character transformations”.

Line 275: “plausibly” – I love it, but it should be “plausibly”

Line 402: there is an extra closing parenthesis.

Line 638: “xxx” will have to be populated with the Figshare link upon acceptance.

Line 651: The character in parentheses (the unit for shape parameter values) appears as a square in the PDF, so care will need to be taken during proofing that the correct character has come through. I don't recall seeing this issue on the original Word document, so hopefully it is just a small hiccup.

Line 963: The image caption says that the ‘Extreme’ model in panel e is a pink line, whereas the legend indicates it is blue. I think the typo is in the caption, which mentions pink lines later where they show differences in mass between specimens at the same age.

(Remarks on code availability)

I reviewed the code in the last draft, and the additions here do not appreciably change the code.

Referee #2

(Remarks to the Author)

This new draft of the manuscript is even more exciting than before. It's a major reorganization of the arguments, resulting in a substantial rewrite of both the main text and the SI. But it works really well now in that the narrative is sharper and the argumentation more compelling. It's fun to read...and much easier to read, too! It's impressive that they did new histological analyses, as well as new phylogenetic analyses. We reviewers didn't ask for those new analyses, but they do significantly strengthen the overall analysis and head-off any future critics. Of course, this is a fast-moving area of extraordinarily high interest, so it's a constant battle to “remain current.” In fact, since this resubmission came out, Thomas Carr published a new description of the holotype skull of *T. rex* (<https://doi.org/10.1080/27669645.2025.2539638>), which makes more than 50 references to the holotype skull of *Nanotyrannus*. I'll leave it the authors and the editor to decide whether they should incorporate any changes based on this new Carr article, but obviously it's a very relevant publication.

In general, other than dealing (or not dealing) with the new Carr article, I have relatively few changes to recommend. The revised draft is very well written. The SI has just the right amount of description, and most of it is directed toward meaningful comparisons rather than straight description for its own sake (the latter is legit and valuable but not the emphasis for a Nature article). The responses to the reviewers are generally more than adequate, and I won't argue against any of their decisions. I'll again reveal that this review was prepared by Larry Witmer (Ohio University).

Most of my comments are editorial. Note that the SI was provided as a Word file with no line numbers, so I added line numbers and converted to PDF. I'll try to upload the file, but if I fail, I encourage the authors to shoot me an email (witmerL@ohio.edu), and I'll send it to them.

Main text:

1. Line 52: en-dash should be em-dash
2. Line 229: This may be the first reference to EFS, in which case it should be spelled out as “external fundamental system (EFS)”.
3. Line 273: It would be good to substantiate “several” by listing specimen numbers.
4. Line 274: should be “these”
5. Line 348: needs an end parenthesis. Also, are you saying USNM 555000 is the “largest Tyrannosaurus”? It's not...not even close, right?
6. Lines 364–365: Probably should be “due to the juvenile status of specimens known at the time.” Using “its juvenile status” implies only a single entity and only individuals can be juvenile not a genus (duh)..
7. Line 482: Should be “eutyranosaurians” (plural), unless there's a different intent. Regardless, it needs a minor tweak to read right.
8. Line 491: Should this be “Nanotyrannus or its ancestors” or maybe just “the ancestors of Nanotyrannus.” It reads now as the genus *Nanotyrannus* was in Appalachia as well as Laramidia.

Supplementary Information (see note above about how I handled the Word file with no line numbers):

9. Lines 117–118: For clarity move “(the condition in NCSM 40000 cannot currently be assessed)” to the end of this sentence.
10. Line 173: “Na.” should be “N.”
11. Line 180 but maybe elsewhere: You use both “alioramins” and “alioramines.” If these are the same clade then you should pick one and be consistent.
12. Line 193: “spp.” should not be in italics
13. Line 246: “tuber-like”? As in looking like a potato? Odd metaphor.
14. Line 257: should be “evident in MOR 1130” (missing “in”)
15. Line 270: Again, “spp.” should not be in italics.
16. Line 320: should be “proatlantal”
17. Line 403: should be “Daspletosaurus”
18. Lines 405 & 409: should be “lancensis”
19. Lines 464–466: “Only the lateralmost rim of the proximal end of MCIII articulates with the carpals or antebrachium. Otherwise, MCIII appears genuinely splint-like, despite being robust proximally.” Does this passage pertain to NCSM 40000 or to the previous tyrannosaurids?

20. Lines 469–470: When you say “(nearly twice the absolute dimensions of one of the largest known *T. rex* individuals”, you should designate which *T. rex* individual.
21. Line 492: should be “peduncle”
22. Line 524: Should be “crista tibiofibularis” (two words)
23. Line 525: Should be “Bistahieversor”
24. Line 532: Need to add a comma after “40000” or delete the comma after “generally”.
25. Lines 575–581: weird font switch
26. Lines 679–682: Nice! No edits, just glad to see the addition.
27. Line 910: Should be “lethaeus
28. Line 1008: Should be “Outgroup”
29. Line 1150: Should be “Nanotyrannidae” now, right?
30. Line 1225: *Nanotyrannus* and *Alioramus* should be italicized.

(Remarks on code availability)

Referee #3

(Remarks to the Author)

I thank the authors for taking the time to fairly evaluate and respond to my comments and am pleased with their modifications of the article. My only final comments are very minor editorial ones...

-- in the Remarks section starting line 166, it's not necessary to have 'former' (line 170) in italics.

-- also, in lines 170-1, 'Whereas, NCSM 40000 compares favorably with CMNH 7541, and critically preserves a shared apomorphy...' would be better worded 'In contrast, NCSM 40000 compares favorably with CMNH 7541: notably, both share the apomorphic presence of....'. 'Critically' is not the right word here.

-- also, line 172, 'contrasting the shallow recess' should be 'in contrast to the shallow recess'

(Remarks on code availability)

Referee #4

(Remarks to the Author)

I want to extend my thanks and gratitude to the authors for their careful and thorough re-organization of both the manuscript text and figures. With these revisions, the paper is much easier to read, and presents a well-organized compelling narrative that will be attractive to a broad swath of the journal's readership. This manuscript now really reads like a Nature paper. The authors should be commended for such an excellent manuscript; and as with the initial submission, the science is top-notch. It is my pleasure to recommend this contribution for publication in Nature after a handful of minor revisions, listed below.

- Diagnosis (lines 112-132, 157-164, 193-199): I apologize that my comment on the genus and species diagnoses was not more clear. For the diagnosis of *Nanotyrannus* as a genus, and the two species (*N. lancensis* and *N. lethaeus*), the authors do explicitly indicate autapomorphies (unique character states), which does make this implicitly differential. However, my comment was about the character states in the diagnoses that are *not* autapomorphies. For these character states, the authors should indicate if they are the same or different from other taxa. i.e., for the generic diagnosis of *Nanotyrannus*, which of the non-autapomorphies are similar/different from other eutyranosaurians, particularly *T. rex*; and for the species diagnoses, which of the non-autapomorphies differ from the other species of *Nano*. For further info on differential diagnoses, see Cifelli & Kielan-Jaworowska 2005 (*Acta Pal Polonica*).

- lines 216-217: I would not call this a "widely accepted consensus" - plenty of paleontologists in recent years accept *Nano* as a valid species. Perhaps say "common hypothesis"

- Figure 6: This figure is improved, but I still find it a bit difficult to read, primarily because the taxon labels are so small. Because this paper really only focuses on the interpreting the portion of the tyrannosauroid evolutionary tree that is *Suskityrannus/Xiongguanlong* + Eutyranosauria, I would suggest they only show this part of the tree in the main text figure (Fig 6), so there is more space to enlarge the topologies to make it easier to read. The full tree can still be showing in Extended Data Figs or Suppl Info, but with the current Figure 6 I had to zoom in to over 200% to be able to read the phylogeny.

(Remarks on code availability)

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Response to the Reviewers

We thank all reviewers for their constructive and positive feedback. Our reviewers' suggestions mostly focused on streamlining the narrative around the evidence for *Nanotyrannus* in the main text, as opposed to describing NCSM 40000. To accommodate this, we moved the anatomical description of NCSM 40000 (which was already couched in a comparative phylogenetic framework in the prior version) to the supplementary information, leaving only key anatomical details needed to advance our argument in the main text. Beyond this, the reviewers provided only minor suggested edits, of which, we have accommodated nearly all in this revision.

In addition, we have made some changes that we felt were essential to improve the rigor of our analyses and ensure its results are as up to date as possible even though these were not requested (or in one case required) by our reviewers. This includes:

1. Coding the Mongolian tyrannosaur *Khankhululuu* (described while our paper was in review) into our matrix and rerunning all 8 of our phylogenetic protocols (4 parsimony and 4 Bayesian). We are happy to report that the addition of this new taxon does not change any of our conclusions. Our supplementary data files have been updated accordingly.

2. Dr. Funston's comments on sensitivity analyses for our growth models inspired us to tackle some additional modeling. These changes were not requested by Dr. Funston (or any of our other reviewers), but we wanted to address the spirit of his comment (providing sensitivity tests of the CGM data). We did this by applying different analytical approaches to growth models, as we did with phylogenetics, as a means to improve the rigor and appropriateness of our results. Thus, in addition to using nonlinear fixed-effect models (reported in our previous draft), our paper now includes retrocalculated ages derived from nonlinear mixed-effect models. Fixed-effect models and mixed-effect models each have strengths and weaknesses, which we detail in our Methods section, and both have been used in recent literature. In short, fixed-effect models are most appropriate for species when modeled from a single specimen (*N. lancensis*, and *N. lethaeus*, as well as specimen-level models of *Tyrannosaurus*) but do not allow flexibility in age retrocalculation between individual specimens when modeling a taxon using multiple specimens (e.g., our higher taxonomic level models). We also decided to explore the plausibility of *Nanotyrannus* specimens representing juvenile *Tyrannosaurus* in an "All *Tyrannosaurus*" model because we believe that readers would want to see how well (or in this case, how poorly) a single model fits a combined *Nanotyrannus/Tyrannosaurus* dataset. Our growth model figure and supplemental files have been updated to reflect these new data. Although we feel they add additional rigor to our study, the new mixed-effect models do not change any of our previous conclusions.

We detail our responses below in red text and provide a reviewer copy with changes marked in red, and a clean copy with our resubmission.

Referee #1 (Remarks to the Author):

I have read the manuscript by Zanno and Napolitano. The study describes a new specimen of tyrannosauroid dinosaur from the Late Cretaceous Hell Creek Formation, which is directly relevant to the debated taxonomy of *Tyrannosaurus/Nanotyrannus*. In my opinion, the paper is comprehensive, strongly argued, and about as decisive on the issue as the fossil record can be.

I feel that it is important to contextualize some of the philosophical issues at play in the *Nanotyrannus/Tyrannosaurus* debate. This, at its core, is a lumpers/splitters debate. That is, it centres around how different scientists interpret the same data, and whether, when presented with variation in the fossil record, our default assumption should be that it represents a taxonomic difference (splitters) or simply intraspecific variation

(lumpers). There is no correct answer, and the problem is impossible to escape. Through self reflection, I have identified that my philosophy is that of a lumper: I treat species as alternative hypotheses, meaning that we must falsify the default assumption of shared taxonomy. This will necessarily impart a bias in my review, and other reviewers and scientists will have different perspectives that impart their own biases.

However, despite my initial perspective, the information that the authors present in this manuscript is, in my eyes, incontrovertible evidence that *Nanotyrannus* and *Tyrannosaurus* are two different taxa. The new specimen shows a suite of differences across the skeleton that cannot be explained by ontogenetic transformation, and the authors demonstrate that they are outside of the range of intraspecific variation. Even if several of the characters are likely controlled by allometry, the histological evidence of skeletal maturity (or nearly so) in this specimen confirms that these differences remain useful diagnostic characters. As the authors outline, this is the key point: establishing skeletal maturity for a *Nanotyrannus*-morph individual is the ‘smoking gun’ that has been sought in this debate.

I was initially a little more hesitant to accept that the magnitude of differences between BMRP 2002.4.1 and NCSM 40000 are sufficient to establish a new species, but I will concede that this may simply be my human reaction to rejecting too much change when it comes all at once. Upon reflection, I have no arguments against any of the characters listed, and I agree with the authors that they are substantial differences unlikely to be attributable to ontogeny. Indeed, some of my own work shows that characters like 2nd dentary tooth reduction are established prenatally, so I can’t really argue that they’re not valid.

There are two main emphases in the manuscript: tyrannosaur anatomy, and palaeohistology. I am familiar with both fields but I am not as well versed in tyrannosaur anatomy as the authors, nor, likely, some of the other reviewers (although if you feel you need suggestions for experts in this field, I can recommend some). Accordingly, my focus will be on the palaeohistology, as I feel that I can comment more authoritatively, but I have a few comments about the anatomy as well.

Anatomy:

- In my reading through the main text and supplementary information, I cannot identify any major anatomical inconsistencies, although others may have a better knowledge (or stronger opinions) of the details of tyrannosaur anatomy and the referenced specimens in particular.

No edits requested.

- To me, the differences noted between *Nanotyrannus* and *Tyrannosaurus* are substantial, and characters like the opposite locations of cornual processes, presence/absence of foramina in the quadratojugal, and especially highly divergent forelimbs, are highly unlikely to be intraspecifically or ontogenetically variable. Therefore, they support the taxonomic distinction of these specimens.

No edits requested.

- I am unclear on one of the autapomorphic features the authors identify: the lack of a subnarial foramen. To my eyes, there is a gap between the maxilla and premaxilla on both sides of NCSM 40000, which is similar in expanse to the subnarial foramen described in ‘Sue’ by Brochu (2003). Indeed, the pointers on Extended Data Fig. 1i seem to point to such a foramen. [[Note, I cannot seem to find captions for the Extended Data Figures, so it could be that this panel is intended to show the presence of the feature, and has been mis-annotated. In any case, it would be useful to have Extended Data captions somewhere in the manuscript.]] In any case, it would be useful if the authors could provide a more detailed comparison figure showing what this feature looks like when it’s present, compared to what exists in NCSM 40000, especially because it is a key trait in the manuscript.

The appearance of a subnarial foramen in *Nanotyrannus* specimens is an artifact of damage. This region of the maxilla is commonly broken in tyrannosaur specimens, but even with damage the margins of the subnarial foramen are usually apparent. We do not see any clear evidence of one in *Nanotyrannus*, and additionally could not find a corresponding channel on the articular surface of the premaxilla in NCSM 40000 or BMRP 2002.4.1. A channel is present in tyrannosaurids bearing a subnarial foramen in this region. Although we cannot exclude the possibility that this foramen was extremely minute in *Nanotyrannus*, all signs point to absence. We have clarified this point further in the text.

Also, we have added extended data figure captions.

Palaeohistology:

- Overall, the palaeohistological analysis is done well. Based on the images and data provided, I come to the same conclusion as the authors, that the new specimen represents an individual in the asymptotic growth phase, which corresponds with skeletal maturity. This is an animal that is highly unlikely to grow to the size of an adult *T. rex*, or indeed, much more at all. The authors emphasize that their approach underestimates age and maturity, and I agree that they have been maximally conservative.

No edits requested.

- I think the authors' reinterpretation of Woodward et al.'s (2020) data is reasonable, and in comparison with the new data the other specimen provides, the patterns make more sense.

No edits requested.

- I was able to replicate the growth curve analysis using the script provided, and I cannot identify any errors in the code, underlying data, or resulting analyses.

No edits requested.

- The authors comprehensively outline the terminology they follow, which is important because histological terminology is a mess, and these thin sections are quite complex. While the authors choose to follow Woodward et al.'s (2013) definition of LAG as an annual CGM, they should be aware that some other groups have essentially equated LAGs with rest lines, as component parts of CGMs, which may or may not be annual (e.g., Ch. 31 in de Buffrénil et al. 2021). If the authors wish to avoid this discrepancy, they could use the term "Annual mark" in place of LAG in their figures, which would make clearer to readers the interpretations of these structures. If they do choose to retain their terminological scheme, I would recommend that they outline this in the main text methods, so that readers familiar with the term LAG don't have to go too far to determine which definition is being used.

We agree that the terminology for bone histology is, lamentably, inconsistent in the literature. Because of this, we felt it essential to specify the definitions we follow (Woodward) and to provide an extensive discussion of these issues in the supplement, which, as Dr. Funston notes, we have done, even including a figure that illustrates our usage. However, we agree that this information is currently buried in the supplement, which is not ideal. Therefore, at Dr. Funston's helpful suggestion, we have added the definitions we are following to the main text methods. Although no reviewer requested it, we also reconsidered our new term "CGM couplet" and have changed it to "CGM cluster" because we recognize the term "couplet" refers to a pair, and sometimes these closely spaced CGMs are found in triplet or more, thus the term "cluster" would be more appropriate.

- The authors outline their logic for selecting which CGMs within CGM complexes they select as annual bands in NCSM 40000, used for calculating body mass for the growth curve. If they want to fully dispel any uncertainty, they could present a sensitivity analysis that shows growth curves for the alternative interpretations of the CGMs that they consider. Essentially, this would further demonstrate that there's no way to interpret the observed marks as indicating an individual in the exponential phase of growth. This is optional in my eyes, but wouldn't be very difficult to implement, seeing as their data analysis pipeline is automated.

Dr. Witmer also asked us to clarify what the Woodward et al. (2013) approach would yield in terms of an age estimate for NCSM 40000. Put simply, Woodward counted each growth marker as an annual marker, so in this case, the Woodward approach would yield an age estimate for NCSM 40000 of at least 26 years at death. As we note in our manuscript, our estimate is the most conservative test of the juvenile *T. rex* hypothesis because it yields the shortest life span and highest annual growth rates for NCSM 40000 that can be reasonably interpreted from the data. We do appreciate Dr. Funston's suggestion, but for several reasons (including his statement that it is not an essential addition) we have decided not to make this change. First, as we have 20 models that include NCSM 40000 already summarized and reported in the main text and supplement, we feel that reporting results for an additional 20 models that represent *a less conservative test* of the "*Nanotyrannus* as juvenile *Tyrannosaurus*" hypotheses would not strengthen the manuscript. Additionally, we have already met our extended data figure limit, and would not be able to figure these models. Instead we have included the new mixed-model approach to test the sensitivity of our CGM data to variation in model approach.

I have not attempted to reproduce the phylogenetic analyses because of the computational power required, but I have taken a look at the priors for the Bayesian analysis and they seem appropriate. There are no aberrant results that would cause me to suspect an error in the analyses, and the authors do a good job of addressing unexpected findings and urging caution where necessary.

No edits requested.

I don't think it's reasonable to expect the authors to incorporate the recently-named *Khankhuuluu* into their phylogenetic dataset, even if it might have an impact on the evolutionary and biogeographic scenarios they discuss. This would require a considerable amount of extra work in scoring the taxon, as well as non-negligible computing time re-running the analyses. Instead, I think this recent study is better dealt with via discussion of the implications of the Voris et al. (2025) paper in the last paragraph of the Discussion. The authors may also wish to emphasize some of the anatomical comparisons they draw, for example in the pectoral girdle. These provide stronger evidence for a non-tyrannosaurid affinity of *Nanotyrannus* now that MPC-D 100/50 is understood as a stem eutyranosaurian itself.

Khankhuuluu was published after the initial submission of this MS. While we appreciate Dr. Funston not requiring us to repeat computationally intensive analyses with a new species, we felt it was essential to rerun our phylogenetic analyses to include this taxon and accommodate any changes to character polarity introduced by a relatively well-represented mid-grade tyrannosauroid. We received high-resolution images from the authors of the recent description of *Khankhuuluu* and have included it in revised versions of all phylogenetic analyses. Happily, *Khankhuuluu* had a minimal impact on our phylogenetic topologies, and none of our interpretation or argument is affected by inclusion of it in our analyses.

In addition, we now draw anatomical comparisons to *Khankhuuluu* and discuss the implications of the Voris et al. (2025) manuscript throughout, as requested by both Drs Funston and Witmer.

In addition to these comments, I have made some minor suggestions to the text and corrections to typographical errors in the attached documents, using the "Track changes" features of Microsoft Word. I realize that Nature prefers

all edits spelled out, but this would be very difficult to do because the document provided does not have page or line numbers.

Below we summarize the changes requested by Dr. Funston directly on our manuscript files and our response. All minor typographical errors were corrected as suggested and we thank Dr. Funston for his careful read through of the manuscript!

Edits requested to the Main Text:

If there are quantitative ranges of intraspecific variation established in these groups, it would be helpful to compare these to the 15% documented for *N. lancensis* and *T. rex*, to contextualize that this is much larger than expected for intraspecific variation

We added a citation for range of variation in fish (~5%)

Edits requested to the Supplementary Information:

It was requested that we combine the traits of a humerus longer than femur, and a hand longer than femur.

We feel these are best treated separately as our observation is that arm reduction in tyrannosaurs does not proceed uniformly across the forelimb elements, but is instead modular.

It was requested that we reiterate characters previously published as being shared with *Nanotyrannus* and *Tyrannosaurus*.

We have added a new section to the in text manuscript that discusses key characters in this argument so this has now been addressed in the main text.

It was requested that we add an interpretive figure clarifying the articular surfaces of the forelimb elements.

Unfortunately, we are at our maximum limit for extended data figures; however, a paper on the unique forelimb morphology of *Nanotyrannus* is underway that will soon alleviate this concern.

It was requested that we provide ratios of PI-1 and femur lengths for other taxa.

We have added ratios from additional taxa in the supplementary information as requested.

It was requested that we provide comments about whether the shape and size of the maxillary fenestra is individually or ontogenetically variable.

We have added a note about how this feature varies ontogenetically: “The maxillary fenestra does elongate with positive allometry in tyrannosaurid ontogeny, but even the smallest juvenile *Gorgosaurus* spp. specimens have maxillary fenestrae that are proportionally similar to adult conspecifics.”

In addition, as requested by Dr. Funston, we:

- added figure citations to the supplementary description of NCSM 40000
- changed “caudals” to “caudal vertebrae”
- added the specimen number for the isolated quadratojugal from the Dinosaur Park Formation

-specified the species in multispecific genera in our description or added 'spp.'

-added stratigraphic overlap of *Tyrannosaurus* and a scaled silhouette of *Tyrannosaurus* to Figure 1.

As there is identifying information in my review and annotated files, I am willing to waive anonymity.

Sincerely,

Gregory F. Funston, PhD
Visiting Assistant Professor
University of California, Davis

Referee #2 (Remarks to the Author):

This manuscript is very much anticipated, to say the least. The discovery of the “Dueling Dinosaurs” reached the attention of the public about 15 years ago, and then in 2013 Peter Larson presented a poster on the tyrannosaur at the Society of Vertebrate Paleontology meeting in LA. As the specimen was still in private hands it remained in purgatory until the North Carolina Museum of Natural Sciences purchased it in 2021. At that point the game was on, leading up to this manuscript. This manuscript is very compelling, presenting diverse lines of evidence that show conclusively that *Nanotyrannus* is not only a valid genus but holds two species, findings that have more implications than this manuscript can really address (as the authors state), although they touch on a few. I won't go over the osteohistology and phylogenetics in any detail but both were particularly innovative and well done, perhaps even a quantum advance in both arenas. The biogeography was also really interesting (the idea that nanotyrannosaurids may have had their roots in Appalachia is fascinating!).

A key strength of this manuscript is that it's a dispassionate exposition of scientific reasoning leading to its conclusions rather than an advocacy piece, which is refreshing. The “*Nanotyrannus* debate” has had some solid scientific discourse but has also sometimes degenerated into an eye-rolling weariness of back-and-forth vitriol, often involving whispers about a passel of annoyingly nicknamed specimens in private collections. The fact that the authors here are not among the “usual suspects” in this debate, with little to no prior investment or axes to grind, immediately presents the opportunity for a fresh look, which this manuscript offers—along with a boatload of brand-new analyses. It's important to emphasize that there is much more at stake here than declaring a victor in a pissing match, as there are literally decades of research and dozens (probably hundreds) of publications based on a premise that this manuscript overturns. *Tyrannosaurus rex* has emerged as something of a model species given its great fossil record and has been a centerpiece in evolutionary analyses of functional morphology, ecology, biogeography, and phylogenetics, but these analyses will all need revision. So, yes, this manuscript is very effective. However, it still needs some work to be ready. The authors are permitted to know that this review is by Larry Witmer (Ohio University), in case they want to reach out to me for clarification on any of the points that I raise.

I'll present some general issues and then follow up with a bunch of small things, typos, etc.

1. First, a bookkeeping thing... If there were captions for the Extended Data figures, I couldn't find them. I could kind of figure it out, but captions would be helpful.

We have added extended data figure captions.

2. Line 1: The title (“*Nanotyrannus* and *T. rex* cohabited at the close of the Cretaceous”) is okay, but “co-occurred” or “were contemporaneous” might be better. “Cohabit” has more of a “shacking up” vibe, and Webster's defines it as “to share a home and have a sexual relationship.” Lol.

We struggled with this as well. Although we felt “co-habited” is an appropriate term for two animals inhabiting the same ecosystem, we changed “co-habited” to “coexisted.”

3. New-ish works that should be considered for incorporation.

a. Longrich & Saitta (2024) is indeed cited but only twice (that I counted) in the main text and just in the context of being an advocate for Nanotyrannus being valid. Obviously L&S 2024 present lots of analyses and characters that merit citation and discussion.

b. Voris et al. (2025) just published a major article here in Nature about a new tyrannosauroid. Khankhuuluu itself may not be all that relevant but their SI has relevant discussions of numerous tyrannosauroids, including Nanotyrannus, which they regard as a juvenile T. rex. Their section on Nanotyrannus has relevant discussions of some of the key characters discussed here (e.g., tooth counts, QJ pneumatic foramen).

c. Witton (2025) just published a book titled “King Tyrant.” Although it’s a “popular book,” it’s well referenced and has a lot of interesting discussions, including a presentation of Nanotyrannus (which he regards as a juvvu rex).

d. Paul (2025: <https://doi.org/10.11646/mesozoic.2.2.1>) came out so recently (last night, as I write this) that I haven’t had a chance to do much more than buzz through it, but there are lots of citable and discussable points. For example, he also thinks Jane might be a different species of Nanotyrannus and tentatively refers NCSM 40000 to Stygivenator.

• In general, all these recent publications reflect how hot this topic is right now. They also highlight how important and timely the Zanno & Napoli manuscript is, given the detailed careful analyses and their unique access to perhaps the most relevant specimen (NCSM 40000). I regard the scholarship in the above four works as worthy of attention. This debate has sometimes had a somewhat disturbing tendency to hinge on elite academics versus non-degreed, non-party-line outsiders...which kinda ain’t right.

We now cite Longrich and Saitta (2024) in more locations in-text and have added a few sentences on how their growth model approach compares to our own in the main text (some of this information was previously included in the supplementary information due to space constraints). We also include discussion of Voris et al. (2025) and Paul (2025) where appropriate in the main text. While we do not doubt that Witton (2025) is a valuable summarization of the *Nanotyrannus* debate, neither author has yet been able to read it and given limits on reference number, do not consider it prudent to cite it at the expense of peer-reviewed work more directly relevant to our research here.

4. Thoughts on basic organization. I struggled with the organization when I hit the sections “Ontogenetic Assessment” (starting on line 196) and “Differential description” (starting on line 225). The headers don’t say it, but I eventually figured out that these were basically dedicated to NCSM 40000.

a. As I’ll advocate below, there might be a better way to organize the main text, but first a couple comments on the “Differential description” section as it stands now. The section headers don’t indicate that the focus is on NCSM 40000. And, given its position under the Nanotyrannus section, shouldn’t it also be focusing on CMNH 7541 and Jane? It’s hard to tell which specimens/species the description pertains to. Also, there’s no clear organization to these sentences or their sequence. Sometimes sequential sentences pertain to the same character, but then it can be hard to know whether the subsequent sentences pertain to the previous one or is a new character. Maybe this needs to be broken into a series of numbered items. It’s also pretty detailed “inside baseball” stuff, which I’m loving but may be too much for the general readership of Nature. The SI also has a lot of description of NCSM 40000 (and a separate monographic treatment is promised), so there’s some redundancy. The description here in the main text runs on for almost four pages and maybe should be more focused.

We moved the description to the supplement and edited it for clarity.

b. I’ll pull this out as a separate point... In truth, the manuscript isn’t (or shouldn’t be, in my view) **about** NCSM 40000 but rather about establishing the validity of Nanotyrannus. Obviously the new specimen is a

key document in this argument, but the distinction is important. It shouldn't be "hey, look at this new specimen which has implications" but rather, "hey, look at this important scientific hypothesis, which now has an important new test based on the new specimen.” The authors may disagree with my assessment because they have this sweet new specimen, but I’m positive that the rest of the world will see this publication as being *about* the validity of *Nanotyrannus* and how decades of research on the most famous dinosaur may be wrong. So please don’t bury the lede. :)

c. The authors actually present the following summary statement in the Discussion (lines 467–471), which is super important as a summary statement, but it may also suggest a new and better outline for presentation of the argument: “In combination, four independent lines of evidence—osteohistological indicators of somatic maturity, shared autapomorphies between CMNH 7541 and NCSM 40000, absence of synapomorphies exclusive to *Nanotyrannus* and *Tyrannosaurus*, and ontogenetically invariant characters differentiating *Nanotyrannus* from *Tyrannosaurus*—demonstrate beyond reasonable doubt that *Nanotyrannus* is a valid taxon.” These four “independent lines of evidence” could be four sections, probably in that order. In other words, hit the main points hard—so that they can’t be missed—in the main text. You can fold in a pile of anatomy/description as you go, but it’ll be just the anatomy that is central to the main point; the rest will be in the SI. Yes, this may require a rethink and a rewrite, but it may make the manuscript that much more compelling.

We appreciate the helpful feedback about the organization of the manuscript, and upon consideration agree with Dr. Witmer’s proposal. In accordance, we have significantly restructured our manuscript to focus on our four independent lines of evidence. We hope that this new organization will simultaneously highlight new data derived from NCSM 40000 and its implications for the *Nanotyrannus* debate. We feel it essential to provide a description of NCSM 40000 and summary of important characters of *Nanotyrannus* in a comparative framework in this publication. Thus we have moved our detailed description of NCSM 40000 to the Supplemental Information.

5. As for the ontogenetic assessment (“osteohistological indicators of somatic maturity”), this probably should indeed be the first topic to take on. It might be beneficial to state at the outset of the section that it’s particularly important to establish the ontogenetic status of NCSM 40000 given that so many attributes of putative *Nanotyrannus* specimens have been regarded (even dismissed) as early stages of the ontogeny of *T. rex*.

Alleviated by the reorganization of the text.

a. In truth, the osteohistology/skeletochronology here will be the target of those likely to be resistant to the validity of *Nanotyrannus*. I’m no expert on osteohistology, but I’m pretty well acquainted with the issues involved, and I have to say that I’m very impressed with how the authors carried out this component. Still, the fact that NCSM 40000 is almost at somatic maturity is so important to the argument that critics will be looking very closely at all the skeletochronology. Longrich & Saitta (2024) and Paul (2025) also discuss histology (based mostly on literature reports in both cases), and their discussions are relevant.

Thank you. We have added additional citations to the recent Longrich and Saitta manuscript and some methodological comparisons in text.

b. Carr (1999) made a big deal about “immature bone grain” in CMNH 7541—it was the first piece of evidence that he listed in the abstract—and it was influential for years (it was all the rage in the late ‘90s, with Scott Sampson’s team also using it as supposedly a size-independent indicator of age). That line of argumentation seems to have faded but was mentioned in Mark Witton’s recent book (*King Tyrant*) and by Longrich & Saitta. It’d be useful to discuss that here. Does NCSM 40000 have surface bone textures that shed any light?

We did not investigate the periosteal texture of the bones on NCSM 40000. We feel that despite its wide usage as an ontogenetic indicator several decades ago, most of the research on this topic remains unpublished/peer reviewed,

and the categorization of “immature bone grain” remains coarsely defined and subjective. Although we find this topic interesting and agree it is worthy of further investigation, we feel it is beyond the scope of this manuscript and more importantly, that the osteohistological data we present is a more rigorous way to approach an assessment of skeletal maturity.

6. “Shared autapomorphies between CMNH 7541 and NCSM 40000” also needs to be prominent. Another (maybe a better) way to put it would be “basis for referral of NCSM 40000 to *Nanotyrannus lancensis*.” This basis was frankly a little hard to extract from the current text. In terms of the logical flow of ideas, the two key elements are (1) NCSM 40000 is not a juvenile but rather is close to somatic maturity and (2) it has unique features that resemble CMNH 7541 and dictate referral to the same species.

a. The holotype CMNH 7541 is only cited a few times in the main text outside of introductory material; same with the SI. There’s maybe just a single image of the holotype skull and it’s just a single CT slice (Extended Data Fig. 1n). If anything at all is *Nanotyrannus*, it’s the holotype, CMNH 7541. **Thus, it seems that a more formal accounting of why NCSM 40000 can be referred to *N. lancensis* is in order, probably with illustrations, and in the main text. The SI (lines 97–109) has a “Differential Diagnosis [of?] *Nanotyrannus* and *Tyrannosaurus*” but again there’s no means of easily checking what features of the skull of NCSM 40000 justify referral to the same species as the holotype.**

b. My team has some of the bony elements of CMNH 7541 segmented, including the braincase with columella, and would be happy to provide them to the authors, if that would help.

This is accommodated by the Systematic Paleontology section, which lays out the anatomical argument for referral of NCSM 40000 to *N. lancensis* as well as *N. lancensis* and *N. lethaeus* to *Nanotyrannus*. We think its sufficiently covered in the Sys Paleo portion of the manuscript and simply lack space to repeat this information in the discussion.

7. The last two remaining sections—“absence of synapomorphies exclusive to *Nanotyrannus* and *Tyrannosaurus*, and ontogenetically invariant characters differentiating *Nanotyrannus* from *Tyrannosaurus*”—also would merit their own sections. My intent here is to suggest an organization that would help convey the compelling nature of the evidence the authors have amassed, which will help convince the readers that the conclusions are inescapable. If you can’t convince the readers of the validity of *Nanotyrannus*, then the phylogenetics, biogeography, etc. won’t have much impact.

With the restructuring, these are now subheadings of the main text : “*Nanotyrannus* is Diagnosable By Ontogenetically Invariant Characters” and “*Nanotyrannus* Shares no Exclusive Synapomorphies with *Tyrannosaurus*”.

More minor points, typos, etc...

8. Lines 48– 51: The second sentence of the opening paragraph (“As one of the last surviving non-avian dinosaurs, a crucial datum for assessing terrestrial biodiversity, ecosystem structure and stability, and biogeographic exchange immediately preceding the end-Cretaceous mass extinction event—one of Earth’s greatest biological catastrophes.”) is not a complete sentence.

Corrected

9. Line 54: The term “hypodigm” may be too jargony for the opening paragraph. It’s not all that widely used in paleontology, and its meaning is not apparent from the roots of the word.

Perhaps, but we prefer to keep the term.

10. Lines 60–61: Regarding “ontogenetic invariance in extant archosaurs” doesn't really seem to factor in here in this manuscript, at least not enough to merit mention in the opening paragraph.

Our restructuring has brought more emphasis to this point, so we have chosen to retain a reference to it in the opening paragraph.

11. Lines 110–111: Regarding listing BMRP 2006.4.4 as referred material directly under *Nanotyrannus* seems a little weird here. I get that you're not referring this specimen to either species (it's *Nanotyrannus* sp.), but it seems odd, if only because it seems like the only specimen referred to the genus. Maybe there's a different way to notate this sense.

No longer relevant due to restructuring.

12. Line 133: “absolutely larger forelimb elements.” This could be interpreted as ALL forelimb elements are absolutely larger. Figure 6 indicates that the humerus is absolutely shorter. Is it just the hand that's absolutely longer than in *T. rex*. If so, say that.

We have changed “forelimb” to “manus.”

13. Line 142: *N. lethaeus* sp. nov. is presented first. Shouldn't the existing species, *N. lancensis*, be presented before the new species?

This was also requested by anonymous reviewer 4. We had a reason for the prior order that is now irrelevant in the restructuring, so we have adjusted the order as requested.

14. Line 157: “was” should be “were.”

Corrected.

15. Line 172: For the name *Nanotyrannus lancensis*, shouldn't Bakker et al. 1988 be listed?

According to the ICZN, the authorship attribution does not change when a species is transferred to a new genus name; however, it should be enclosed in parentheses: article 50.3.2. “Change in generic combination of a species-group name does not affect its authorship” and 51.3. “When a species-group name is combined with a generic name other than the original one, the name of the author of the species-group name, if cited, is to be enclosed in parentheses (the date, if cited, is to be enclosed within the same parentheses).” We have attributed “*Nanotyrannus*” to Bakker et al. but not *N. lancensis*, which should remain listed as (Gilmore 1946)

16. Line 227: Are you trying to reference the skull figure? Seems like it might be Ext Data Fig. 7, not 6.

No longer relevant due to restructuring.

17. Line 251: missing words. It should be “between *Nanotyrannus* and *Tyrannosaurus*”

No longer relevant due to restructuring.

18. Lines 257–258: Regarding “*Tyrannosaurus* entirely lacks a lacrimal cornual process,” *T. rex* has lacrimal osteoderms, so does the attachment area on the lacrimal count as a cornual process?

No, we don't consider this homologous since it is not a process.

19. Line 263: "marred" probably isn't the best word here. Maybe "Instead, it has rugose striations...." would be adequate.

Changed

20. Line 273: Probably should be "most other tyrannosaurines"

No longer relevant due to restructuring.

21. Lines 277–279: Regarding “The lateral surface of the quadratojugal is pierced by a small pneumatic foramen, a trait also present in the mid-Cretaceous tyrannosauroid MPC-D 100/50...” Voris et al. 2025 talk about this character and these specimens and should be minimally cited or even discussed. Also, should this be MPC-D 100/05 rather than 100/50? Voris et al. (2025) make reference to MPC-D 107/5 having a QJ pneumatic foramen. Whether people use the leading 0 (05 vs. 5) seems variable.

We have added some discussion of this feature to the manuscript. For your convenience, we summarize it herein. Jared Voris has kindly shared high-resolution images of *Khankhuuloo* now that the taxon is described, and we have changed our interpretation of its quadratojugal. What we thought was a foramen in low-resolution images appears to be a break, though it is possible that some margin of it is natural; we note that Voris et al. did not report a foramen here in their discussion of the feature in other theropods, and surmise that they also consider it an artefact of damage. We have added some discussion of the quadratojugal pneumatic recess to the main text, and disagree with Voris et al. We interpret the foramina they identify as neurovascular, not pneumatic, based on their small size. By chance, both Jared Voris and one of us (JGN) overlapped in collections work at the Royal Tyrrell Museum of Paleontology, and Jared showed him putative “quadratojugal recesses” in *Gorgosaurus* that we interpret as small neurovascular foramina. An isolated quadratojugal in that museum (TMP 1997.12.17), from the Dinosaur Park Formation, does clearly have a quadratojugal recess like *Nanotyrannus*. This has been interpreted as a juvenile *Gorgosaurus* quadratojugal (and thus, as evidence for this being a feature of young tyrannosaurids), but the specimen does not have autapomorphies facilitating a specific referral; in fact, the rostrally-displaced dorsal jugal facet is most reminiscent of *Daspletosaurus*. Given that *Daspletosaurus horneri* has been shown to have a quadratojugal recess, it seems very possible that this is simply a *Daspletosaurus* quadratojugal, which would make the quadratojugal recess unremarkable. [REDACTED]

22. Lines 284–285: Regarding “The braincase of *N. lancensis* is only preserved in articulated specimens, where it is difficult to visualize...” We segmented the braincase out of CMNH 7541 (W&R 2010) and illustrated it with labeled stereopairs in multiple views. I can provide an STL, if needed.

Thank you for this kind offer. We feel the comparisons we needed to make in this manuscript were visible with the data we had at hand but would welcome the STL for future work.

23. Lines 309–311: Tooth counts were already discussed earlier in this section, so this might be a bit redundant.

No longer relevant due to restructuring.

24. Line 355: Regarding “of one of the largest known *T. rex* individuals”, state which individual (presumably FMNH PR 2081).

Added

25. Line 358: Did you want "is" italicized (e.g., for emphasis) or is it left over from the taxon name?

Corrected

26. Lines 394–400: The manuscript needs more passages like this that really distinguish *Nanotyrannus* from *T. rex* and why they can't be the same species.

This text is now combined under the subheading: “*Nanotyrannus* Shares no Exclusive Synapomorphies with *Tyrannosaurus*”.

Also, "precipice" is spelled incorrectly.

Corrected

27. Lines 448–450: Regarding tooth count reductions, Voris et al. 2025 (the Khankhuuluu article) says in the SI that "tooth count reduction in *Tyrannosaurus* is present in the CT scans of the adult specimen FMNH PR 2081 where a resorbed 13th alveolus is present at the posterior end of the left maxillary tooth row." Also, what about mysticetes that kinda develop teeth as fetuses but then switch over to baleen? <https://doi.org/10.1111/joa.12579> Is that tooth count reduction that's known in amniotes?

We have added discussion to our main text to address the points raised by Voris et al. (2025), with which we disagree. We have also now clarified that we are speaking about developmental loss of tooth positions *postnatally*, rather than a developmental process involving a complete loss of teeth and replacement with some other tissue (e.g., a beak or baleen). Unfortunately, we do not have room in text to include discussion of cetaceans in our manuscript, but note here that we consider the above reference to corroborate our interpretation. In mysticetes, tooth position patterning occurs early in embryonic development, tooth loss is a prenatal process, and it involves a complete loss of the dentition, rather than merging or obliteration of select tooth positions later in life. We also feel it important to mention the inherent disagreement of Carr (1999) and Voris et al. (2025). Carr (1999) posited that the mesial-most alveoli were lost during *T. rex* ontogeny, while Voris et al. (2025) posits loss from the distal end of the toothrow. We have added this consideration to our manuscript and hope the revised text is more circumspect in describing only postnatal loss of select tooth positions, which to our knowledge is not a part of the normal (i.e., non-pathological) developmental program of any amniote that does not entirely replace its dentition with another tissue (e.g., ramphotheca or baleen).

28. Line 460: Should be MPC-D 107/7

Corrected

29. Line 495–497: I understand use of "failure" here but pitching it differently may raise fewer hackles...and I think most workers who accepted *Jane* as a juvvy *rex* were honest and thought they were following consensus thought.

We agree and did not intend to imply dishonesty with the use of the word. We have modified the text.

Also, saying "did not mirror the spatial niche partitioning of their prey" is a little convoluted and obscures the point you're trying to make.

30. Line 506: Should be "Tyrannosaurus"

Corrected

31. Line 512: There is no Fig. 5e

Corrected

32. Line 523: There is no Fig. 5f

Corrected

33. Line 582: You could mention that CMNH 7541 was also scanned on that Philips scanner in June 2023. Maybe not a transformative scan but still another attempt.

Although these data ultimately were not used for this research, we agree that this should not be omitted and have updated our methods and acknowledgements accordingly.

34. Line 631: Should be "constrained"

Corrected

35. Line 654: What do you mean about "our" specimens? Better to state specimen numbers.

In lieu of relisting all specimen numbers, we just changed "our" to "all"

36. SI.1.1 Table of specimens: Under CM 9380, it should be "Firsthand" not "Firsthead" (although that's kinda true, too!).

Corrected

Also, I'm virtually positive that RTMP uses "TMP" as the museum prefix in catalog numbers. That is, they drop the "R". (I guess they're not fans of the Royal Family...which is on-brand for Alberta.)

Corrected

37. SI Line 100: Should be "absolutely"

Corrected

38. SI Line 102: As noted in #21 above, the SI for Voris et al. (2025, Khankhuuluu) has a discussion of this character and Nanotyrannus in general that will need to be incorporated.

We have addressed this.

39. SI Line 111: As noted above, how the description of NCSM 40000 is handled may need a bit of an overhaul, particularly if my suggestions for the reorganization of the main text are accepted.

We have moved the description to the supplement as requested.

40. SI Line 117: I think it'd be legit and helpful to remind the reader that the histology of NCSM 40000 suggests somatic maturity. As I was reading the descriptions I couldn't help thinking of the authors who have regarded the attributes as juvenile or "ontogenetic characters" and had to remind myself that you're arguing for somatic maturity. Thus, maybe it'd be beneficial to the argumentation to remind the reader from time to time, or at least with some of the more "classic" characters.

This is now accommodated in the restructured sections.

41. SI Line 162: The "A" in "as" should be capitalized.

Corrected

42. SI Line 208: My point #21 above pertains here, too. Should this be MPC-D 100/05? Voris et al. (2025) make reference to MPC-D 107/5 having a QJ pneumatic foramen.

No, we were referring to MPC-D 100/50 here, but this is no longer relevant as new high-resolution photos suggest this is more likely damage (see above)

43. SI Line 239: Italicize the "T. " in T. rex

Corrected

44. SI Line 276: Should be "pneumatopores"

Corrected

45. SI Lines 313–314: Regarding “We also take a conservative approach by not adding conditions observed to the species-level diagnoses for these taxa.” Not sure what you mean by this statement. Reword?

We have reworded for clarity. It now reads “Apomorphies that can only be confirmed in one species of *Nanotyrannus* are conservatively listed in the genus diagnosis.”

46. SI Line 528: Do you mean "cortex" here...or "cortical"? "Cortice" seems like an improperly constructed singular of "cortices" which should be "cortex."

Cortice is used, but we have changed to the more familiar term “cortex.”

47. SI Line 533: "redacted" doesn't seem like the right word here.

Corrected to “reduced.”

48. SI Lines 562–564: Regarding “A more stringent 1:1 interpretation of CGM to growth cycle count, as employed in other studies of tyrannosauroid growth (e.g., Woodward et al.), would only strengthen the argument for a growth trajectory in NCSM 40000 distinct from that of FMNH PR 2081.” Can you provide an age estimate using the criteria of Woodward et al.?

It would be 1:1, meaning every CGM would be interpreted as an annual marker (in this case, 25 annual markers plus one incomplete year of growth periosteally, which equals an age at death of 26 years or greater). We added this as requested in the supplement because this sentence no longer appears in the main text.

49. SI Line 644: Should be "CGMs"

Corrected

50. SI Line 966: Should be "permitted"

Corrected

51. SI Line 1027: As you start to present the different topologies, it would be super helpful if you could relate these different topologies to the figures in the Extended Data and main text. Also, the character list in the "Parsimony Matrix" file is not particularly readable and looks like program output rather a more readable formatted document.

For space, we have reduced discussion of alternative topologies, and added appropriate references to the ED phylogeny figures. We have also added a phylogenetic character list to Supplementary Information, as section SI 1.12; we retain the list provided in the parsimony matrix file for convenience for any colleagues who wish to load it into Mesquite, MorphoSource, or similar programs while retaining character and state names.

52. SI Line 1080: Should be "Supplementary"

Corrected

53. SI Line 1094: Regarding *Stygivenator*, both Longrich and Saitta (2024) and Paul (2025) raise the question of whether NCSM 40000 could be *Stygivenator*. Paul even illustrates NCSM 40000 and labels it as “*Stygivenator? incertae sedis*”.

We have updated this section to cite Paul (2025) now that it is published, but our opinion on “*Stygivenator*” is not altered by this publication. It is distressing to see several publications (e.g., Longrich and Saitta [2024] and Paul [2025]) pass through peer review that discuss the “Dueling Dinosaurs” tyrannosaur specimen given that these researchers did not contact the NCSM to request access to work on the specimen, did not examine the specimen in person at the NCSM, and did not ensure the specimen had been accessioned and was available to the research community at the time they published on it (as evidenced by the lack of a specimen number in these publications).

• Respectfully submitted by Larry Witmer (Ohio University)

Referee #3 (Remarks to the Author):

Before diving into assorted minutiae relevant to this manuscript, I have two main points that I would like the authors and editors to consider.

Point 1. This is a fascinating, well-crafted and surprising manuscript, but also a troubling one since it indicates that mistakes in interpretation made by a previous set of authors misled an entire generation of dinosaur workers (maybe more than one generation) into making arguments (pertaining to histology and ontogeny, anatomical character states, and phylogeny) that are here stated to be erroneous, and based on misinterpretation.

The current ms does emphasize this point (lines 663-678 in particular; the Introduction – lines 76-81 in particular – does too) but this is such an important point that I wonder if it should be flagged more than it is, especially seeing as Carr et al. are accused of making “pervasive errors in character construction and definition” (lines 676-7) – ouch! What we’re saying is that social inertia – and/or ‘in-group’ membership – led to mass adoption of an incorrect conclusion. That’s a non-trivial issue that should have everyone more worried than they already are. Needless to say, further discussion of this issue would be scope for a social science study, not appropriate for the current ms, but I wonder if it might be appropriate to emphasize this even further. **I seriously wonder if words to the effect of ‘Reversing an erroneous consensus’ or such should be worked into the abstract or even the title. I personally find the title lacklustre given the massive interest there will be in this paper, and in the fallout and subsequent discussion... though I also recognise that the authors are being good, conservative scientists in using understated language.**

We know that there are (and will continue to be) strong feelings around this topic in the scientific community. Within our own pool of reviewers we received feedback that our language was too strong and not strong enough. We respectfully prefer to maintain a more “matter of fact” title and discussion of the data throughout our manuscript. We hope this approach will allow us to avoid the possible perception of courting controversy or inflicting judgement on previous researchers with our paper. Unfortunately, we are certain that the controversy will appear whether or not we court it!

Point 2. Given the heated nature of discussions on *Nanotyrannus*, the authors need to be as clear as possible in stating that there is no ‘massaging’ of the data in order to win the incredibly gratifying conclusions they report. While I congratulate the authors in being as transparent and forthright as possible in stating the work that was done and what conclusions were reached, I see points in which the wording implies data massaging. My suggestion is that the wording is changed such that things are better explained, or that extra text is added to precisely explain the relevant text segments. Consider the following...

In line 381, it is stated that inferred hatching age and growth rates are estimated by “[applying] an isometric allometric scaling mass adjustment”. The growth trajectory here is based on patterns presented in Erickson & Tumanova’s 2000 *Psittacosaurus* analysis. Rather than refer obliquely to an “isometric allometric scaling mass adjustment”, I recommend that the authors instead describe that a growth model was inferred based on a standardized or averaged (non-bird) dinosaurian pattern established for the ornithischian *Psittacosaurus*. I would also like the authors to state why a growth model for *Psittacosaurus* was used and not one incorporating data from multiple dinosaurian taxa – is this really because that for *Psittacosaurus* is the only one available?

We appreciate this comment, but it stems from a misunderstanding. The isometric allometric scaling mass adjustment is a standard correction used to account for allometry in body mass and body size during ontogeny, and is employed in all recent dinosaurian growth models. It allows for estimating the body mass of juvenile individuals from regression analyses that produce mass estimates only for adults. It is not based on *Psittacosaurus* (it is a standard equation applied to all dinosaurian taxa); instead, it was first introduced in that study, and that paper is cited as the source.

In line 395, it’s stated that published models positing an ontogenetic transition from *Nanotyrannus* into *Tyrannosaurus* present a “biologically implausible bimodal life history”. A typical response to assertions like this is that implausibility is not the same as impossibility, and the authors who’ve argued for this transition of course already regard *Tyrannosaurus* as an unusual, possibly unique, animal. It might be more appropriate to refer instead to a ‘bimodal life history that would be wholly unique within reported archosaur diversity’ or such. In addition, while I accept and agree with the authors’ assertion that the aforementioned ‘bimodal life history’ would indeed be ‘wholly unique’, the authors would better demonstrate this assertion if they listed appropriate citations: space is an issue, of course, but there are select good studies that make this point, and I see a dearth of citations in this section.

We have made the aforementioned edit.

Finally, lines 403–4 refer to a “new protocol for handling logical character inapplicability”. This sounds scarier than it is (the authors are referring to the moderately familiar Goloboff et al. 2021). I would reword the text here, something along the lines of ‘following accepted protocols of rejecting inapplicable phylogenetic characters’, since otherwise the text reads as if the authors have devised and are implementing a new way of excluding characters they don’t like.

Appreciative of the feedback. We did not intend to imply that we had developed a new phylogenetic algorithm; rather, our choice of words was intended to underscore the relative novelty of the approach, which has not yet been adopted by most dinosaur systematists. We have modified the sentence to more directly identify the method as that of Goloboff et al. (2021).

Taxonomy and phylogenetic definition. Any ‘family-level’ group anchored on *Nanotyrannus* cannot be ‘Nanotyrannosauridae’ because there is no ‘Nanotyrannosaurus’: it must instead be Nanotyrannidae. As precedent, the authors may not be aware that there is an extant dinosaur family based on *Tyrannus* (kingbirds), namely Tyrannidae. Use of ‘Nanotyrannosauridae’ and ‘nanotyrannosaurids’ later in the ms (lines 516–531, Fig. 5) needs to be changed in view of this.

Yes, we agree and have changed the clade name to Nanotyrannidae.

The phylogenetic definition is noted as being ‘stem’. That looks dated given that workers now mostly prefer to refer to ‘node-based’ vs ‘branch-based’ definitions, and this is a branch-based definition. This issue may be redundant anyway, as a ‘family-level’ term is itself redundant (in terms of phylogenetic nomenclature) with respect to *Nanotyrannus*... viz, there’s no need for a Nanotyrannidae in a system where we employ phylogenetic nomenclature. On the use of ‘stem’, line 511 (which refers to ‘stemward outgroups’) should be tweaked such that the lineages concerned are described as ‘early-diverging’ or such.

We have changed the phylogenetic definition to “branch-based,” and changed the term “stemward.”

Minor final observations...

Line 120: I’m of the unpopular (but anatomically correct according to *Nomina Anatomica* works) opinion that a bone like the quadrate does not and cannot have a ‘proximal’ end because proximal-distal terminology applies only to appendages. A quadrate has a ventral end and a dorsal end. ‘Proximal’ makes no sense when applied to this element.

Corrected, we agree.

Line 215: typo for ‘osteohistological’

Corrected

Lines 219 and 222: ‘cranialmost caudals’ should be ‘proximalmost caudals’ as per anatomical convention otherwise mostly used throughout ms

Line 303: ‘bounded caudally’ should be ‘bound caudally’ I think

Changed

Line 330: vertebral variation is not unique to the groups listed; some cetacean species are variable in vertebral count too.

This is certainly true! However, we are already over the recommended number of main text references, and since this is far afield phylogenetically from our study group, we have not added this additional reference.

Lines 343 and 344: are 'supraradiocondular' and 'ectepicondular' correctly formulated? I would think that they should be 'supraradiocondylar' and 'ectepicondylar'.

Yes, thank you for catching these typos!

Line 364: double use of 'is'

Corrected

Line 431: 'lacking exclusive synapomorphies with T. rex' should be "lacking exclusive synapomorphies shared with T. rex", though I appreciate the redundancy given the meaning of the word 'synapomorphies'.

Line 675: space missing in 'N. lethaeus'.

Corrected

Darren Naish

Referee #4 (Remarks to the Author):

This paper presents a comprehensive re-evaluation of the debate surrounding whether the theropod dinosaur *Nannotyrannus* is a juvenile of *Tyrannosaurus rex* or a distinct smaller-bodied species. The manuscript presents a stunning new fossil specimen of *Nannotyrannus*, along with a host of new gross anatomical, histological, and phylogenetic data. The authors have provided a comprehensive and incredibly convincing case that not only is *Nannotyrannus* a distinct and valid species separate from *T. rex*, but that there are actually two different species of *Nannotyrannus* from the Hell Creek/Lance Formation assemblage. As *T. rex* is the most iconic non-avian dinosaur species with a worldwide cultural saturation, there is no doubt this paper will appeal to the broad scientific readership of *Nature* (and when published, will certainly receive worldwide coverage from news media). More importantly though, it is an exemplary case study of how one should approach questions about the interplay of variation, growth, speciation, and phylogenetic evolution in the fossil record, where the fourth dimension of deep time can muddy the waters that are artificially clear for neontologists. Further, the results of this paper have important implications for the paleoecology of latest Cretaceous ecosystems. Nearly all Jurassic and Cretaceous non-marine ecosystems have a diversity of predatory dinosaurs occupying a wide variety of body sizes and ecological roles. The Hell Creek/Lance ecosystem has always appeared aberrant in lacking medium-sized theropod dinosaurs that would fill the 'mesopredator' role. Now we know that these dinosaurs were present - they had just been confused for juveniles of the giant *T. rex*!

The science presented in this manuscript is of the highest quality. Below, I note some issues with overall organization and the figures that should be rectified in revision. However, after these changes are made, the MS is certainly worthy of publication in *Nature*.

- Right now, the paper is couched in the context of the taxonomy debate about *T. rex*. The MS should be written for the broad readership of *Nature*, so should introduce the topic with questions that will interest those readers. Alpha taxonomy is boring for the non-theropod specialist. What is interesting is the implications of this taxonomic debate for how we interpret species in the fossil record, and what it tells us about the paleoecology of latest Cretaceous ecosystems. So that is what I would stress in the first two paragraphs, rather than the taxonomic debate itself.

We respect this opinion and prefer to leave the introduction narrative as drafted as we feel the history of the debate is both of interest to *Nature*'s readership and relevant to set the foundation for the research to follow.

- The diagnosis of *Nannotyrannus* should be differential (i.e., with some comparisons to other taxa) - if the debate has centered on whether it's synonymous with *T. rex*, then the authors need to emphasize in the main text diagnosis how it is different rather than referring reader to Supplementary Info.

We are a bit confused by this comment and unsure if we are misunderstanding. Taxonomic diagnoses are inherently differential by nature. Our diagnoses for the genus *Nannotyrannus* and the species *N. lancensis* and *N. lethaeus* include many autapomorphies, which are by definition, traits that differ from all other eutyranosaurians (therefore including *Tyrannosaurus*) and are explicitly marked with an asterisk. Moreover, we previously had an entire four-page description that made explicit comparisons to character states shared with and distinguishable from other eutyranosaurian species but were asked to move that section to the supplementary information by this same reviewer, which would seem to be in opposition to this comment. Regardless, we have now reorganized the text in such a way as to hopefully alleviate this concern. Specifically laying out the argument that *Nannotyrannus* does not share exclusive traits with *Tyrannosaurus* and adding some text in the sys paleo section explaining the specific traits that allow referral of NCSM 40000 to *N. lancensis*.

- Flip the order of *N. lancensis* & *N. lethaeus* in the Systematic Paleontology section. Now that *Nannotyrannus* is no longer monotypic, it's important to give a revised diagnosis of the existing species *N. lancensis* *before* you introduce the new species (*N. lethaeus*)

This was also requested by Dr. Witmer. We have flipped these in order.

- Radioisotopic dating is cited as "submitted". What is the guarantee that this will be accepted or published by the time this *Nature* paper is published? As a reviewer, I can't evaluate stratigraphic arguments because I have no access to this submitted geochron manuscript and none of the details are presented here. If for some reason the geochron MS is delayed or rejected, the reader has to take it on faith that the geochron data are correct and interpreted correctly. I don't know if this was submitted as a companion MS to *Nature* (much like is done with fossil hominids), or to another journal within NPG that will coordinate publication timing?

We have now submitted this in revision manuscript as a preprint so it is available to the reviewer for perusal and can be cited in this paper even if it is eventually published afterwards.

- The 'differential description' is difficult to read for anyone except a tyrannosaurid specialist. I suggest that it be rewritten a bit so it has a stronger, easier-to-read, narrative. It can remain organized in anatomical order, but should basically center around three things: 1) how *Nanno* differs from *T. rex* but there are shared apomorphic similarities the two *Nannotyrannus* species; 2) differences between the two *Nanno* species; and 3) character states that support the placement of *Nannotyrannosauridae* outside of *Tyrannosauridae*. In a *Nature* paper, the osteological description should focus on the anatomical highlights that support the main arguments of the paper, rather than trying to touch on every possible character state.

This comment mirrors that of Dr. Witmer's. To make our paper more readable for non-specialists, we have modified the way in which we present our data. We focus on key characters in the text in the context in which they factor into the lines of evidence we use to assess the validity of *Nanotyrannus*, rather than providing a dedicated osteological description in the main body. We have moved all descriptive text to the extended description in the Supplemental Information, so that it is preserved in the publication and available to the community while we draft the planned long-form description of this specimen. As we noted above, the main text is now reorganized into the following subheadings: "NCSM 40000 (*N. lancensis*) is Skeletally Mature," "*Nanotyrannus* is Diagnosable By Ontogenetically Invariant Characters," "*Nanotyrannus* Shares no Exclusive Synapomorphies with *Tyrannosaurus*," and "Evolutionary Relationships of Nanotyrannidae"

- There's no transition between the description, CGM, phylogeny, etc sections - the text just abruptly changes topic. Tell the reader a story, and provide some sort of bridge between these sections so they understand where you are going.

We have restructured our paper in response to this comment and feedback from the other reviewers, and hope that now forms a stronger and more easily understandable narrative.

- lines 450-451: you could also emphasize here that *Limusaurus* is not closely related to tyrannosaurs

We have done so in the revised text.

- Figure 1: The 'strat column' isn't really helpful because there's no detail here - it's just a box with dates at top and bottom. Also, the radioisotopic date for NCSM 40000 has uncertainty/error associated with it and should always be reported as such; stripping the uncertainty is misleading.

We did not refer to the age graphic in this figure as a "strat column" because as the reviewer notes, it is not a strat column. Our new data on Hell Creek stratigraphy casts doubt on the existing stratigraphic divisions within the formation, specifically the use of marker beds sometimes referred to as the "middle member." Our data suggest the stratigraphy is more complex and additional work is needed to define and trace a contact between the "upper" and "lower" beds across the study area. For this reason, we have made this part of Figure 1, very general, and tried to visualize the associated uncertainty. However, we respectfully disagree with the reviewer that it is not valuable as a component of the figure and Dr. Funston has asked us to add additional elements to this figure (see above), so we prefer to leave this component.

Age uncertainty was stated in the main text. We have added to the figure as well.

- Figure 1: the photo of the snout of NCSM 40000 is really dark - could be lightened slightly (similar to Figure 2)

We have modified the figure to lighten the snout of NCSM 40000.

- Figure 1: Each element should have its own letter - it's hard for the reader to interpret when three bones each are grouped under (b) and (c). Further, I would find it more helpful if the two palatines were next to each other and the two postorbitals were next to each other. Finally, the figure caption is incomplete - it doesn't actually say what bones are figured.

We prefer to maintain our original arrangement for this figure, but have improved the caption to make it more helpful to the reader. To avoid excess visual clutter, we have not opted to give each bone a distinct letter label, but have also improved the caption to explicitly state which image pertains to each bone, and in which view the bone is shown.

- Figure 3: the lambda filtered image for (i) is really dark and hard to see much detail - could be helpful to brighten just a touch.

We have lightened the lambda-filtered image.

- Figure 3: this figure takes up a lot of space. I think with just one histological transect of the femur you can make your point convincingly and use less space. The rest can go in an extended data figure.

We appreciate this comment and respectfully disagree. The age assessment of NCSM 40000 is arguably the most important argument for the validity of *Nanotyrannus* in our manuscript. It is essential to show that we sampled across the entire femur (ruling out pathology and/or shape change) and corroborated femoral CGM patterns with a tibia section within the main text.

- Figure 4: Graph (a) to me is difficult to interpret, because you're comparing the growth curve of a single species (*T. rex*) to a composite growth curve of a genus (two species of *Nanotyrannus*). Similar to (b), the two *Nanotyrannus* species should be plotted separately (or only plot one species). Part (a) of Figure 4 compares growth trajectories at the genus level for both "*Tyrannosaurus*" and "*Nanotyrannus*" using all available data for both genera. It does not compare species-level curves for either genus. Part (b) divides and graphs the data by *Nanotyrannus* individual to show the variation in the genus (each, in this case, representing a designated species, *N. lethaeus*, and *N. lancensis*). This is mirrored by part (c), which likewise graphs each *Tyrannosaurus* individual separately to show the variation in the genus.

We understand the reviewer's confusion regarding the data labeled as "*Tyrannosaurus*" in parts (a) and (c), as we had a typo in our figure caption stating that part (a) graphs "species-level" curves and also probably because it is most commonly accepted that *Tyrannosaurus* is a monospecific genus. We have corrected the caption, which should clear up the confusion. We also want to explain our reasoning in graphing at the genus level for *Tyrannosaurus* in part (d) and using "*Tyrannosaurus*" not "*T. rex*" throughout the manuscript. Multiple species of *Tyrannosaurus* have been proposed in the published literature, one of which designates FMNH PR 2081 (used in our growth curves) as a different species of *Tyrannosaurus*, *Tyrannosaurus imperator* [REDACTED]. The other *Tyrannosaurus* specimen plotted in our graphs is an isolated femur and cannot be assigned to any putative *Tyrannosaurus* species. Although we co-authored a rebuttal paper to [REDACTED], our challenge was that [REDACTED] conclusions were based on analytical errors and that his diagnoses were inoperable, not that the fundamental hypothesis of multiple species of *Tyrannosaurus* is incorrect. In fact, our manuscript here presents an argument that *Tyrannosaurus* [REDACTED] over-lumped at the species level and should be revisited with rigorous analyses. However, we cannot tackle the issue of species-level identifications for these specimens (FMNH PR 2081 and TCM 2003.66.1) in this paper. Nor do we want to assign the species-level diagnosis as *T. rex*. If *Tyrannosaurus rex* is multispecific, we will never be able to assign TCM 2003.66.1 to a specific *Tyrannosaurus* species, thus, the growth curves using this specimen will always reflect a genus-level curve. For these reasons, we do not label the graphs in Figure 4 "*Tyrannosaurus rex*" but rather, "*Tyrannosaurus*." Beyond this, Figure 4 has had a substantial rework in the revision due to the addition of mixed-effect model plots and we hope this is no longer a concern.

- Figure 5: This is a really confusing figure. Its trying to communicate too many different things to the reader. Please simplify. Pick one phylogenetic topology and put the other in extended data. The implied weighting results, while interesting, are not important for your main conclusions, and can also be put in extended data or supplementary info.

We have simplified this figure by removing the alternative parsimony topology, removing the unequal comparisons, rearranging the orientation of the phylogenetic trees shown, and removing some "stylized" graphics. We consider it important to show one tree from each analytical modality, so we have selected one parsimony tree and one Bayesian

tree to feature in the main text and discussion; alternative topologies are found in the extended data figures. This has saved manuscript space and simplified the figure for the reader as suggested.

- Figure 6: This figure is not that important to the main points of the paper and can be moved to the extended data section.

We have modified this figure to retain only data and images describing the apomorphically long forelimbs of NCSM 40000, which we consider essential to the main text of the paper given its importance to taxonomy, systematics, and paleobiology of *Nanotyrannus*. For space, we have omitted the hindlimb component, and present this original figure unaltered in our extended data.

Response to the Reviewers

We thank the reviewers for their final comments. We detail our responses below in red text and provide a reviewer copy with changes marked in red, and a clean copy with our resubmission.

Referee #1 (Remarks to the Author):

The authors have satisfied my suggestions on the previous draft, and have also undertaken extra work that further improves the manuscript. I am satisfied with the content of the manuscript, and have noted only a few small typos here and there, outlined below. I have one optional suggestion for moving a paragraph between sections, which I will leave to the authors.

Lines 205–213, beginning with “over the past two decades, consensus [...]” and ending “Nanotyrannus is a valid taxon.” : I see why this short paragraph is located here, as a segue from the systematic palaeontology section to the remainder of the manuscript, but because it doesn’t have its own header, it’s easily missed if readers jump around the manuscript. Optionally, the authors could move it to the introduction, somewhere towards the end before setting up the stinger about describing NCSM 40000, or they could add a “Results and Discussion” header before this paragraph, making the following headings (NCSM 40000 is skeletally mature, etc.) into subheadings of that broader section. Realistically, this is a very minor issue and does not need to be fixed, but could help with the ‘polish’ of the manuscript.

Thank you, we moved the Discussion subheader before this paragraph and adjusted the subheadings accordingly.

Line 229: This is the first appearance of the abbreviation EFS in the text, so it should be defined here.

Thank you, we made this change.

Line 239: “caudals” should be “caudal vertebrae”

Thank you, we made this change.

Line 274: “this proposed character transformations” should be “these proposed character transformations”.

Thank you, we corrected the language.

Line 275: “plausibly” – I love it, but it should be “plausibly”

Thank you, we corrected the typo.

Line 402: there is an extra closing parenthesis.

Thank you, we corrected the typo.

Line 638: “xxx” will have to be populated with the Figshare link upon acceptance.

We have done so.

Line 651: The character in parentheses (the unit for shape parameter values) appears as a square in the PDF, so care will need to be taken during proofing that the correct character has come through. I don't recall seeing this issue on the original Word document, so hopefully it is just a small hiccup.

Thank you, this does not appear in our version. We will check the proof.

Line 963: The image caption says that the 'Extreme' model in panel e is a pink line, whereas the legend indicates it is blue. I think the typo is in the caption, which mentions pink lines later where they show differences in mass between specimens at the same age.

Not a typo, but certainly unclear, we were referring to the mass comparisons in pink. We have edited to clear up the confusion.

Referee #1 (Remarks on code availability):

I reviewed the code in the last draft, and the additions here do not appreciably change the code.

Referee #2 (Remarks to the Author):

This new draft of the manuscript is even more exciting than before. It's a major reorganization of the arguments, resulting in a substantial rewrite of both the main text and the SI. But it works really well now in that the narrative is sharper and the argumentation more compelling. It's fun to read...and much easier to read, too! It's impressive that they did new histological analyses, as well as new phylogenetic analyses. We reviewers didn't ask for those new analyses, but they do significantly strengthen the overall analysis and head-off any future critics. Of course, this is a fast-moving area of extraordinarily high interest, so it's a constant battle to "remain current." In fact, since this resubmission came out, Thomas Carr published a new description of the holotype skull of *T. rex* (<https://doi.org/10.1080/27669645.2025.2539638>), which makes more than 50 references to the holotype skull of *Nanotyrannus*. I'll leave it the authors and the editor to decide whether they should incorporate any changes based on this new Carr article, but obviously it's a very relevant publication.

Although we would like to refer to this publication, we are now in the process of removing 13 references to meet Nature's editorial guidelines. Unfortunately, we lack the ability to add this reference without removing another, and all are critical in our opinion.

In general, other than dealing (or not dealing) with the new Carr article, I have relatively few changes to recommend. The revised draft is very well written. The SI has just the right amount of description, and most of it is directed toward meaningful comparisons rather than straight description for its own sake (the latter is legit and valuable but not the emphasis for a Nature article). The responses to the reviewers are generally more than adequate, and I won't argue against any of their decisions. I'll again reveal that this review was prepared by Larry Witmer (Ohio University).

Most of my comments are editorial. Note that the SI was provided as a Word file with no line numbers, so I added line numbers and converted to PDF. I'll try to upload the file, but if I fail, I encourage the authors to shoot me an email (witmerL@ohio.edu), and I'll send it to them.

Main text:

1. Line 52: en-dash should be em-dash

Thank you, we corrected the typo.

2. Line 229: This may be the first reference to EFS, in which case it should be spelled out as "external fundamental system (EFS)".

Thank you, we made this change.

3. Line 273: It would be good to substantiate "several" by listing specimen numbers.

Thank you, we made this change.

4. Line 274: should be "these"

Thank you, we corrected the language.

5. Line 348: needs an end parenthesis. Also, are you saying USNM 555000 is the "largest Tyrannosaurus"? It's not...not even close, right?

Thank you, we added the end parentheses. Our meaning was intended to refer to multiple specimens representing the largest specimens of Tyrannosaurus. According to our measurements, USNM 555000 has longer metatarsals and a longer femur than Sue. Sue has a thicker femur and longer tibia, so we think it is plausible that it was a larger individual overall. We added FMNH PR 2081 to this sentence because it also has metatarsals of approximately the same length as NCSM 40000 and will hopefully clarify that we are not trying to enter the debate into which proxy best approximates the "largest" Tyrannosaurus specimen.

6. Lines 364–365: Probably should be "due to the juvenile status of specimens known at the time." Using "its juvenile status" implies only a single entity and only individuals can be juvenile not a genus (duh)..

We added "specimens of" to clarify that we are not referring to the genus, but rather the specimens representing it.

7. Line 482: Should be "eutyranosaurians" (plural), unless there's a different intent. Regardless, it needs a minor tweak to read right.

Thank you, we corrected the typo.

8. Line 491: Should this be "Nanotyrannus or its ancestors" or maybe just "the ancestors of Nanotyrannus." It reads now as the genus Nanotyrannus was in Appalachia as well as Laramidia.

Good catch, we added this.

Supplementary Information (see note above about how I handled the Word file with no line numbers):

9. Lines 117–118: For clarity move "(the condition in NCSM 40000 cannot currently be assessed)" to the end of this sentence.

Thank you, we added this phrase.

10. Line 173: "Na." should be "N."

11. Line 180 but maybe elsewhere: You use both "alioramins" and "alioramines." If these are the same clade then you should pick one and be consistent.

12. Line 193: "spp." should not be in italics

Thank you, we corrected the typos.

13. Line 246: “tuber-like”? As in looking like a potato? Odd metaphor.

Point taken, we improved the language.

14. Line 257: should be “evident in MOR 1130” (missing “in”)

15. Line 270: Again, “spp.” should not be in italics.

16. Line 320: should be “proatlantal”

17. Line 403: should be “Daspletosaurus”

18. Lines 405 & 409: should be “lancensis”

Thank you, we corrected the typos.

19. Lines 464–466: “Only the lateralmost rim of the proximal end of MCIII articulates with the carpals or antebrachium. Otherwise, MCIII appears genuinely splint-like, despite being robust proximally.” Does this passage pertain to NCSM 40000 or to the previous tyrannosaurids?

NCSM 40000. We made note of it in the text.

20. Lines 469–470: When you say “(nearly twice the absolute dimensions of one of the largest known T. rex individuals”, you should designate which T. rex individual.

We have added “such as FMNH PR 2081 and MOR 980.”

21. Line 492: should be “peduncle”

22. Line 524: Should be “crista tibiofibularis” (two words)

23. Line 525: Should be “Bistahieversor”

24. Line 532: Need to add a comma after “40000” or delete the comma after “generally”.

Thank you, we corrected the typos.

25. Lines 575–581: weird font switch

Thank you. Unclear why this is happening, we will check the proof.

26. Lines 679–682: Nice! No edits, just glad to see the addition.

27. Line 910: Should be “lethaeus

Thank you, we corrected the typo.

28. Line 1008: Should be “Outgroup”

Thank you, we corrected the typo.

29. Line 1150: Should be “Nanotyrannidae” now, right?

Thank you, we corrected the typo.

30. Line 1225: *Nanotyrannus* and *Alioramus* should be italicized.

Thank you, we corrected the typos.

Referee #3 (Remarks to the Author):

I thank the authors for taking the time to fairly evaluate and respond to my comments and am pleased with their modifications of the article. My only final comments are very minor editorial ones...

-- in the Remarks section starting line 166, it's not necessary to have 'former' (line 170) in italics.

We appreciate this opinion; however, we feel the emphasis is valuable here and prefer to leave the word in italics.

-- also, in lines 170-1, 'Whereas, NCSM 40000 compares favorably with CMNH 7541, and critically preserves a shared apomorphy...' would be better worded 'In contrast, NCSM 40000 compares favorably with CMNH 7541: notably, both share the apomorphic presence of....'. 'Critically' is not the right word here.

-- also, line 172, 'contrasting the shallow recess' should be 'in contrast to the shallow recess'

Thank you, we have edited the text in line with these two suggestions.

Referee #4 (Remarks to the Author):

I want to extend my thanks and gratitude to the authors for their careful and thorough re-organization of both the manuscript text and figures. With these revisions, the paper is much easier to read, and presents a well-organized compelling narrative that will be attractive to a broad swath of the journal's readership. This manuscript now really reads like a Nature paper. The authors should be commended for such an excellent manuscript; and as with the initial submission, the science is top-notch. It is my pleasure to recommend this contribution for publication in Nature after a handful of minor revisions, listed below.

- Diagnosis (lines 112-132, 157-164, 193-199): I apologize that my comment on the genus and species diagnoses was not more clear. For the diagnosis of *Nanotyrannus* as a genus, and the two species (*N. lancensis* and *N. lethaeus*), the authors do explicitly indicate autapomorphies (unique character states), which does make this implicitly differential. However, my comment was about the character states in the diagnoses that are *not* autapomorphies. For these character states, the authors should indicate if they are the same or different from other taxa. i.e., for the generic diagnosis of *Nanotyrannus*, which of the non-autapomorphies are similar/different from other eutyrannosaurians, particularly *T. rex*; and for the species diagnoses, which of the non-autapomorphies differ from the other species of *Nano*. For further info on differential diagnoses, see Cifelli & Kielan-Jaworowska 2005 (*Acta Pal Polonica*).

We fully agree that this is best practice, and we initially had these comparisons in the manuscript for that reason. Unfortunately, we had to cut these to reduce word count before the first submission. Although cuts to minimize manuscript length could arguably be made elsewhere, extensive lists of taxonomic names in the three diagnoses were appealing as they are less important for Nature's wide audience than all other text currently in the main manuscript. For specialists, to whom such information would appeal, non-autapomorphic diagnostic characters of *Nanotyrannus* can be obtained from the phylogenetic matrix, included as a supplemental file, as the distribution of

nearly all of these features across all tyrannosauroids is recorded there and is also discussed in the extended description SI 1.

- lines 216-217: I would not call this a "widely accepted consensus" - plenty of paleontologists in recent years accept *Nano* as a valid species. Perhaps say "common hypothesis"

Although we disagree that a large proportion of paleontologists in recent years accept *Nanotyrannus* as a valid species, we have changed this to say simply "hypothesis."

- Figure 6: This figure is improved, but I still find it a bit difficult to read, primarily because the taxon labels are so small. Because this paper really only focuses on the interpreting the portion of the tyrannosauroid evolutionary tree that is *Suskityrannus*/*Xiongguanlong* + Eutyranosauria, I would suggest they only show this part of the tree in the main text figure (Fig 6), so there is more space to enlarge the topologies to make it easier to read. The full tree can still be showing in Extended Data Figs or Suppl Info, but with the current Figure 6 I had to zoom in to over 200% to be able to read the phylogeny.

While we had hoped to show our full tree topologies in the main text, we agree that the trees were difficult to read and have made this recommended change to increase clarity. We have truncated our trees to show *Dilong* and all more derived tyrannosauroids (corresponding to the usual conception of the clade Pantyrannosauria), pruning *Juratyrant* and *Stokesosaurus*, all proceratosaurids, and all of our outgroup taxa from the topology, which allowed us to significantly increase the size of the phylogeny and text labels in Figure 6. We hope the new version of this figure achieves the desired clarity.