New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna

Chase Doran Brownstein

Article citation details
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Review timeline
Original submission: 26 March 2019
1st revised submission: 10 July 2019
2nd revised submission: 16 October 2019
Final acceptance: 22 October 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSOS-190533.R0 (Original submission)

Review form: Reviewer 1

Is the manuscript scientifically sound in its present form?
No

Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No
2

Have you any concerns about statistical analyses in this paper?
Yes

Recommendation?
Major revision is needed (please make suggestions in comments)

Comments to the Author(s)

This manuscript hinges upon the claim that you have a non-tyrannosaurid tyrannosauroid with affinities to eastern taxa (i.e. Dryptosaurus) and a dromaeosaurid with western affinities in the same formation. Therefore, the manuscript requires both these identifications and these different affinities to be well-supported.

The text in the descriptions does a good job of comparing these teeth to other comparable taxa (I should note, however, that a twisted mesial carina on lateral teeth is only documented from D. Albertensis and not from other similar isolated teeth or Utahraptor).

However, your data and analyses either do not support your main claim or are insufficient to do so. Starting with your dataset, your measurements of NJSM GP 12456 for DB, DC, and DA do not appear congruent with the specimen figured in Fig. 1J, though do seem to match the scale if Fig. 1E. In Fig. 1J, measurements closer to 4 would appear to be more accurate than 2, 2, and 2.5. The scale bars for the photos and your measurements should be double-checked. You also have a substantial amount of missing data for your new specimens in your dataset, and you haven’t discussed how this was handled in your PCA. The default in PAST is to fill missing data with column average substitution, which in the Smith et al. (2005) dataset will bias all of your specimens towards the tyrannosaur part of your plot (as there are more tyrannosaurs in the dataset than any other group). Given that all three of the new teeth plot in areas of your plots where no other theropod teeth plot (partway between dromaeasaurids and tyrannosaurs), it appears that column average substitution of your dataset is having a substantial contribution to the position of your specimens on these plots. As well, eastern taxa are notably excluded. Dryptosaurus is not plotted in Fig. 2A, and the Tar Heel dromaeosaurid is not plotted in Fig. 4B and 4C, making the argument that either of these teeth have eastern or western affinities insufficiently supported by these analyses. Additions of those specimens and the exclusion of variables with missing data are necessary for these plots to be informative.

In the phylogenetic analysis, you only list shared derived characters between your tyrannosaur specimen and T. rex, but do not list shared derived characters that unite all tyrannosauroids. However, even this analysis does not support your argument that the specimen is a non-tyrannosaurid tyrannosauroid with affinities with Dryptosaurus. Also, one of the four characters you do list, 94) biconvex apical distal denticles, is not mentioned in your description at all nor is it visible in Fig. 1.

As well, Fig. 1B, 1C, and 1D depict fossils that are not described in the manuscript. If these specimens are figured in this manuscript, they should be described systematically in the text. Alternatively, these figures could easily be excluded from the manuscript. The entire datasets used for analysis, including the Smith et al. (2005) and Larson and Currie (2013) should be reproduced in the supplemental data for ease of replication.

This description is of specialist interest given the new records from eastern North America, but any discussion of faunal interchange in premature. In your description, you have demonstrated that you have teeth of a dromaeosaurid and a tyrannosauroid from this formation, but your analyses in their current form are insufficient to demonstrate that these teeth have any biogeographic affinities.
Review form: Reviewer 2 (Terry A. Gates)

Is the manuscript scientifically sound in its present form?
No

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
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Recommendation?
Major revision is needed (please make suggestions in comments)

Comments to the Author(s)
The author of this paper has identified two theropod dinosaur teeth from the east coast of North America they attribute to Tyrannosauroidea and Dromaeosauridae.

Further the author suggests ways that these teeth contribute to our knowledge of faunal interchange between eastern and western North America at the Campano-Maastrichtian boundary.

This paper is important for the acknowledgement of the taxa found in this New Jersey formation. Outside of this finding there is much more difficulty in acquiring significance. This problem of lack of greater significance is not the fault of the author but the nature of the Appalachian dinosaur record. Fossiliferous formations are poorly dated, fossils are not terribly abundant, and when known are typically in rough condition. Because there is not a proper framework for the dinosaurs, determining faunal interchange is problematic...you need to know what is around when, and the organism's phylogenetic relationships. Without this it is difficult to say anything concrete about paleobiology. Especially, in these days when doing rigorous biogeographic analyses is so easy. In my opinion you can't really say anything about faunal interchange until a solid, dated fossil record is assembled.

I am glad to see the author using quantitative techniques to identify the teeth. However, I have some issues with the methods and/or the results presented. First, I firmly do not think that a phylogenetic analysis should be used on a single tooth, much less a single partial tooth. The phylogenetic analysis of teeth is not a proper use of phylogenetics in my opinion at any rate. To my mind this part of the paper should be eliminated.

Second, the author should use a more recent ordinal analysis of teeth. This is not a deal breaker, but the primary dataset chosen is 13 years old (or 5 yrs old in the case of Larson and Currie) and many others have been produced since then.
Third, the tyrannosaur tooth should absolutely be removed from the PCA analysis. It is a fragmentary tooth, therefore any measurements taken are not going to be the correct measurement and will provide erroneous results. Or there will be too little data to say much about.

Fourth, the dromaeosaurid tooth falls outside the dromaeosaurids in the Smith/Brownstein matrix. And is just part of the miasma of teeth in the Larson and Currie matrix. I would suggest pulling individual taxa from the analyses and talk about comparisons with them instead of consistently saying it is a Sauornitholestesine theropod. Remember that the PCA is using data you input. If there is more information supporting your taxonomic claim that is not included in the quantitative data, then you should discuss this in the text. In PAST you can change the symbol and the color, meaning that you can label individual dinosaur taxa and the higher level taxonomic groups at the same time. This should be done to help you see which species the Tar Heel and Mt Laurel specimens are mostly similar to.

Fifth, this is very important! When using PCA on variables that are measurements, the first axis is almost invariably a reflection of size, not shape. Therefore, you need to show axes 2 and 3. You are welcome to retain axis 1 and 2, but 2 and 3 must be shown in addition. You may also want to consider Centering or z-transforming your data because it can help remove the effect of size, bring outliers closer together, and reflect shape better.

I have provided a marked PDF with more comments and suggestions (Appendix A).

Hopefully these suggestions help the paper and the author.

Sincerely,
Terry Gates

Decision letter (RSOS-190533.R0)

10-Jul-2019

Dear Mr Brownstein:

Manuscript ID RSOS-190533 entitled "New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America" which you submitted to Royal Society Open Science, has been reviewed. The comments from reviewers are included at the bottom of this letter.

In view of the criticisms of the reviewers, the manuscript has been rejected in its current form. However, a new manuscript may be submitted which takes into consideration these comments.

Please note that resubmitting your manuscript does not guarantee eventual acceptance, and that your resubmission will be subject to peer review before a decision is made.

You will be unable to make your revisions on the originally submitted version of your manuscript. Instead, revise your manuscript and upload the files via your author centre.

Once you have revised your manuscript, go to https://mc.manuscriptcentral.com/rsos and login to your Author Center. Click on "Manuscripts with Decisions," and then click on "Create a
Resubmission” located next to the manuscript number. Then, follow the steps for resubmitting your manuscript.

Your resubmitted manuscript should be submitted by 07-Jan-2020. If you are unable to submit by this date please contact the Editorial Office.

We look forward to receiving your resubmission.

Kind regards,
Alice Power
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Robert Sansom (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

Subject Editor Comments to Authors:

Both reviewers (and I) appreciate the great amount of work that has gone into this manuscript and the level of painstaking analysis. That said, neither reviewer is happy with the level of biogeographic inference, and this is largely because they are not happy with the taxonomic identifications and use of phylogenetic inference. Without these the paper becomes considerably more limited in scope, and that would be a different paper.

I will be glad to entertain a resubmission if the advice of the reviewers is followed, or, alternatively, if you can refute their concerns to their satisfaction. Best wishes.

Reviewer: 1
Comments to the Author(s)
This manuscript hinges upon the claim that you have a non-tyrannosaurid tyrannosauroid with affinities to eastern taxa (ie. Dryptosaurus) and a dromaeosaurid with western affinities in the same formation. Therefore, the manuscript requires both these identifications and these different affinities to be well-supported.

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Reviewer: 2

Comments to the Author(s)
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I have provided a marked PDF with more comments and suggestions.

Hopefully these suggestions help the paper and the author.

Sincerely,
Terry Gates

Author's Response to Decision Letter for (RSOS-190533.R0)

See Appendix B.

RSOS-191206.R0

Review form: Reviewer 2 (Terry A. Gates)

Is the manuscript scientifically sound in its present form?
No
Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
The paper is much improved since I last reviewed it. There are comments posted in another annotated pdf attached to this review (Appendix C).

Important changes that still need to be made.
First and foremost—the phylogenetic analysis of teeth. You must use the super matrix of Hendrickx and Mateo, not just the tooth matrix. Please recode and rerun the analysis. Also, you should add Dryptosaurus and potentially one other tyrannosaurid to the matrix so that you might get some resolution as to the phylogenetic affinities of your tooth. Without this there is little that can be said except it is a tyrannosauroid tooth.

Put some or all of the Discriminant Analysis results in the paper, not the SM. We need to see the data.

The last sentence of the abstract does not make sense. I suggest deleting it, but you can try to modify it.

Good luck with further revisions.

Terry Gates

Review form: Reviewer 3

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No
Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
This revision of the original paper is much better present and the interpretations are supported. I think it is nearly ready for publication. I made minor corrections to the MS on the PDF (Appendix D). Please be careful with the use of the clade names. Tyrannosaurids = members of Tyrannosauridae. I noted these throughout. Also, put the description before the identification of each tooth section.

Review form: Reviewer 4 (Thomas Carr)

Is the manuscript scientifically sound in its present form?
No

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
Dear Editor,

I submit to you my review of MS RSOS-191206, “New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America” by Brownstein. This article is a long-overdue consideration of the possibility of faunal exchange between Laramidia and Appalachia during the latest Cretaceous. Virtually all paleogeographic maps of this time show Laramidia and Appalachia joined across what is now western Canada, where previously they were decisively separated by the Western Interior Seaway (WIS). However, the complete absence of Appalachian dinosaurs from the Hell Creek Formation and its equivalents sets the null hypothesis that faunal exchange, at least from east to west, did not occur. In his manuscript, Brownstein compares these hypotheses from the perspective of the east.

If dispersal went in the opposite direction (west to east), then fossils of, say, Tyrannosaurus rex and Triceratops should be present in late Maastrichtian sedimentary rocks of Appalachia. Indeed, if T. rex did disperse from Central Asia to Laramidia, becoming nearly instantaneously widespread across that landmass, then Appalachia should have been occupied in the same
fashion. But that isn’t what the fossil record shows: certainly, opportunity for faunal exchange presented itself at 76, 74, and 68 million years ago, but there is no evidence of it in Laramidia, and the basal nature of Appalachiosaurus (Campanian) and Dryptosaurus (Maastrichtian) are consistent with that pattern. In the end, the author does conclude that the tooth specimens that he describes provide evidence for the refugium hypothesis, a conclusion that I agree with.

I suggest publication with minor revision; in addition to the specific comments below, I think the author should more clearly couch the article in terms of the refugium versus exchange models. In the introduction and conclusion, he leans heavily on the exchange model and that needs to be balanced, in both places, by a skeptical assessment of the case for the exchange model. An explicit statement of the evidence in favor of the refugium hypothesis must also be included in the abstract and the title must be adjusted accordingly.

The author may know my identity: Thomas D. Carr

Sincerely,
Thomas D. Carr, PhD
Associate Professor of Biology
Carthage College
2001 Alford Park Drive
Kenosha, WI 53140
p/262-551-5887

Specific comments:

Abstract: the phrase “fine detail” does not need to be hyphenated.
The phrase “heavily mediolaterally compressed” is too wordy and misleading; the word “narrow” with a width to length ratio (in per cent) would suffice. My quibble is this: narrow teeth (w:l ratio less than 60%) is merely the plesiomorphic condition for tyrannosaurids. Since narrow teeth are the ancestral condition, there is no process of “compression” to account for their form. Replace “this fossil supports” with “this fossil is evidence for”.
Replace the word “common” with “widespread”.

Introduction
Page 9, line 60: delete “rectangular”.
Page 10, lines 74 to 74: move “come” up to follow “have”.
Page 11, lines 97, 98: replace the em-dashes with “to”.
Page 11, line 111: replace “border” with “boundary”.

Tyrannosauroid tooth
Identification
Page 13, line 147: insert a space between the parentheses.
Page 13, lines 151-152: replace “highly mediolaterally compressed” with “narrow” and give a width to length ratio (mentioning, of course, that the tooth is incomplete and so the ratio is an overestimate).
Page 13, line 155: replace “high mediolateral compression” with “narrow”.
Page 13, line 158: delete “pers. obs. of”.
Page 14, line 161: mention that the crown is incomplete and that you only have the apical third to half, otherwise your inability to take all measurements, as said here, is unclear.
Page 14, line 169: insert a space between the parentheses.
Table 1: the specimen number “NJSM GP 12456” does not match the number in the text (NJSM GP 14256); which is correct?
Is there a caption that explains the abbreviations? If not, please include.
Why is the basal width to basal length ratio not included?

Page 15, line 181: modern erosion or ancient erosion? Clarify.
Page 15, line 183: a single tooth cannot be “ziphodont”, which is a term used for the entire dentition; “ziphiform” is appropriate for a single tooth; replace “compressed” with “narrow”.
Page 15, line 184: in which direction is the mesial carina convex: labial or lingual? Please clarify.
Page 15, line 185: replace “run” with “extent”.
Page 15: are the apical denticles worn down; i.e., through use, as produced the subtle wear facet on the lingual surface? Please include that observation, if you can.
Page 15, line 193: replace “interspersed with diminutive” with “separated by small”.

Figures: I did not receive any figure captions with the manuscript, so I cannot comment on those.

Dromaeosaurid tooth
Identification
Page 16, line 219: separate the parentheses with a space.
Page 17, line 223: explicitly state the crown height here.
Page 17, line 238: separate the parentheses with a space.
Page 18, lines 248, 251: placing a word or phrase between apostrophes implies that you are disowning what you are saying; since this clearly isn’t the case, please delete them – they are distracting and self-contradictory. If you are insecure about using slender as a qualitative term, you could quantify the condition of slender with a ratio of, say, basal length to crown height or the like.
Page 18, line 249: give the ratio!
Page 18, line 252: is the term “western” necessary? Or do you mean exclusively Laramidia?
Clarify.
Page 18, line 254: give a ratio to quantify this contrast in slenderness.
Page 18, line 258: delete “conducted”.
Page 18, line 262: separate the parentheses with spaces.
Page 19, line 274: replace “and” with “from”.
Page 19, line 281: the name B. feinbergi should not be enclosed in apostrophes.
Page 19, line 288: replace “analysis” with “analyses”; delete “in which…included”.

Description
Page 20, line 295: replace “ziphodont” with “ziphiform”.
Page 20, line 308: replace “project” with “extend”.

Discussion
Page 21, line 315: insert “the” ahead of “Maastrichtian”.
Page 21, line 321: is “largish” a real word? Please fix!
Page 23: I’m skeptical of the claim for interchange – why can’t the ceratopsian and lambeosaurine material simply reflect descendants of those clades before the inundation of the WIS? For example, lambeosaurines do have Santonian representatives in Asia. My impression is that the opportunities for exchange between Asia and Laramidia were generally episodic, whereas it was sustained during the late Maastrichtian. Regardless, the evidence for exchange between Laramidia and Appalachia isn’t strong even though it is a worthwhile hypothesis to test.
Page 23, line 381: separate the parentheses with a space.
Page 24, line 395: argh – “largish” again! Please fix.
Methods

Page 25, line 406: change “provide support for the assignment” to “quantitatively test the identity”.

Page 26, line 429: change “provide additional support for” to “test”.

Figure 3: Perhaps it is in the caption, but please make it clear what the “ML” specimens are.

Decision letter (RSOS-191206.R0)

23-Sep-2019

Dear Mr Brownstein

On behalf of the Editor, I am pleased to inform you that your Manuscript RSOS-191206 entitled "New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and Subject Editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript. The reviewers have provided comments in PDF format to assist you - as these appear to be large files, and sometimes the ScholarOne mail server strips messages of large attachments, please let me know if you do not receive these.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link: http://datadryad.org/submit?journalID=RSOS&manu=RSOS-191206

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.
• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please note that we cannot publish your manuscript without these end statements included. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 02-Oct-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under “Manuscripts with Decisions”. Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees.

When uploading your revised files please make sure that you have:

1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document".
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format)
3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account.

4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript.

5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://figshare.com). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Robert Sansom (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author (Dr Robert Sansom):

The reviewers are impressed with this revised version and suggest only minor revisions. I apologise for the long delay in getting this back to you; I have never had more difficulty in procuring reviewers than for this submission.

Reviewer comments to Author:
Reviewer: 2

Comments to the Author(s)
The paper is much improved since I last reviewed it. There are comments posted in another annotated pdf attached to this review.

Important changes that still need to be made.
First and foremost—the phylogenetic analysis of teeth. You must use the super matrix of Hendrickx and Mateo, not just the tooth matrix. Please recode and rerun the analysis. Also, you should add Dryptosaurus and potentially one other tyrannosaurid to the matrix so that you might get some resolution as to the phylogenetic affinities of your tooth. Without this there is little that can be said except it is a tyrannosauroid tooth.
Put some or all of the Discriminant Analysis results in the paper, not the SM. We need to see the data.

The last sentence of the abstract does not make sense. I suggest deleting it, but you can try to modify it.

Good luck with further revisions.

Terry Gates

Reviewer: 3

Comments to the Author(s)
This revision of the original paper is much better present and the interpretations are supported. I think it is nearly ready for publication. I made minor corrections to the MS on the PDF. Please be careful with the use of the clade names. Tyrannosaurids = members of Tyrannosauridae. I noted these throughout. Also, put the description before the identification of each tooth section.

Reviewer: 4

Comments to the Author(s)

Dear Editor,

I submit to you my review of MS RSOS-191206, “New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America” by Brownstein. This article is a long-overdue consideration of the possibility of faunal exchange between Laramidia and Appalachia during the latest Cretaceous. Virtually all paleogeographic maps of this time show Laramidia and Appalachia joined across what is now western Canada, where previously they were decisively separated by the Western Interior Seaway (WIS). However, the complete absence of Appalachian dinosaurs from the Hell Creek Formation and its equivalents sets the null hypothesis that faunal exchange, at least from east to west, did not occur. In his manuscript, Brownstein compares these hypotheses from the perspective of the east.

If dispersal went in the opposite direction (west to east), then fossils of, say, Tyrannosaurus rex and Triceratops should be present in late Maastrichtian sedimentary rocks of Appalachia. Indeed, if T. rex did disperse from Central Asia to Laramidia, becoming nearly instantaneously widespread across that landmass, then Appalachia should have been occupied in the same fashion. But that isn’t what the fossil record shows: certainly, opportunity for faunal exchange presented itself at 76, 74, and 68 million years ago, but there is no evidence of it in Laramidia, and the basal nature of Appalachiosaurus (Campanian) and Dryptosaurus (Maastrichtian) are consistent with that pattern. In the end, the author does conclude that the tooth specimens that he describes provide evidence for the refugium hypothesis, a conclusion that I agree with.

I suggest publication with minor revision; in addition to the specific comments below, I think the author should more clearly couch the article in terms of the refugium versus exchange models. In the introduction and conclusion, he leans heavily on the exchange model and that needs to be balanced, in both places, by a skeptical assessment of the case for the exchange model. An explicit statement of the evidence in favor of the refugium hypothesis must also be included in the abstract and the title must be adjusted accordingly.
The author may know my identity: Thomas D. Carr

Sincerely,
Thomas D. Carr, PhD
Associate Professor of Biology
Carthage College
2001 Alford Park Drive
Kenosha, WI 53140
p/262-551-5887

Specific comments:

Abstract: the phrase “fine detail” does not need to be hyphenated.
The phrase “heavily mediolaterally compressed” is too wordy and misleading; the word “narrow” with a width to length ratio (in per cent) would suffice. My quibble is this: narrow teeth (w:l ratio less than 60%) is merely the plesiomorphic condition for tyrannosaurids. Since narrow teeth are the ancestral condition, there is no process of “compression” to account for their form. Replace “this fossil supports” with “this fossil is evidence for”. Replace the word “common” with “widespread”.

Introduction
Page 9, line 60: delete “rectangular”.
Page 10, lines 74 to 74: move “come” up to follow “have”.
Page 11, lines 97, 98: replace the em-dashes with “to”.
Page 11, line 111: replace “border” with “boundary”.

Tyrannosauroid tooth Identification
Page 13, line 147: insert a space between the parentheses.
Page 13, lines 151-152: replace “highly mediolaterally compressed” with “narrow” and give a width to length ratio (mentioning, of course, that the tooth is incomplete and so the ratio is an overestimate).
Page 13, line 155: replace “high mediolateral compression” with “narrow”.
Page 13, line 158: delete “pers. obs. of”.
Page 14, line 161: mention that the crown is incomplete and that you only have the apical third to half, otherwise your inability to take all measurements, as said here, is unclear.
Page 14, line 169: insert a space between the parentheses.

Table 1: the specimen number “NJSM GP 12456” does not match the number in the text (NJSM GP 14256); which is correct? Is there a caption that explains the abbreviations? If not, please include. Why is the basal width to basal length ratio not included?

Page 15, line 181: modern erosion or ancient erosion? Clarify.
Page 15, line 183: a single tooth cannot be “ziphodont”, which is a term used for the entire dentition; “ziphiform” is appropriate for a single tooth; replace “compressed” with “narrow”.
Page 15, line 184: in which direction is the mesial carina convex: labial or lingual? Please clarify.
Page 15, line 185: replace “run” with “extent”.
Page 15: are the apical denticles worn down; i.e., through use, as produced the subtle wear facet on the lingual surface? Please include that observation, if you can.
Page 15, line 193: replace “interspersed with diminutive” with “separated by small”.


Figures: I did not receive any figure captions with the manuscript, so I cannot comment on those.

Dromaeosaurid tooth Identification
Page 16, line 219: separate the parentheses with a space.
Page 17, line 223: explicitly state the crown height here.
Page 17, line 238: separate the parentheses with a space.
Page 18, lines 248, 251: placing a word or phrase between apostrophes implies that you are disowning what you are saying; since this clearly isn’t the case, please delete them – they are distracting and self-contradictory. If you are insecure about using slender as a qualitative term, you could quantify the condition of slender with a ratio of, say, basal length to crown height or the like.
Page 18, line 249: give the ratio!
Page 18, line 252: is the term “western” necessary? Or do you mean exclusively Laramidia? Clarify.
Page 18, line 254: give a ratio to quantify this contrast in slenderness.
Page 18, line 258: delete “conducted”.
Page 18, line 262: separate the parentheses with spaces.
Page 19, line 274: replace “and” with “from”.
Page 19, line 281: the name B. feinbergi should not be enclosed in apostrophes.
Page 19, line 288: replace “analysis” with “analyses”; delete “in which…included”.

Description
Page 20, line 295: replace “ziphodont” with “ziphiform”.
Page 20, line 308: replace “project” with “extend”.

Discussion
Page 21, line 315: insert “the” ahead of “Maastrichtian”.
Page 21, line 321: is “largish” a real word? Please fix!
Page 23: I’m skeptical of the claim for interchange – why can’t the ceratopsian and labeosaurine material simply reflect descendants of those clades before the inundation of the WIS? For example, labeosaurines do have Santonian representatives in Asia. My impression is that the opportunities for exchange between Asia and Laramidia were generally episodic, whereas it was sustained during the late Maastrichtian. Regardless, the evidence for exchange between Laramidia and Appalachia isn’t strong even though it is a worthwhile hypothesis to test.
Page 23, line 381: separate the parentheses with a space.
Page 24, line 395: argh – “largish” again! Please fix.

Methods
Page 25, line 406: change “provide support for the assignment” to “quantitatively test the identity”.
Page 26, line 429: change “provide additional support for” to “test”.

Figure 3: Perhaps it is in the caption, but please make it clear what the “ML” specimens are.

Author’s Response to Decision Letter for (RSOS-191206.R0)

See Appendix E.
Decision letter (RSOS-191206.R1)

22-Oct-2019

Dear Mr Brownstein,

I am pleased to inform you that your manuscript entitled "New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna" is now accepted for publication in Royal Society Open Science.

You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience_proofs@royalsociety.org and openscience@royalsociety.org) to let us know if you are likely to be away from e-mail contact -- if you are going to be away, please nominate a co-author (if available) to manage the proofing process, and ensure they are copied into your email to the journal.

Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers. As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Kind regards,

Lianne Parkhouse
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of the Associate Editor and Professor Kevin Padian (Subject Editor)
openscience@royalsociety.org

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### Appendix A

**New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America**

| Journal:  | *Royal Society Open Science* |
|-----------|-----------------------------|
| Manuscript ID | RSOS-190533                |
| Article Type: | Research                   |
| Date Submitted by the Author: | 26-Mar-2019               |
| Complete List of Authors: | Brownstein, Chase; Stamford Museum and Nature Center, |
| Subject: | Palaeontology < EARTH SCIENCES, evolution < BIOLOGY, ecology < BIOLOGY |
| Keywords: | Dinosaur, Biogeography, Appalachia, Cretaceous |
| Subject Category: | Biology (whole organism) |
**Author-supplied statements**

Relevant information will appear here if provided.

**Ethics**

*Does your article include research that required ethical approval or permits?:*
This article does not present research with ethical considerations

*Statement (if applicable):*
CUST_IF_YES_ETHICS :No data available.

**Data**

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*
Yes

*Statement (if applicable):*
The data is included in the supplementary material.

**Conflict of interest**

*I/We declare we have no competing interests*

*Statement (if applicable):*
CUST_STATE_CONFLICT :No data available.

**Authors’ contributions**

*I am the only author on this paper*

*Statement (if applicable):*
CUST_AUTHOR_CONTRIBUTIONS_TEXT :No data available.
New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America

Chase Doran Brownstein

Research Associate, Dept. of Collections and Exhibitions, Stamford Museum and Nature Center, Stamford, CT, chasethedinosaur@gmail.com
Abstract.

The faunal changes that occurred in the few million years before the Cretaceous-Paleogene extinction are of much interest to vertebrate paleontologists. Western North America preserves arguably the best fossil record from this time, whereas terrestrial vertebrate fossils from the eastern portion of the continent are usually limited to isolated, eroded postcranial remains. Here, I report on two theropod teeth from the Mount Laurel Formation, a lower-middle Maastrichtian unit from northeastern North America. One of these preserves in fine-detail the structure of the outer enamel and closely resembles the dentition of the tyrannosaurid *Dryptosaurus aquilunguis*. The other is assignable to a dromaeosaurid and represents both the youngest occurrence of a non-avian maniraptoran in eastern North America and the first from the Maastrichtian reported east of the Mississippi. Unlike other dromaeosaurid teeth from the northeastern portion of the continent, the Mt. Laurel specimen is closely comparable with western North American ones. Taken together, these fossils suggest a complex biogeography for dinosaurs in the American east. Although the tyrannosaurid tooth provides an additional record of non-tyrannosaurid tyrannosauroids in the Maastrichtian of eastern North America, the dromaeosaurid specimen indicates faunal interchange between eastern and western North America began to take place as early as the early Maastrichtian, several million years earlier than previous discoveries indicated. Along with recent research on coeval dispersals between Asia and western North America, the description of the new Mt. Laurel teeth emphasizes that dinosaur biogeography during the Maastrichtian was characterized by extensive faunal interchange.

Keywords: Dinosaur; Appalachia; Cretaceous; Biogeography; Tyrannosaur; Teeth
Introduction.

The extinction of the non-avian dinosaurs at the end of the Mesozoic Era is a topic that has continued to intrigue vertebrate paleontologists (e.g., Alvarez et al., 1980; Sloan et al., 1986; Sarjeant and Currie, 2001; Le Loeuff 2012, Brusatte et al., 2012, 2015; Sakamoto et al., 2016). However, a poor global terrestrial record from the Maastrichtian has hindered attempts to assess the diversity dynamics of important groups like the Dinosauria during this period (e.g., Le Loeuff, 2012; Brusatte et al., 2015). Western North America preserves arguably the most well-characterized vertebrate record from the last 20 million years of the Mesozoic Era (Brusatte et al., 2015), whereas that from the eastern portion of the continent is far more obscure. During the majority of the Late Cretaceous, eastern and western North America were separated, the former existing as a rectangular landmass called Appalachia. Appalachian dinosaur faunas included intermediate-grade tyrannosaurs (Carr et al., 2005; Brusatte et al., 2011), basal hadrosaurids and derived non-hadrosaurid hadrosauroids (Langston, 1960; Prieto-Márquez et al., 2006; Prieto-Márquez et al., 2016), nodosaurids (Gallagher, 1993; Burns and Ebersole, 2016), and ornithomimosaurs (Miller, 1967; Schwimmer et al., 1993; Weishampel and Young, 1996; Schwimmer et al., 2015; Brownstein, 2018a).

Despite the amount of knowledge of Cretaceous faunal change to be gleaned from the fossil record of Appalachia, the assemblages of this landmass have remained fundamentally understudied since the mid-19th century (e.g., Weishampel & Young, 1996; Gallagher, 1997; Weishampel, 2006; Brownstein, 2018a). The scarcity of terrestrial sedimentary units known from the eastern half of the United States has also contributed to the obscurity of Appalachian faunas compared to western North American ones (Weishampel and Young, 1996; Gallagher, 1997;
Weishampel, 2006). Only in the past few years have indications of complex faunal changes in the latest Cretaceous of the American east come, and all from isolated, fragmentary finds. Although a ceratopsian tooth from the uppermost Maastrichtian of Mississippi (Farke and Phillips, 2017) and lambeosaurine bones from the upper Maastrichtian of New Jersey (Gallagher, 1993) have hinted that faunal exchanges occurred between Appalachia and Laramidia following the regression of the Western Interior Seaway in the latest Campanian-earliest Maastrichtian, the timing of these events remains poorly constrained. Characterizing faunal dispersals leading up to the K-Pg extinction is essential for modeling changes to terrestrial vertebrate communities that occurred before the event. Thus, further sampling of enigmatic assemblages from the Maastrichtian, such as those of the eastern United States, is important for studying this subject.

In the Campanian-Maastrichtian of New Jersey, a set of formations corresponds to a period of transgressions and regressions of the Atlantic Ocean (e.g., Gallagher, 1993; Sugarman et al., 1995; Miller et al., 2004; Gallagher et al., 2014). The majority of these Cretaceous units are known for producing marine vertebrate and invertebrate fossils (Gallagher, 1993), although some, such as the Woodbury and New Egypt formations, are notable for producing some of the first partial dinosaur skeletons from the Americas (e.g., Leidy, 1858; Cope, 1866; Gallagher, 1993, Weishampel and Young, 1996; Gallagher, 1997). One of the most fossiliferous of these formations is the Mount Laurel Formation, which is either uppermost Campanian or lowermost Maastrichtian (Miller et al., 2004) and in New Jersey has produced the remains of several groups of dinosaurs, including hadrosaurs, tyrannosaurs, and ornithomimosauras (Gallagher, 1993; Gallagher, 2014). Because of the sheer diversity of the community represented in the Mt. Laurel,
the formation serves as a window into eastern North American faunas. However, the terrestrial fossils it produces are often eroded postcranial fragments (Gallagher, 2014).

Here, I describe some theropod teeth from the Mt. Laurel Formation of New Jersey. These include a large tooth assignable to a mid-sized (est. 6—8 m) tyrannosauroid and a smaller, heavily recurved one assignable to a smallish (est. 2—3 m) dromaeosaurid. These teeth are among the most diagnostic records of theropods from the Mt. Laurel Formation, allowing for a more precise understanding of the faunal composition and ecology of the eastern seaboard during the Maastrichtian, a globally under-sampled time period (Le Loeuff, 2012; Brusatte et al., 2012).

The dromaeosaurid tooth, representing the youngest occurrence of a non-avian maniraptoran in the American east, is very closely allied with Maastrichtian western North American saurornitholestines, suggesting Laramidian maniraptorans dispersed into eastern North America as early as the latest Campanian. The tyrannosauroid tooth is comparable to the dentition of *Dryptosaurus aquilunguis*, providing the first strong morphological support for the presence of *Dryptosaurus* or a closely related form in the Mt. Laurel ecosystem and representing a probable additional record of phylogenetically-intermediate tyrannosaurs in eastern North America. These specimens indicate that Appalachian vertebrate faunas were already becoming heterogenous during the early Maastrichtian, five million years earlier than previous discoveries have indicated. Along with other finds in North America, Europe, and Asia, these Mt. Laurel theropod teeth indicate complex interchanges occurred across northern hemisphere only a few million years before the end of the Mesozoic Era.

**Results.**

Geological setting.
Both theropod teeth described here were collected from sediments of the Mount Laurel Formation (Gallagher, 1993; pers. obs.), a marine deposit that represents a regression of the Atlantic Ocean during the Late Cretaceous period and is the oldest unit included in the Monmouth Group (Gallagher, 1993; Miller et al., 2004). The tyrannosauroid tooth described here, NJSM GP 12456, was recovered from Big Brook (Fig. 1A), a highly fossiliferous locality famous for producing an extensive marine fauna (Gallagher, 1993; Weishampel and Young, 1996). At Big Brook, the stratigraphic column is exposed along the banks, with the Mt. Laurel smoothly transitioning from the underlying Wenonah Formation such that the border between the two are indistinguishable (Gallagher, 1993). The contact between the Mt. Laurel and the overlying Navesink Formation is highly irregular (Miller et al., 2004; Gallagher et al., 2014). The Mt. Laurel Formation appears as gray to dark brown, pebbly quartz sands. The Big Brook tyrannosauroid tooth (Fig. 1E—H) is unusual among the terrestrial vertebrate teeth collected from the site in possessing a well-preserved enamel surface. Whereas other terrestrial vertebrate fossils from Big Brook are known for being heavily water-worn and lacking morphological details, NJSM GP 12456 preserves both its outermost enamel layer and many of its denticles. NJSM GP 22949, the dromaeosaurid tooth, was recovered from Mt. Laurel deposits in Burlington County, New Jersey (Fig. 1A). In this area, which makes up a portion of the southwestern-most range of the Monmouth Group, the sands of the Mt. Laurel are more glauconitic than farther north and are intermixed with iron compounds (Gallagher, 1993). The thickness of this unit is also far greater to the southwest of its range (e.g., Gallagher, 1993).

Tyrannosauroid tooth.

Systematic Paleontology.
Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Tyrannosauroidea Osborn 1905

Tyrannosauroidea indet., cf. *Dryptosaurus aquilunguis* Cope 1866

Material.

New Jersey State Museum collections (NJSM) GP 14256, the partial tooth of a large theropod dinosaur (Fig. 1E—H).

Locality and Horizon.

Mt. Laurel Formation sediments at Big Brook, Monmouth County, New Jersey, latest Campanian to early Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.

NJSM GP 14256 (Fig. 1E—H) closely resembles the dentition of tyrannosaurid theropods in several respects. The tooth resembles those of adult tyrannosauroids in its size, which is closely comparable to tyrannosaur crowns known from both western and eastern North America (Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et al., 2011; Williamson and Brusatte, 2014). In addition to its size, the Mt. Laurel tooth resembles those of tyrannosaurs among theropods known from Late Cretaceous North America in possessing packed denticles (2–2.5/mm) on its distal carina (15+ mm), the presence of denticles along both carinae, the straightness of its distal margin, the presence of numerous transverse undulations (density = 2/mm) on its main surface, and its smooth but irregular surface texture (Fig 1E—H)(Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et
al., 2011; Williamson and Brusatte, 2014). However, despite the size of the Mt. Laurel tooth, which indicates the ontogenetic maturity of the individual it represents, NJSM GP 14256 is notably unlike the teeth of tyrannosaurids, which possess incrassate teeth with D-shaped basal cross-sections (e.g., Williamson and Brusatte, 2014). Instead, NJSM GP 14256 shows is highly mediolaterally compressed and possesses a lens-shaped basal cross-section, indicative it came from a more basal tyrannosaur outside Tyrannosauridae. Among large Late Cretaceous tyrannosaurs, only *Dryptosaurus aquilunguis* from the Maastrichtian New Egypt Formation of New Jersey is known to possess this combination of features in its teeth (e.g., Brusatte et al., 2011). NJSM GP 14256 is also closely comparable with the mediolaterally compressed teeth of *Dryptosaurus aquilunguis* in its dimensions, curvature, and prominence and density of its denticles (1.7—1.8 mm in *Dryptosaurus*) and enamel crenulations (Brusatte et al., 2011; pers. obs. of YPM PU 22208). Given the Mt. Laurel tooth’s very close spatiotemporal proximity to the holotype of *Dryptosaurus*, I suggest the former belongs to *D. aquilunguis* or a close relative.

The principle components analysis including NJSM GP 14256 in a modified version of the dataset of Smith et al. (2005) found this tooth to cluster more closely to those of tyrannosauroid theropods than to dromaeosaurids and troodontids (Fig. 2). Furthermore, phylogenetic analysis of the tooth within the dataset of Hendrickx and Mateus (2014) found NJSM GP 14256 to be the sister taxon of *Tyrannosaurus rex* in a clade united by four characters. These are characters 94 (biconvex apical denticles present on distal carinae of lateral teeth), 100 (subequal number of denticles apically than at mid-crown portion of distal carinae on lateral teeth), 103 (interdenticular space between mid-crown denticles on distal carinae of lateral teeth broad), and 105 (interdenticular sulci between mid-crown denticles on distal carinae of lateral
teeth present, long, and well-developed) (Hendrickx and Mateus, 2014). The clade comprised of NJSM GP 14256 and other derived tyrannosaurs (*Alioramus, Tyrannosaurus, “Raptorex”*) is united by the presence of a sub-symmetric crown with a centrally-positioned distal carina in distal view (char. 83). The strict consensus tree (tree length = 688, consistency index = 0.340, retention index = 0.561) is shown in Fig. 1B.

Description.

NJSM GP 14256 (Fig. 1) is the apical half of the tooth of a theropod dinosaur. Measurements of the specimen may be found in Table 1. The tooth is well-preserved for a terrestrial fossil collected from one of the marine deposits of the Cretaceous Atlantic Coastal Plain, preserving details of the outer enamel layer and denticle morphology. Unfortunately, the basal half of the crown and the entirety of the root of the tooth are not preserved. This is probably due to erosion, as the tooth is broken transversely and heavily rounded at its preserved base (Fig. 1E—F).

The tooth displays the ziphodont condition in being labiolingually compressed and only slightly recurved. The preserved mesial carina is slightly convex, whereas the distal carina is straightened along its entire run. The labial and lingual portions of the enamel are well-preserved (Fig. 1G), bearing developed transverse undulations that develop out of the distal margin of the tooth to become bands (Brusatte et al. 2007). In NJSM GP 14256, these undulations (= marginal bands) are relatively strongly developed, although they are less prominent than in carcharodontosaurids (e.g., Sereno et al., 1996; Brusatte et al., 2007). The labial and lingual surfaces of the tooth are slightly convex, as in most other theropod dinosaurs (Hendrickx et al.,
2015a). The apex of the tooth bears a slight wear facet on its lingual surface. The tooth is lenticular in basal cross-section.

The distal carina preserves many denticles (Fig. 1E—F, H), which are small, dense (6/mm), and apicobasally straightened. The denticles are interspersed with diminutive interdenticular sulci (the “blood grooves” of Currie et al. (1990)). These are encompassed by the apical ends of the denticles. These denticles maintain a similar density along the entirety of the distal carina. However, their density may have changed along the missing portion of the tooth. The mesial carina preserves a few denticles, although these are too eroded for much morphological description. These denticles appear to be similar in size to those on the distal carina.

### Table 1. Measurements of teeth described in this study (in/per mm).

| Specimen | CH  | CBL | CBW | AL  | CA  | MB  | MC  | MA  | DB  | DC  | DA  |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| NJSM GP 12456 | 15 (est. 25) | 8.99 | 4.90 |     |     |     |     |     | 2   | 2   | 2.5 |
| NJSM GP 22949 | 15.5 | 8.0 | 2.0 | 18.00 | 55.5 |     |     |     | 6   | 5   | 5   |

Dromaeosaurid tooth.

Systematic Paleontology.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Maniraptora Gauthier 1986
Dromaeosauridae Matthew & Brown 1922

Sauornitholestinae Sues 1978

Sauornitholestinae indet.

Material.

NJSM GP 22949, the tooth of a mid-sized theropod dinosaur.

Locality and Horizon.

Mt. Laurel Formation sediments in Burlington County, New Jersey, latest Campanian to early Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.

NJSM GP 22949 is identified as the lateral tooth of a dromaeosaurid theropod based on the following combination of features: (1) its extreme apicobasal curvature created by its concave distal carina and distally offset apex, (2) the presence of apically hooked distal denticles, (3) the absence of mesiodistal constriction along the crown base, and (4) distal denticles that decrease in size towards the apex of the tooth (Fig. 3A—E)(Currie et al., 1990; Turner et al., 2012; Larson and Currie, 2013; Williamson and Brusatte, 2014). NJSM GP 22949 is smaller than the majority of Appalachian theropod teeth assigned to tyrannosaurids, in which crown heights surpass 50 mm (Schwimmer et al., 1993; Carr et al., 2005; Brusatte et al., 2011; Denton et al., 2011; Schwimmer et al., 2015). However, the tooth is somewhat larger than most North American dromaeosaurid teeth, which are often less than 10 mm in height (Ostrom, 1969; Currie et al., 1990; Currie and Varricchio, 2004; Larson and Currie, 2013; Williamson and Brusatte, 2014; Wick et al., 2015). *Dakotaraptor*, which possessed crowns up to ~25 mm high, represents the exception among Maastrichtian forms (Palma et al., 2015). NJSM GP 22949 is also
distinguished from Appalachian tyrannosauroids in lacking subquadrangular distocentral
denticles (Hendrickx et al., 2015). The first principle components analysis on the Mt. Laurel
dromaeosaurid tooth supports this hypothesis by placing the specimen closer to the convex hulls
formed by dromaeosaurid teeth than to those formed by tyrannosauroids (Fig. 4).

NJSM GP 22949 is notable for being very similar to the teeth of western North American
saurornitholestine dromaeosaurs (Fig. 3A—E, G)(Larson and Currie, 2013) and unlike those
previously discovered from the American east (Kiernan and Schwimmer, 2004; Schwimmer et
al., 2015; Brownstein, 2018a). Teeth assigned to “cf. Saurornitholestes” have been described
from the Cretaceous of the southeastern United States (Kiernan and Schwimmer, 2004;
Schwimmer et al., 2015), but these are extremely small (< 6 mm), far less recurved than NJSM
GP 22949, and have proportionally large denticles that are more strongly apically hooked (e.g.,
fig. 1 in Kiernan and Schwimmer, 2004). One tooth from Alabama measuring 4.9 mm in crown
height and preserving 7 distal denticles and 8 mesial denticles per mm is less recurved than
NJSM GP 22949 and far less slender (see Kiernan and Schwimmer, 2004). Some
‘saurornitholestine’ teeth from South Carolina (Schwimmer et al., 2015) also lack the ‘slender’
condition in NJSM GP 22949, where the width of the heavily recurved tooth crown steadily
shortens towards the apex to produce a tall, mesiodistally shortened crown. All these teeth are
very similar to dromaeosaurid crowns described from the mid-Cretaceous of Idaho
(Krumenacker et al., 2016) and Utah (Frederickson et al., 2018). Teeth from the Ellisdale site of
New Jersey include dromaeosaurid crowns (Denton et al., 2011; Brownstein, 2018c). However,
large crowns from Ellisdale are not ‘slender’ like NJSM GP 22949, are much larger in size, and
bear distal denticles that are considerably more apically hooked than the Mt. Laurel tooth and
western saurornitholestines (Brownstein, 2018c). A dromaeosaurid tooth from North Carolina is slightly larger than NJSM GP 22949, but is less recurved and far less slender (Brownstein, 2018b).

When compared to dromaeosaurid teeth from outside eastern North America, NJSM GP 22949 most closely resembles the teeth of western North American saurornitholestine dromaeosaurids. Unlike the western North American velociraptorine Acheroraptor temertyorum (Evans et al., 2013) and the Mongolian Velociraptor mongoliensis (Turner et al., 2012; Fig. 3F), NJSM GP 22949 lacks strongly developed striations along its crown surface, is more strongly recurved, and is far more slender. In contrast to Utahraptor ostrommaysorum, Dromaeosaurus albertensis, and ‘dromaeosaurine’ teeth from western North America, the mesial carina in NJSM GP 22949 is not twisted onto the mesiolingual face of the crown, the distal denticles are apically hooked, and the tooth is more strongly recurved (Fig. 3H—I; Turner et al., 2012; Larson and Currie, 2013). The Mt. Laurel tooth is also smaller, much more strongly recurved, and possesses denticles more apically hooked than those of the giant Maastrichtian dromaeosaurid Dakotaraptor steini (DePalma et al., 2015). NJSM GP 22949 lacks the ‘figure-8’ basal cross-section seen in the teeth of Deinonychus (Ostrom, 1969; Brownstein, 2018b; pers. obs.).

Although the strongly recurved maxillary teeth of Deinonychus (Ostrom, 1969; Turner et al., 2012; pers. obs.) are somewhat comparable with NJSM GP 22949, the differing basal cross-sections among these specimens and the slightly asymmetrical morphology of the teeth in Deinonychus distinguish D. antirrhopus and the Mt. Laurel form.

NJSM GP 22949 closely resembles the teeth of western North American Maastrichtian saurornitholestines in having a slender, tall outline in labial and lingual views (the “Lancian”
saurornitholestine morphotype of Larson and Currie, 2013). The tooth is closely comparable with the crowns of the juvenile saurornitholestine ‘Bambiraptor feinbergi,’ which are extremely recurved and slender and possess apically-hooked denticles (Fig. 3G). A principle components analysis of the Late Cretaceous western North American paravian tooth dataset of Larson and Currie (2013) found NJSM GP 22949 to nest within the convex hulls formed by four tooth morphotypes (Saurornitholestinae, Dromaeosaurinae, Zapsalis, and Atrociraptor). However, unlike in teeth assigned to Dromaeosaurus or other ‘dromaeosaurines,’ the mesial carina in NJSM GP 22949 is not twisted onto the mesiolingual face of the crown and the distal denticles are apically hooked (Fig. 3H—I; Larson and Currie, 2013). NJSM GP 22949 is also quantifiably unlike YPM VPPU.021397, the large dromaeosaurid tooth from the Campanian of North Carolina (Brownstein, 2018b), plotting far from the southeastern North American specimen in both morphometric analysis in which these teeth were included (Fig. 4). Thus, NJSM GP 22949 is identifiable as the crown of a dromaeosaurid with affinities to coeval western saurornitholestines.

Description.

NJSM GP 22949 is the complete crown of a dromaeosaurid dinosaur. Measurements of this specimen are in Table 1. This tooth is heavily recurved, displaying the ziphodont condition present in the teeth of other Appalachian theropods (e.g., Brusatte et al. 2011; Schwimmer et al., 2015). The crown is also mediolaterally compressed and possesses an ovoid basal cross-section. In distal view, the middle portion of tooth is convex labially and distally, although the crown becomes labiolingually straightened towards its apex. The labial and lingual surfaces are flattened, and the lack of a root attached to this crown indicates it was shed. Although both the
mesial and distal carinae are preserved, the mesial denticles have been eroded away. Some portions of the tooth crown are cracked, and the outer enamel layer is poorly preserved towards the distal end of the specimen. Small portions of the middle of the crown are missing. The distal profile of NJSM GP 22949 is strongly concave and more developed in basal cross-section than the mesial. The preserved portions of the outer enamel layer are smooth, although at the apex several slightly developed ridges appear. These ridges could represent features of the original morphology of the tooth or be damage from feeding or taphonomic processes.

The distal carina preserves a large number of apically hooked denticles that become smaller towards the apex of the crown. These denticles are separated by interdenticular sulci that, along with the serrations, project slightly onto the tooth surface. Unfortunately, the shape and density of the mesial denticles could not be determined, as the mesial carina is heavily eroded in NJSM GP 22949.

Discussion.

The two theropod teeth described here add to one of the most complete Maastrichtian faunas from eastern North America. The dromaeosaurid tooth NJSM GP 22949 is the first occurrence of this clade in the Mount Laurel Formation and more generally Maastrichtian of eastern North America. Until now, only tyrannosaurid and ornithomimosaur remains have been reported from this area (Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997; Brusatte et al., 2011; Brusatte et al., 2012; Gallagher et al., 2014), with the latest records of dromaeosaurids in the American east hailing from mid-Campanian units in the Carolinas (Schwimmer et al., 2015; Brownstein, 2018b) and the Ellisdale site of New Jersey (Denton et al., 2011). Although NJSM GP 22949 is most comparable to the crowns of mid-sized to largish
dromaeosaurids like *Deinonychus antirrhopus* and *Dakotaraptor steini* (Ostrom, 1969; DePalma et al., 2015) and small tyrannosauroids (Denton et al., 2011; Williamson and Brusatte, 2014; Schwimmer et al., 2015) in its dimensions, it is most closely allied with dromaeosaurids in the morphometric analyses conducted (Fig. 4) and in several key features of its morphology. Indeed, this tooth is of great biogeographical significance for being the youngest record of a non-avian maniraptoran in the eastern half of the North American continent, greatly increasing theropod diversity in this area.

The tyrannosauroid tooth NJSM GP 14256 supports the presence of *Dryptosaurus*-like tyrannosauroids in the early Maastrichtian of New Jersey. Isolated teeth and postcranial fragments from the Mount Laurel were previously assigned to *Dryptosaurus* sp. based on little more than their geographic proximity to the site where the holotype of this taxon was recovered (Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997), but no detailed description of early Maastrichtian tyrannosauroids from New Jersey has appeared in the literature. The well-preserved nature of NJSM GP 14256 thus allows for the formal recognition of the presence of intermediate-grade tyrannosauroids in the earliest Maastrichtian of the Atlantic Coastal Plain. Furthermore, the excellent condition of the outer enamel layer of NJSM GP 12456 allows for further documentation of the dental anatomy of Appalachian tyrannosauroids, the isolated teeth of which are often found highly abraded among stream deposits (e.g., Weishampel & Young, 1996). The presence of non-tyrannosaurid tyrannosauroids in the Mt. Laurel Formation was expected, given the presence of *Dryptosaurus aquilunguis* and non-tyrannosaurid tyrannosaurs of similar phylogenetic position in both the middle-late Maastrichtian Navesink and New Egypt formations (Gallagher, 1993; Brusatte et al., 2011) and Campanian Marshalltown Formation.
(Denton et al., 2011). However, that NJSM GP 14256, originally discovered in 1984, is only described now attests to the understudied nature of these deposits.

The late recognition of dromaeosaurids in the Maastrichtian sediments of New Jersey is somewhat more intriguing, given that the dinosaurs of the Mt. Laurel and other Cretaceous units in the Atlantic Coastal Plain have been studied for over a century and a half (e.g., Leidy, 1858; Cope, 1866; Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997). Teeth from locations like the Ellisdale site of the Marshalltown Formation of New Jersey originally assigned to tyrannosaurs have more recently been reclassified as the crowns of dromaeosaurids (Gallagher et al., 1986; Gallagher, 1993, 1997; Denton et al., 2011), so it is entirely possible that the lack of diversity in dinosaur faunas from the Maastrichtian of the Atlantic Coastal Plain reflects systematic misidentification of these isolated fossils. Only further work on Appalachian fossils will allow for more comprehensive revision of the identification of fossils from this area.

On a larger biogeographical scale, the two teeth described here are important for illuminating early trends to faunal homogenization in the latest Cretaceous of the northern hemisphere. The trend in faunal composition for the majority of the Cretaceous was evolution in isolation, which coincided with the breakup of supercontinents like Gondwana and Laurasia and the inundation of smaller landmasses like North America and Europe (e.g., Russell, 1995; Sereno et al., 1996; Csiki et al., 2010; Sampson et al., 2010; Csiki-Sava et al., 2015). In particular, the faunas of Appalachia and Laramidia, which became isolated from each other as the Western Interior Seaway flooded the middle of North America (e.g., Russell, 1995; Roberts and Kirschbaum, 1997; Schwimmer, 2002; Sampson et al., 2010), have been recognized as highly distinctive (e.g., Gallagher, 1993; Weishampel and Young, 1996; Gallagher, 1997; Sampson et
al., 2010; Denton et al., 2011; Schwimmer et al., 2015). However, in the past thirty years, a
handful of discoveries from the eastern margin of the North American continent have indicated
some faunal interchange occurred between Laramidian and Appalachian dinosaur communities
during the latest Maastrichtian. These include the tooth of a ceratopsid from the latest
Maastrichtian of Mississippi and the forelimb material of possible lambeosaurines from the
Maastrichtian of New Jersey and earliest Maastrichtian of Nunavut, Canada (Gallagher, 1995;
Gallagher, 1997; Farke and Phillips, 2017). The discovery of a dromaeosaurid tooth in the latest
Campanian-earliest Maastrichtian Mt. Laurel Formation with affinities to western North
American saurornitholestine dromaeosaurids is particularly interesting in the context of these
other finds, indicating such faunal dispersals could have occurred as early as the late Campanian.
At the same time, Appalachian faunas continued to harbor endemic forms like intermediate
tyrannosauroids, represented by Dryptosaurus aquilunguis and comparable forms through the
Campanian-Maastrichtian transition in the Atlantic Coastal Plain (Gallagher, 1993; Brusatte et
al., 2011; this paper).

Faunal homogenization in the last 10 million years of the Mesozoic seems to have
occurred throughout the northern hemisphere. The presence of Tyrannosaurus rex in the
Maastrichtian of the western United States and Canada seems to represent a dispersal of Asian
tyrannosauroids into the Americas (Brusatte et al., 2010; Brusatte and Carr, 2016). A dispersal
event between Asian and North Americans faunas during the Maastrichtian may have occurred
over Beringia (Fiorillo, 2008), given the similarity of Maastrichtian polar faunas from Russia,
Alaska, and lower latitudes in the United States and Canada (e.g., Weishampel et al., 2004;
Gangloff, 2012; Godefroit et al., 2012; Le Loeuff, 2012). The new teeth illuminate the presence
of this trend in the Campanian-Maastrichtian of the Atlantic Coastal Plain, showing that the
transition from a solely endemic Appalachian fauna to one including immigrant genera occurred
during the beginning of the closure of the Western Interior Seaway (Schwimmer, 2002; Farke
and Phillips, 2017; Brownstein, 2018a).

Conclusions.

Two theropod teeth from the Campanian-Maastrichtian Mount Laurel Formation of New
Jersey preserve the detailed morphology of their denticles and enamel surfaces, allowing for their
assignment to dromaeosaurids and tyrannosauroids. The dromaeosaurid tooth, which plots with
western North American saurornitholestine teeth in principle components and discriminant
analyses, is the youngest record of a non-avian maniraptoran from eastern North America and the
first from the Maastrichtian of the American east. Along with the tyrannosauroid tooth, which is
the first specimen to strongly suggest the presence of *Dryptosaurus aquilunguis* or a closely
related tyrannosauroid in the Mt. Laurel ecosystem, this dromaeosaurid crown provides new
information in faunal interchanges in the latest Cretaceous of the northern hemisphere, pushing
back the dispersal of western North American taxa into the eastern half of the continent into the
Campanian-Maastrichtian boundary.

Methods.

Measurements and nomenclature.

Measurements of both teeth were taken in accordance with the methodology of Smith et al.
(2005) and Larson and Currie (2013). The dimensions of the Mt. Laurel teeth were determined
using digital calipers. I follow the nomenclature of Hendrickx et al. (2015) when describing the
two teeth on which this paper focuses.
Principle components analyses.

In order to provide statistical support for the assignment of the two described teeth to specific groups of theropod dinosaurs, I included them in principle components analyses conducted in the program PAST v. 3.18 (Hammer et al., 2001). In order to assess the morphological similarity of the Mt. Laurel teeth to theropod clades present in the Cretaceous of the northern hemisphere, I used a modified version (Brownstein, 2018b) of the dataset of Smith et al. (2005) that includes tooth data on tyrannosauroids, troodontids, and dromaeosaurids. A principle components analysis was run on this dataset, which included data on fifteen measurements: crown height (CH), crown base length (CBL), crown base width (CBW), apicobasal length (length of the tooth along the longest apicobasal axis), serration density per 5mm for the basal (MB), mid-crown (MC), and apical (MA) mesial carina, and the same for the distal carina (DB, DC, DA). An additional principle components analysis (PCA) was conducted using the dataset of Larson and Currie (2013) in order to better assess the similarity of the Mt. Laurel dromaeosaurid specimen to other North American paravian teeth. This principle components analysis assessed for five measurements: CH, CBL, CBW, and the mesial (MD) and distal (DD) denticles per millimeter. The summary statistics and loadings from the results of the PCAs conducted are included in the Supplementary Information.

Discriminant analyses.

To further assess the affinities of the Mt. Laurel dromaeosaurid tooth, I performed a discriminant analysis on the tooth datasets of Smith et al. (2005, modified in Brownstein, 2018b) and Larson and Currie (2013). This analysis creates a morphospace by maximally separating objects sorted
into pre-determined groups. This analysis was also run in PAST v. 3.18 (Hammer et al., 2001), and the summary statistics can be found in the supplementary information.

Phylogenetic analysis.

To provide additional support for the referral of the incomplete tyrannosauroid tooth to that family, I coded the specimen for the phylogenetic matrix of Hendrickx and Mateus (2014), a dataset of theropod dentition that includes 64 taxa/specimens coded for 141 characters. The matrix was entered into the phylogenetics program TNT 1.5 (Goloboff and Catalano, 2016) for a phylogenetic analysis. The matrix was first analyzed using the “New Technology Search,” with default parameters for ratchet, tree drift, tree fuse, and sectorial search. A total of 10 trees of length 688 were retained. These topologies were then subjected to traditional (TBR) branch swapping, which allows for a more extensive exploration of each tree island. This found over >99,999 most parsimonious topologies of 688. These were summarized in a strict consensus topology.

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Availability of data and material.

All data is available in the Supplementary Information.

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Figure 1. Locality information, Maastrichtian eastern North American dinosaurs, and Mount Laurel tyrannosauroid tooth anatomy. (A) map of New Jersey showing the location of Burlington and Monmouth counties and the Big Brook site (pink dot), (B) possible partial Lambeosaurine forelimb, (C) cast of the manual ungual of *Dryptosaurus aquilunguis*, and (D) pedal phalanx of an ornithomimosaur. NJSM GP 14256 in labial (E—F) distal (G), and basal (H) views with a closeup of the enamel wrinkles (I) and distal denticles (J). Map is public domain, access to photograph the cast of the manual ungual of *Dryptosaurus aquilunguis* courtesy of the Yale Peabody Museum (peabody.yale.edu).
Figure 2. Support for the assignment of NJSM GP 12456 in Tyrannosauroidia. (A) Principle components analysis of coelurosaurian teeth including a large dromaeosaurid tooth from North Carolina and the Mt. Laurel tyrannosauroid tooth (Smith et al., 2005; Brownstein, 2018b). Principle component 1 accounted for 91.677% of variance, whereas principle component 2 accounted for 4.0981%. (B) Phylogenetic topology of theropod teeth, with Tyrannosauroidia highlighted in red.
Figure 3. Anatomy of the Mt. Laurel dromaeosaurid tooth. NJSM GP 22949 in labial (A), lingual (B), basal (C), and distal (D) views, with a closeup (E) of the distal denticles. (F), teeth of *Velociraptor*, (G) dentary and teeth of “*Bambiraptor*,” (H) premaxilla and teeth of *Utahraptor*, and (I) dentary and teeth of *Dromaeosaurus*. r, enamel ridge; tc, twisted mesial carina.
Figure 4. Principle components and discriminant analyses of the Mt. Laurel dromaeosaurid tooth. (A), Principle components analysis of coelurosaurian teeth including a large dromaeosaurid tooth from North Carolina and the Mt. Laurel dromaeosaurid tooth (Smith et al., 2005; Brownstein, 2018b). Principle component 1 accounted for 91.722% of variance, whereas principle component 2 accounted for 4.0932%. (B), Principle components analysis of North American paravian teeth including the Mt. Laurel dromaeosaurid tooth (Larson and Currie, 2013). Principle component 1 accounted for (C), Discriminant analysis of North American paravian teeth including the Mt. Laurel dromaeosaurid tooth (Larson and Currie, 2013).
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Finally, I’ve removed the biogeographic speculations in line with the comments of the reviewers and editor. I agree that these were presented far too strongly, and I have reorganized the manuscript to act as a faunal characterization. I’ve also revised the manuscript in accordance with the many minor comments presented in reviewer 2’s annotated PDF.

I hope the manuscript is now suitable for publication, and thank you for your reviews.

Regards,

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Collections & Exhibitions, Stamford Museum & Nature Center
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Responses to Reviewers.

Chase D. Brownstein

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Done. I’ve double checked the scale bars to make sure they are correct. Please see the revised figure.

*You also have a substantial amount of missing data for your new specimens in your dataset, and you haven’t discussed how this was handled in your PCA. The default in PAST is to fill missing data with column average substitution, which in the Smith et al. (2005) dataset will bias all of your specimens towards the tyrannosaur part of your plot (as there are more tyrannosaurs in the dataset than any other group). Given that all three of the new teeth plot in areas of your plots where no other theropod teeth plot (partway between dromaeosaurs and tyrannosaurs), it appears that column average substitution of your dataset is having a substantial contribution to the position of your specimens on these plots. As well, eastern taxa are notably excluded. Dryptosaurus is not plotted in Fig. 2A, and the Tar Heel dromaeosaurid is not plotted in Fig. 4B and 4C, making the argument that either of these teeth have eastern or western affinities insufficiently supported by these analyses. Additions of those specimens and the exclusion of variables with missing data are necessary for these plots to be informative.*

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Done.
### Appendix C

#### ROYAL SOCIETY
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**New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America**

| Journal                  | Royal Society Open Science |
|--------------------------|----------------------------|
| Manuscript ID            | RSOS-191206                |
| Article Type             | Research                   |
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| Complete List of Authors | Brownstein, Chase; Stamford Museum and Nature Center, |
| Subject                  | Palaeontology < EARTH SCIENCES, evolution < BIOLOGY, ecology < BIOLOGY |
| Keywords                 | Dinosaur, Biogeography, Appalachia, Cretaceous |
| Subject Category         | Biology (whole organism)   |

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Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

Statement (if applicable):
CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The data is included in the supplementary material.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors' contributions

I am the only author on this paper

Statement (if applicable):
CUST_AUTHOR_CONTRIBUTIONS_TEXT :No data available.
Cover Letter

July 10, 2019

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New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna

Chase Doran Brownstein
Research Associate, Dept. of Collections and Exhibitions, Stamford Museum and Nature Center, Stamford, CT, chasethedinosaur@gmail.com
Abstract.

The faunal changes that occurred in the few million years before the Cretaceous-Paleogene extinction are of much interest to vertebrate paleontologists. Western North America preserves arguably the best fossil record from this time, whereas terrestrial vertebrate fossils from the eastern portion of the continent are usually limited to isolated, eroded postcranial remains. Examination of fragmentary specimens from the American east, which was isolated for the majority of the Cretaceous as the landmass Appalachia, is therefore important for better understanding dinosaur diversity at the end of the Mesozoic. Here, I report on two theropod teeth from the Mount Laurel Formation, a lower-middle Maastrichtian unit from northeastern North America. One of these preserves in fine-detail the structure of the outer enamel and resembles the dentition of the tyrannosauroid *Dryptosaurus aquilunguis* among latest Cretaceous forms in being heavily mediolaterally compressed and showing many moderately developed enamel crenulations. Along with previously reported tyrannosauroid material from the Mt. Laurel and overlying Cretaceous units, this fossil supports the presence of non-tyrannosaurid tyrannosauroids in the Campanian-Maastrichtian of eastern North America. The other tooth is assignable to a dromaeosaurid and represents both the youngest occurrence of a non-avian maniraptoran in eastern North America and the first from the Maastrichtian reported east of the Mississippi. This tooth, which belonged to a medium-sized dromaeosaurid based on size comparisons with the teeth of taxa for which skeletons are known, increases the diversity of the Maastrichtian dinosaur fauna of Appalachia. Along with previously reported dromaeosaurid teeth, the Mt. Laurel specimen supports the presence of mid-sized to large dromaeosaurids in eastern North America throughout the Cretaceous. This indicates that dromaeosaurids...
approaching or exceeding 3 meters in length were more common in the Late Cretaceous than previously thought.

Keywords: Dinosaur; Appalachia; Cretaceous; Fauna; Tyrannosaur; Teeth

Introduction.

The extinction of the non-avian dinosaurs at the end of the Mesozoic Era is a topic that has continued to intrigue vertebrate paleontologists (e.g., Alvarez et al., 1980; Sloan et al., 1986; Sarjeant and Currie, 2001; Le Loeuff 2012, Brusatte et al., 2012, 2015; Sakamoto et al., 2016). However, a poor global terrestrial record from the Maastrichtian has hindered attempts to assess the diversity dynamics of important groups like the Dinosauria during this period (e.g., Le Loeuff, 2012; Brusatte et al., 2015). Western North America preserves arguably the most well-characterized vertebrate record from the last 20 million years of the Mesozoic Era (Brusatte et al., 2015), whereas that from the eastern portion of the continent is far more obscure. During the majority of the Late Cretaceous, eastern and western North America were separated, the former existing as a rectangular landmass called Appalachia. Appalachian dinosaur faunas included intermediate-grade tyrannosauroids (Carr et al., 2005; Brusatte et al., 2011), basal hadrosaurids and derived non-hadrosaurid hadrosauroids (Langston, 1960; Prieto-Márquez et al., 2006; Prieto-Márquez et al., 2016), nodosaurids (Gallagher, 1993; Burns and Ebersole, 2016), and ornithomimosaurs (Miller, 1967; Schwimmer et al., 1993; Weishampel and Young, 1996; Schwimmer et al., 2015; Brownstein, 2018a).

Despite the amount of knowledge of Cretaceous faunal change to be gleaned from the fossil record of Appalachia, the assemblages of this landmass have remained fundamentally understudied since the mid-19th century (e.g., Weishampel & Young, 1996; Gallagher, 1997;
Weishampel, 2006; Brownstein, 2018a). The scarcity of terrestrial sedimentary units known from
the eastern half of the United States has also contributed to the obscurity of Appalachian faunas
compared to western North American ones (Weishampel and Young, 1996; Gallagher, 1997;
Carr et al., 2005; Weishampel, 2006; Brusatte et al., 2011). Only in the past few years have
indications of faunal changes in the latest Cretaceous (late Campanian-Maastrichtian) of the
American east come, and all from isolated, fragmentary finds. Although a ceratopsian tooth from
the uppermost Maastrichtian of Mississippi (Farke and Phillips, 2017) and possible
lambeosaurine bones from the upper Maastrichtian of New Jersey (Gallagher, 1993) have
revealed that faunal exchanges probably occurred between Appalachia and Laramidia following
the regression of the Western Interior Seaway in the latest Campanian-earliest Maastrichtian, the
timing of these events remains poorly constrained. Further sampling of enigmatic assemblages
from the Maastrichtian, such as those of the eastern United States, is therefore important for
understanding faunal change in latest Mesozoic North America.

In the Campanian-Maastrichtian of New Jersey, a set of formations corresponds to a
period of transgressions and regressions of the Atlantic Ocean (e.g., Gallagher, 1993; Sugarman
et al., 1995; Miller et al., 2004; Gallagher et al., 2014). The majority of these Cretaceous units
are known for producing marine vertebrate and invertebrate fossils (Gallagher, 1993), although
some, such as the Woodbury and New Egypt formations, are notable for producing some of the
first partial dinosaur skeletons from the Americas (e.g., Leidy, 1858; Cope, 1866; Gallagher,
1993, Weishampel and Young, 1996; Gallagher, 1997). One of the most fossiliferous of these
formations is the Mount Laurel Formation, which is either uppermost Campanian or lowermost
Maastrichtian (Miller et al., 2004) and in New Jersey has produced the remains of several groups
of dinosaurs, including hadrosaurs, tyrannosaurs, and ornithomimosaurs (Gallagher, 1993;
Gallagher, 2014). Because of the sheer diversity of the community represented in the Mt. Laurel, the formation serves as a window into Campanian-Maastrichtian eastern North American faunas. However, the terrestrial fossils it produces are often eroded postcranial fragments (Gallagher, 2014).

Here, I describe some theropod teeth from the Mt. Laurel Formation of New Jersey. These include a large tooth assignable to a 6—8 m tyrannosaurid and a smaller, heavily recurved one assignable to a 3—4 m dromaeosaurid. These teeth are among the most diagnostic records of theropods from the Mt. Laurel Formation, allowing for a more precise understanding of the faunal composition and ecology of the eastern seaboard during the Maastrichtian, a globally under-sampled time period (Le Loeuff, 2012; Brusatte et al., 2012).

**Results.**

**Geological setting.**

Both theropod teeth described here were collected from sediments of the Mount Laurel Formation (Gallagher, 1993; pers. obs.), a marine deposit that represents a regression of the Atlantic Ocean during the Late Cretaceous period and is the oldest unit included in the Monmouth Group (Gallagher, 1993; Miller et al., 2004). The tyrannosaurid tooth described here, NJSM GP 12456, was recovered from Big Brook (Fig. 1A), a highly fossiliferous locality famous for producing an extensive marine fauna (Gallagher, 1993; Weishampel and Young, 1996). At Big Brook, the stratigraphic column is exposed along the banks, with the Wenonah Formation grading into the Mt. Laurel such that the border between the two are indistinguishable (Gallagher, 1993). The contact between the Mt. Laurel and the overlying Navesink Formation is an unconformity (Miller et al., 2004; Gallagher et al., 2014). The Mt. Laurel Formation appears as gray to dark brown, pebbly quartz sands. The Big Brook tyrannosaurid tooth (Fig. 1E—H) is
unusual among the terrestrial vertebrate teeth collected from the site in possessing a well-
preserved enamel surface. Whereas other terrestrial vertebrate fossils from Big Brook are known
for being heavily water-worn and lacking morphological details, NJSM GP 12456 preserves both
its outermost enamel layer and many of its denticles.

NJSM GP 22949, the dromaeosaurid tooth, was recovered from Mt. Laurel deposits in
Burlington County, New Jersey (Fig. 1A). In this area, which makes up a portion of the
southwestern-most range of the Monmouth Group, the sands of the Mt. Laurel are more
glaucicotic than farther north and are intermixed with iron compounds (Gallagher, 1993). The
thickness of this unit is also far greater to the southwest of its range (e.g., Gallagher, 1993).

Tyrannosauroid tooth.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Tyrannosauroidea Osborn 1905

Tyrannosauroidea indet.

Material.

New Jersey State Museum collections (NJSM) GP 14256, the partial tooth of a large theropod
dinosaur (Fig. 1E—H).

Locality and Horizon.

Mt. Laurel Formation sediments at Big Brook, Monmouth County, New Jersey, latest
Campanian to early Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.
NJSM GP 14256 (Fig. 1E—H) closely resembles the dentition of tyrannosauroid theropods in several respects. The tooth resembles those of adult tyrannosauroids in its size, which is closely comparable to tyrannosaur crowns known from both western and eastern North America (Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et al., 2011; Williamson and Brusatte, 2014). In addition to its size, the Mt. Laurel tooth resembles those of tyrannosaurs to the exclusion of other theropods known from Late Cretaceous North America in possessing a combination of packed denticles (2–2.5/mm) on its distal carina (15+ mm), the presence of denticles along both carinae, its slight, rather than pronounced, curvature, the presence of numerous transverse undulations (density = 2/mm) on its main surface, the presence of slightly biconvex denticle outlines for denticles all along the tooth (Fig. 1J), and its smooth but slightly irregular surface texture (Fig 1E—H)(Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et al., 2011; Williamson and Brusatte, 2014).

However, despite the size of the Mt. Laurel tooth, NJSM GP 14256 is notably unlike the teeth of tyrannosaurids, for which incrassate teeth are a synapomorphy (e.g., Williamson and Brusatte, 2014; Brusatte and Carr, 2016). Instead, NJSM GP 14256 shows is highly mediolaterally compressed and possesses a lens-shaped basal cross-section, indicative it came from a tyrannosauid outside Tyrannosauridae. Among large Late Cretaceous tyrannosaurs, only *Dryptosaurus aquilunguis* from the Maastrichtian New Egypt Formation of New Jersey is known to possess a combination of high mediolateral compression and tyrannosaurid-like features of the denticles and tooth surface (e.g., Brusatte et al., 2011). NJSM GP 14256 is also comparable with the mediolaterally compressed teeth of *Dryptosaurus aquilunguis* in its dimensions, curvature, and enamel crenulations (Brusatte et al., 2011; pers. obs. of YPM PU 22208). Given the Mt.
Laurel tooth’s very close spatiotemporal proximity to the holotype of *Dryptosaurus*, I suggest the tooth belongs to a closely related form.

Given the number of measurements unable to be taken from this tooth, I did not include it in a morphometric analysis. However, phylogenetic analysis of the tooth within the dataset of Hendrickx and Mateus (2014) found NJSM GP 14256 to be the sister taxon of *Tyrannosaurus rex* in a clade united by four characters. These are characters 94 (biconvex apical denticles present on distal carinae of lateral teeth), 100 (subequal number of denticles apically than at mid-crown portion of distal carinae on lateral teeth), 103 (interdenticular space between mid-crown denticles on distal carinae of lateral teeth broad), and 105 (interdenticular sulci between mid-crown denticles on distal carinae of lateral teeth present, long, and well-developed)(Hendrickx and Mateus, 2014). The clade comprised of NJSM GP 14256 and other derived tyrannosaurs (*Alioramus*, *Tyrannosaurus*, “*Raptorex*”) is united by the presence of a sub-symmetric crown with a centrally-positioned distal carina in distal view (char. 83). Characters uniting the tyrannosauroid clade include 3, 5, 19, 27, 37, 38, 41, and 48 in the list of Hendrickx and Mateus (2014). The strict consensus tree (tree length = 688, consistency index = 0.340, retention index = 0.561) is shown in Fig. 1B.

Description.

NJSM GP 14256 (Fig. 1) is the apical half of the tooth of a theropod dinosaur. Measurements of the specimen may be found in Table 1. The tooth is well-preserved for a terrestrial fossil collected from one of the marine deposits of the Cretaceous Atlantic Coastal Plain, preserving details of the outer enamel layer and dentine morphology. Unfortunately, the basal half of the crown and the entirety of the root of the tooth are not preserved. This is
probably due to erosion, as the tooth is broken transversely and heavily rounded at its preserved base (Fig. 1E—F).

The tooth displays the ziphodont condition in being labiolingually compressed and only slightly recurved. The preserved mesial carina is slightly convex, whereas the distal carina is vertical along its entire run. The labial and lingual portions of the enamel are well-preserved (Fig. 1G), bearing transverse undulations that develop out of the distal margin of the tooth to become bands (Brusatte et al. 2007). In NJSM GP 14256, these undulations (= marginal bands) are relatively strongly developed, although they are less prominent than in carcharodontosaurids (e.g., Sereno et al., 1996; Brusatte et al., 2007). The labial and lingual surfaces of the tooth are slightly convex, as in most other theropod dinosaurs (Hendrickx et al., 2015a). The apex of the tooth bears a slight wear facet on its lingual surface. The tooth is lenticular in basal cross-section.

The distal carina preserves many denticles (Fig. 1E—F, H), which are small, dense (6/mm), and apicobasally straightened. The denticles are interspersed with diminutive interdenticular sulci (Currie et al., 1990). These are encompassed by the apical ends of the denticles. These denticles maintain a similar density along the entirety of the distal carina. However, their density may have changed along the missing portion of the tooth. The mesial carina preserves a few denticles, although these are too eroded.

Table 1. Measurements of teeth described in this study (in/per mm).

| Specimen       | CH    | CBL  | CBW  | AL  | CA  | DB  | DC  | DA  |
|----------------|-------|------|------|-----|-----|-----|-----|-----|
| NJSM GP 12456  | 15 (est. 25) | 8.99 | 4.90 | N/A | N/A | 2   | 2   | 2.5 |
| NJSM GP 22949  | 15.5  | 8.0  | 2.0  | 18.00 | 55.5 | 6   | 5   | 5   |
for much morphological description. These denticles appear to be similar in size to those on the

distal carina.

Dromaeosaurid tooth.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Maniraptor Gauthier 1986

Dromaeosauridae Matthew & Brown 1922

Saurornitholestinae Sues 1978

cf. Saurornitholestinae indet.

Material.

NJSM GP 22949, well-preserved, complete isolated tooth.

Locality and Horizon.

Mt. Laurel Formation sediments in Burlington County, New Jersey, latest Campanian to early
Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.

NJSM GP 22949 is identified as the lateral tooth of a dromaeosaurid theropod based on the following combination of features: (1) its extreme apicobasal curvature created by its concave distal carina and distally offset apex, (2) the presence of apically hooked distal denticles, (3) the absence of mesiodistal constriction along the crown base, and (4) distal denticles that decrease in size towards the apex of the tooth (Fig. 3A—E)(Currie et al., 1990; Turner et al., 2012; Larson and Currie, 2013; Williamson and Brusatte, 2014). NJSM GP 22949 is smaller than the majority of Appalachian theropod teeth assigned to tyrannosauruids, in which crown
heights surpass 50 mm (Schwimmer et al., 1993; Carr et al., 2005; Brusatte et al., 2011; Denton et al., 2011; Schwimmer et al., 2015). However, the tooth is notably larger than most North American dromaeosaurid teeth, which are often less than 10 mm in height and mostly measure around 5 mm in that dimension (Ostrom, 1969; Currie et al., 1990; Currie and Varricchio, 2004; Larson and Currie, 2013; Williamson and Brusatte, 2014; Wick et al., 2015). Dakotaraptor, which possessed crowns up to ~25 mm high, represents the exception among Maastrichtian dromaeosaurids, the teeth of which usually are below 10 mm in height (Larson and Currie, 2013; DePalma et al., 2015). Instead, the Mt. Laurel dromaeosaurid tooth is more comparable to the teeth of the 3—4 meter Deinonychus and an indeterminate specimen from the Tar Heel Formation of North Carolina in its dimensions (Ostrom, 1969; Brownstein, 2018b). NJSM GP 22949 is also distinguished from Appalachian tyrannosauroids in lacking subquadrangular distocentral denticles (Hendrickx et al., 2015). The first discriminant analysis on the Mt. Laurel dromaeosaurid tooth supports this hypothesis by placing the specimen within the convex hull formed by the teeth of Velociraptor and not in the convex hull formed by the teeth of tyrannosaurs or troodontids (Fig. 4A).

NJSM GP 22949 is notable for being similar to the teeth of western North American saurornitholestine dromaeosaurids (Fig. 3A—E, G)(Larson and Currie, 2013) and somewhat unlike those previously discovered from the American east (Kiernan and Schwimmer, 2004; Schwimmer et al., 2015; Brownstein, 2018a). Teeth assigned to Saurornitholestes have been described from the Cretaceous of the southeastern United States (Kiernan and Schwimmer, 2004; Schwimmer et al., 2015). These teeth are extremely small (< 6 mm), far less recurved than NJSM GP 22949, and have proportionally large denticles that are more strongly apically hooked (e.g., fig. 1 in Kiernan and Schwimmer, 2004). One tooth from Alabama measuring 4.9 mm in crown
height and preserving 7 distal denticles and 8 mesial denticles per mm is less recurved than

NJSM GP 22949 and far less elongate in labial and lingual views (see Kiernan and Schwimmer,
2004). Some saurornitholestine teeth from South Carolina (Schwimmer et al., 2015) also lack the
‘slender’ condition in NJSM GP 22949, where the mesiodistal width of the heavily recurved
tooth crown is much smaller than the crown height. Teeth from the Ellisdale site of New Jersey
include dromaeosaurid crowns (Denton et al., 2011; Brownstein, 2018c). However, large crowns
from Ellisdale are not ‘slender’ like NJSM GP 22949, are larger in size, and bear distal denticles
that are considerably more apically hooked than the Mt. Laurel tooth and western
saurornitholestines (Brownstein, 2018c). A dromaeosaurid tooth from North Carolina is slightly
larger than NJSM GP 22949, but is less recurved and far less slender (Brownstein, 2018b).

When compared to dromaeosaurid teeth from outside eastern North America, NJSM GP
22949 most closely resembles the teeth of western North American saurornitholestine
dromaeosaurids. Despite the fact that NJSM GP 22949 was placed in the convex hull formed by
the teeth of Velociraptor in the first discriminant analysis conducted, the tooth is unlike those of
the western North American velociraptorine Acheroraptor temertyorum (Evans et al., 2013) or
the Mongolian Velociraptor mongoliensis (Turner et al., 2012; Fig. 3F) in lacking strongly
developed striations along its crown surface, in being more strongly recurved, and in being far
more slender (lower CBL/CH value)(Fig. 2A—B, F)(Smith et al., 2005; Evans et al., 2013). In
contrast to Dromaeosaurus albertensis, and ‘dromaeosaurine’ teeth from western North
America, the mesial carina in NJSM GP 22949 is not twisted onto the mesiolingual face of the
crown, the distal denticles are apically hooked, and the tooth is more strongly recurved (Fig.
3H—I; Turner et al., 2012; Larson and Currie, 2013). The Mt. Laurel tooth is far less robust and
has far less developed carinae than the teeth of Utahraptor (Fig. 2H). The Mt. Laurel tooth is

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also smaller, much more strongly recurved, and possesses denticles more apically hooked than
those of the giant Maastrichtian dromaeosaurid *Dakotaraptor steini* (DePalma et al., 2015).

NJSM GP 22949 lacks the ‘figure-8’ basal cross-section seen in the teeth of *Deinonychus*
(Ostrom, 1969; Brownstein, 2018b; pers. obs.). Although the strongly recurved maxillary teeth
of *Deinonychus* (Ostrom, 1969; Turner et al., 2012; pers. obs.) are somewhat comparable with
NJSM GP 22949, the differing basal cross-sections among these specimens and the slightly
asymmetrical morphology of the teeth in *Deinonychus* distinguish *D. antirrhopus* and the Mt.
Laurel form. The discriminant analysis of the Larson and Currie (2013) dataset supports
saurornitholestine affinities for NJSM GP 22949, classifying the tooth as a saurornitholestine
crown (Supplementary Information).

NJSM GP 22949 resembles the teeth of western North American Maastrichtian
saurornitholestines in having a slender, tall outline in labial and lingual views (the “Lancian”
saurornitholestine morphtype of Larson and Currie, 2013). The tooth is closely comparable with
the crowns of the juvenile saurornitholestine ‘*Bambiraptor feinbergi*,’ which are extremely
recurved and slender and possess apically-hooked denticles (Fig. 3G). A discriminant analysis of
the Late Cretaceous western North American paravian tooth dataset of Larson and Currie (2013)
found NJSM GP 22949 to nest within the convex hulls formed by four tooth morphotypes
(Saurornitholestinae, Dromaeosaurinae, *Zapsalis*, and *Atrociraptor*). NJSM GP 22949 is also
quantifiably unlike YPM VPPU.021397, the large dromaeosaurid tooth from the Campanian of
North Carolina (Brownstein, 2018b), plotting far from the southeastern North American
specimen in both morphometric analysis in which these teeth were included (Fig. 4). Thus,
NJSM GP 22949 is most comparable to the crowns of a saurornitholestine-like dromaeosaurid.
Saurornitholestines are small-bodied dromaeosaurids (Turner et al., 2012), and so NJSM GP
291 22949 is important for indicating members of this group may have achieved relatively large body sizes for dromaeosaurs.

293 Description.

294 NJSM GP 22949 is the complete crown of a dromaeosaurid dinosaur. Measurements of this specimen are in Table 1. This tooth is heavily recurved, displaying the ziphodont condition. The crown possesses an ovoid basal cross-section. In distal view, the middle portion of tooth is convex labially, although the crown becomes labiolingually straightened towards its apex. The labial and lingual surfaces are flattened, and the lack of a root attached to this crown indicates it was shed. Although both the mesial and distal carinae are preserved, the mesial denticles have been mostly eroded away, and precise denticle counts for the mesial carina are unable to be taken. Some portions of the tooth crown are cracked, and the outer enamel layer is poorly preserved towards the distal end of the specimen. Small portions of the middle of the crown are missing. The distal profile of NJSM GP 22949 is strongly concave. The preserved portions of the outer enamel layer are smooth, although at the apex several slightly developed ridges appear. These ridges could represent features of the original morphology of the tooth or be damage from feeding or taphonomic processes. The distal carina preserves a large number of apically hooked denticles that become smaller towards the apex of the crown. These denticles are separated by interdenticular sulci that, along with the serrations, project slightly onto the tooth surface. Unfortunately, the shape and density of the mesial denticles could not be determined, as the mesial carina is heavily eroded in NJSM GP 22949.

311 Discussion.

312 The two theropod teeth described here add to one of the most complete Maastrichtian faunas from eastern North America. The dromaeosaurid tooth NJSM GP 22949 is
biogeographically significance for being the first occurrence of this clade in the Mount Laurel
Formation and more generally Maastrichtian of eastern North America. Until now,
tyrannosauroids and ornithomimosaur were the only known theropods from the late Campanian-
Maastrichtian of this area (Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997;
Brusatte et al., 2011; Brusatte et al., 2012; Gallagher et al., 2014), with the latest records of
dromaeosaurids in the American east hailing from mid-Campanian units in the Carolinas
(Schwimmer et al., 2015; Brownstein, 2018b) and the Ellisdale site of New Jersey (Denton et al.,
2011). Although NJSM GP 22949 is most comparable to the crowns of mid-sized to largish
dromaeosaurids like *Deinonychus antirrhopus* and *Dakotaraptor steini* (Ostrom, 1969; DePalma
et al., 2015) and to small tyrannosauroids (Denton et al., 2011; Williamson and Brusatte, 2014;
Schwimmer et al., 2015) in its dimensions, it is most closely allied with dromaeosaurids in the
morphometric analyses conducted (Fig. 4) and in many key features of its morphology.

The tyrannosauroid tooth NJSM GP 14256 supports the presence of *Dryptosaurus*-like
tyrannosauroids in the early Maastrichtian of New Jersey. Isolated teeth and postcranial material
from the Mount Laurel were previously assigned to *Dryptosaurus* sp. based on little more than
their geographic proximity to the site where the holotype of this taxon was recovered
(Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997), but no detailed description of
late Campanian to early Maastrichtian tyrannosauroids from New Jersey has appeared in the
literature. The well-preserved nature of NJSM GP 14256 thus allows for the formal recognition
of the presence of non-tyrannosaurid tyrannosauroids in the latest Campanian to earliest
Maastrichtian of the Atlantic Coastal Plain. Furthermore, the excellent condition of the outer
email layer of NJSM GP 12456 allows for further documentation of the dental anatomy of
Appalachian tyrannosauroids, the isolated teeth of which are often found highly abraded among
stream deposits (e.g., Weishampel & Young, 1996). The presence of non-tyrannosaurid tyrannosaurs in the Mt. Laurel Formation is expected given the presence of *Dryptosaurus aquilunguis* and non-tyrannosaurid tyrannosaurs of similar phylogenetic position in both the middle-late Maastrichtian Navesink and New Egypt formations (Gallagher, 1993; Brusatte et al., 2011) and early Campanian Marshalltown Formation (Denton et al., 2011). However, that NJSM GP 14256, originally discovered in 1984, is only described now attests to the understudied nature of these deposits.

The late recognition of dromaeosaurids in the Maastrichtian sediments of New Jersey is notable, given that the dinosaurs of the Mt. Laurel and other Cretaceous units in the Atlantic Coastal Plain have been studied for over a century and a half (e.g., Leidy, 1858; Cope, 1866; Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997). Teeth from locations like the Ellisdale site of the Marshalltown Formation of New Jersey originally assigned to tyrannosaurs have more recently been reclassified as the crowns of dromaeosaurids (Gallagher et al., 1986; Gallagher, 1993, 1997; Denton et al., 2011), so it is entirely possible that the lack of diversity in dinosaur faunas from the Maastrichtian of the Atlantic Coastal Plain reflects systematic misidentification of these isolated fossils. Only further work on Appalachian fossils will allow for more comprehensive revision of the identification of fossils from this area.

During the Cretaceous, terrestrial faunas became more regionalized as the breakup of supercontinents like Gondwana and Laurasia and the inundation of smaller landmasses like North America and Europe occurred (e.g., Russell, 1995; Sereno et al., 1996; Csiki et al., 2010; Sampson et al., 2010; Csiki-Sava et al., 2015). In particular, the faunas of Appalachia and Laramidia, which became isolated from each other as the Western Interior Seaway flooded the middle of North America (e.g., Russell, 1995; Roberts and Kirschbaum, 1997; Schwimmer,
2002; Sampson et al., 2010), have been recognized as highly distinctive (e.g., Gallagher, 1993; Weishampel and Young, 1996; Gallagher, 1997; Sampson et al., 2010; Denton et al., 2011; Schwimmer et al., 2015). In the past thirty years, a handful of discoveries from the eastern margin of North America have indicated some faunal interchange occurred between Laramidian and Appalachian dinosaur communities during the latest Maastrichtian. These include the tooth of a ceratopsid from the latest Maastrichtian of Mississippi and the fragmentary forelimb material of possible lambeosaurines from the Maastrichtian of New Jersey and earliest Maastrichtian of Nunavut, Canada (Gallagher, 1995; Gallagher, 1997; Farke and Phillips, 2017). At the same time, Appalachian faunas continued to harbor endemic forms like intermediate tyrannosauroids, represented by *Dryptosaurus aquilunguis* and comparable forms through the Campanian-Maastrichtian transition in the Atlantic Coastal Plain (Gallagher, 1993; Brusatte et al., 2011; this paper). Faunal interchange in the last 10 million years of the Mesozoic seems to have occurred throughout the northern hemisphere. Phylogenetic evidence strongly posits that the presence of *Tyrannosaurus rex* in the Maastrichtian of the western United States and Canada represents a dispersal of Asian tyrannosaurids into the Americas (Brusatte et al., 2010; Brusatte and Carr, 2016). A dispersal event between Asian and North Americans faunas during the Maastrichtian may have occurred over Beringia (Fiorillo, 2008), given the similarity of Maastrichtian polar faunas from Russia, Alaska, and lower latitudes in the United States and Canada (e.g., Weishampel et al., 2004; Gangloff, 2012; Godefroit et al., 2012; Le Loeuff, 2012).

Along with previous discoveries, the tyrannosauroid tooth described here supports the ‘refugium’ model for eastern North America, wherein taxa more closely allied with middle Cretaceous forms (e.g., non-tyrannosaurid tyrannosauroids like *Dryptosaurus* and *Appalachiosaurus*) (Carr et
al., 2005; Brusatte et al., 2011; Brusatte and Carr, 2016) persisted in relative isolation as more
derived forms evolved in Laurasia.

Conclusions.

Two theropod teeth from the Campanian-Maastrichtian Mount Laurel Formation of New
Jersey are described in detail. The dromaeosaurid tooth, which plots with western North
American saurornitholestine teeth in principle components and discriminant analyses, is the
youngest record of a non-avian maniraptoran from eastern North America and the first from the
latest Campanian-Maastrichtian of the American east. This tooth provides another record of a
mid-sized to large dromaeosaurid in the Cretaceous of eastern North America. However, this
tooth is more allied with those of saurornitholestines and velociraptorines than with
Deinonychus, dromaeosaurines, or largish dromaeosaurid teeth previously described from
Appalachia, tentatively suggesting that several types of dromaeosaurids might have grown to
relatively large sizes in the Cretaceous of the eastern United States and indicating mid-sized to
largish dromaeosaurids were a usual component of Appalachian faunas. The tyrannosauroid
tooth is the first specimen to suggest the presence of Dryptosaurus aquilunguis or a closely
related tyrannosauroid in the Mt. Laurel ecosystem, further supporting the refugium model for
Appalachian vertebrate evolution.

Methods.

Measurements and nomenclature.

Measurements of both teeth were taken in accordance with the methodology of Smith et al.
(2005) and Larson and Currie (2013). The dimensions of the Mt. Laurel teeth were determined
using digital calipers. I follow the nomenclature of Hendrickx et al. (2015) when describing the
two teeth on which this paper focuses.
Principle components analyses.

In order to provide support for the assignment of the dromaeosaurid tooth to a specific group of theropod dinosaurs, I included it in principle components and discriminant analyses conducted in the program PAST v. 3.18 (Hammer et al., 2001). In order to assess the morphological similarity of the Mt. Laurel teeth to theropod clades present in the Cretaceous of the northern hemisphere, I used a modified version (Brownstein, 2018b) of the dataset of Smith et al. (2005) that includes tooth data on tyrannosauroids, troodontids, and dromaeosaurids. A principle components analysis was run on this dataset, which included data on fifteen measurements: crown height (CH), crown base length (CBL), crown base width (CBW), apicobasal length (length of the tooth along the longest apicobasal axis), and serration density per 5mm for the basal (DB), mid-crown (DC), and apical (DA) distal carina. An additional principle components analysis (PCA) was conducted using the dataset of Larson and Currie (2013) in order to better assess the similarity of the Mt. Laurel dromaeosaurid specimen to other North American paravian teeth. This principle components analysis assessed for five measurements: CH, CBL, CBW, and the mesial (MD) and distal (DD) denticles per millimeter. The summary statistics and loadings from the results of the PCAs conducted are included in the Supplementary Information.

Discriminant analyses.

To further assess the affinities of the Mt. Laurel dromaeosaurid tooth, I performed a discriminant analysis on the tooth datasets of Smith et al. (2005, modified in Brownstein, 2018b) and Larson and Currie (2013). This analysis creates a morphospace by maximally separating objects sorted into pre-determined groups. This analysis was also run in PAST v. 3.18 (Hammer et al., 2001), and the loadings and confusion matrices can be found in the supplementary information.
Phylogenetic analysis.

To provide additional support for the referral of the incomplete tyrannosauroid tooth to that family, I coded the specimen for the phylogenetic matrix of Hendrickx and Mateus (2014), a dataset of theropod dentition that includes 64 taxa/specimens coded for 141 characters. The matrix was entered into the phylogenetics program TNT 1.5 (Goloboff and Catalano, 2016) for a phylogenetic analysis. The matrix was first analyzed using the “New Technology Search,” with default parameters for ratchet, tree drift, tree fuse, and sectorial search. A total of 10 trees of length 688 were retained. These topologies were then subjected to traditional (TBR) branch swapping, which allows for a more extensive exploration of each tree island. This found over >99,999 most parsimonious topologies of 688. These were summarized in a strict consensus topology.

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Availability of data and material.

All data is available in the Supplementary Information.

Competing interests.

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### Appendix D

**New records of theropods from New Jersey inform faunal interchange in Maastrichtian North America**

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Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

Statement (if applicable):
CUST_IF_YES_ETHICS : No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The data is included in the supplementary material.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT : No data available.

Authors’ contributions

I am the only author on this paper

Statement (if applicable):
CUST_AUTHOR_CONTRIBUTIONS_TEXT : No data available.
Dear editor of *Royal Society Open Science,*

I would like to resubmit to you my manuscript “New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna” for consideration at your journal.

In revising my manuscript, I have paid special attention to two major comments given by the reviewers. Firstly, I’ve removed the PCA of the dataset of Smith et al. (2005) with the tyrannosaur tooth included on the advice of reviewer 2, provided additional justification for why the tooth is from a tyrannosauroid and probably not a tyrannosaurid, and provided additional information on the results of the phylogenetic analysis.

Secondly, I’ve redone the PCA and discriminant analyses including the dromaeosaur tooth such that the analyses of the Larson and Currie dataset include the Tar Heel tooth and the discriminant analysis of the Smith et al. dataset does not include characters that could not be scored for the Mt. Laurel tooth.

Finally, I’ve removed the biogeographic speculations in line with the comments of the reviewers and editor. I agree that these were presented far too strongly, and I have reorganized the manuscript to act as a faunal characterization. I’ve also revised the manuscript in accordance with the many minor comments presented in reviewer 2’s annotated PDF.

I hope the manuscript is now suitable for publication, and thank you for your reviews.

Regards,

Chase Brownstein
Research Associate,
Collections & Exhibitions, Stamford Museum & Nature Center
Stamford, Connecticut, United States
Responses to Reviewers.

Chase D. Brownstein

However, your data and analyses either do not support your main claim or are insufficient to do so. Starting with your dataset, your measurements of NJSM GP 12456 for DB, DC, and DA do not appear congruent with the specimen figured in Fig. 1J, though do seem to match the scale if Fig. 1E. In Fig. 1J, measurements closer to 4 would appear to be more accurate than 2, 2, and 2.5. The scale bars for the photos and your measurements should be double-checked.

Done. I’ve double checked the scale bars to make sure they are correct. Please see the revised figure.

You also have a substantial amount of missing data for your new specimens in your dataset, and you haven’t discussed how this was handled in your PCA. The default in PAST is to fill missing data with column average substitution, which in the Smith et al. (2005) dataset will bias all of your specimens towards the tyrannosaur part of your plot (as there are more tyrannosaurs in the dataset than any other group). Given that all three of the new teeth plot in areas of your plots where no other theropod teeth plot (partway between dromaeasours and tyrannosaurs), it appears that column average substitution of your dataset is having a substantial contribution to the position of your specimens on these plots. As well, eastern taxa are notably excluded. Dryptosaurus is not plotted in Fig. 2A, and the Tar Heel dromaeosaurid is not plotted in Fig. 4B and 4C, making the argument that either of these teeth have eastern or western affinities insufficiently supported by these analyses. Additions of those specimens and the exclusion of variables with missing data are necessary for these plots to be informative.

I appreciate this comment, and I have added measurements on the Tar Heel form to the datasets for analysis of the dromaeosaurid tooth. I’ve gone on the suggestion of reviewer 2 and not performed morphometric work on the tyrannosaur tooth. The affinities of that tooth to tyrannosaurs are still supported by several morphological comparisons and the phylogenetic analysis. I’ve also removed measurements that are not known for the new teeth to better perform the analysis. Moreover, instead of performing principle components analyses, I’ve performed a discriminant analysis of the Smith et al. (2005) dataset with characters unknown for the dromaeosaurid tooth removed to better support the referrals. Because the only character in the Larson and Currie dataset unknown for the dromaeosaurid tooth is that of the mesial dentine count, I left the dataset as is for that morphometric analysis.

In the phylogenetic analysis, you only list shared derived characters between your tyrannosaur specimen and T. rex, but do not list shared derived characters that unite all tyrannosaurs. However, even this analysis does not support your argument that the specimen is a non-tyrannosaurid tyrannosauroid with affinities with Dryptosaurus. Also, one of the four characters you do list, 94) biconvex apical distal denticles, is not mentioned in your description at all nor is it visible in Fig. 1.
I have added the shared derived characters that unite all tyrannosauroids to the paper’s text and noted the presence of biconvex denticles along the entirety of the carina.

As well, Fig. 1B, 1C, and 1D depict fossils that are not described in the manuscript. If these specimens are figured in this manuscript, they should be described systematically in the text.

These fossils have been described in previous papers and are there to give the reader a visual map of what fossils are known from the Maastrichtian of NJ.

Alternatively, these figures could easily be excluded from the manuscript. The entire datasets used for analysis, including the Smith et al. (2005) and Larson and Currie (2013) should be reproduced in the supplemental data for ease of replication.

Done. I’ve added the datasets to the Supplemental Data.

This description is of specialist interest given the new records from eastern North America, but any discussion of faunal interchange in premature. In your description, you have demonstrated that you have teeth of a dromaeosaurid and a tyrannosauroid from this formation, but your analyses in their current form are insufficient to demonstrate that these teeth have any biogeographic affinities.

Done. I’ve modified the paper to focus on the significance of these teeth for contributing to our understanding of Appalachian faunas, and removed the biogeographic speculations.

Reviewer: 2

Comments to the Author(s)

This paper is important for the acknowledgement of the taxa found in this New Jersey formation. Outside of this finding there is much more difficulty in acquiring significance. This problem of lack of greater significance is not the fault of the author but the nature of the Appalachian dinosaur record. Fossiliferous formations are poorly dated, fossils are not terribly abundant, and when known are typically in rough condition. Because there is not a proper framework for the dinosaurs, determining faunal interchange is problematic...you need to know what is around when, and the organism's phylogenetic relationships. Without this it is difficult to say anything concrete about paleobiology. Especially, in these days when doing rigorous biogeographic analyses is so easy. In my opinion you can't really say anything about faunal interchange until a solid, dated fossil record is assembled.

I agree. See my comment above.
First, I firmly do not think that a phylogenetic analysis should be used on a single tooth, much less a single partial tooth. The phylogenetic analysis of teeth is not a proper use of phylogenetics in my opinion at any rate. To my mind this part of the paper should be eliminated.

This part of the paper was recommended by another researcher who looked at my paper. As it follows in line with many recent studies (e.g., Hendrickx et al., 2014; Young et al., 2014), I have kept it for the sake of making this paper comparable to other, recent works.

Second, the author should use a more recent ordinal analysis of teeth. This is not a deal breaker, but the primary dataset chosen is 13 years old (or 5 yrs old in the case of Larson and Currie) and many others have been produced since then.

Since the Larson and Currie dataset continues to be the one used the most often for morphometric analysis of Cretaceous North American theropod teeth (see Evans et al., 2013; Williamson and Brusatte, 2014 for examples), I am uncertain what the reviewer here refers to. The Hendrickx et al. (2015) theropod tooth dataset only represents an extension of the Smith et al. (2005) dataset that includes the Larson and Currie dataset and removes a number of continuous characters.

Third, the tyrannosaur tooth should absolutely be removed from the PCA analysis. It is a fragmentary tooth, therefore any measurements taken are not going to be the correct measurement and will provide erroneous results. Or there will be too little data to say much about.

Done. I’ve removed the tooth.

Fourth, the dromaeosaurid tooth falls outside the dromaeosaurids in the Smith/Brownstein matrix. And is just part of the miasma of teeth in the Larson and Currie matrix. I would suggest pulling individual taxa from the analyses and talk about comparisons with them instead of consistently saying it is a Saurornitholestesine theropod. Remember that the PCA is using data you input. If there is more information supporting your taxonomic claim that is not included in the quantitative data, then you should discuss this in the text. In PAST you can change the symbol and the color, meaning that you can label individual dinosaur taxa and the higher level taxonomic groups at the same time. This should be done to help you see which species the Tar Heel and Mt Laurel specimens are mostly similar to.

Done. I’ve instead performed discriminant analyses on the datasets and taking up your suggestion of visualizing the resulting plots using axes 2 and 3. The Mt. Laurel tooth plots firmly within the hull formed by the teeth of Velociraptor in the first DA and firmly with
Fifth, this is very important! When using PCA on variables that are measurements, the first axis is almost invariably a reflection of size, not shape. Therefore, you need to show axes 2 and 3. You are welcome to retain axis 1 and 2, but 2 and 3 must be shown in addition. You may also want to consider Centering or z-transforming your data because it can help remove the effect of size, bring outliers closer together, and reflect shape better.

Done.
New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna

Chase Doran Brownstein

Research Associate, Dept. of Collections and Exhibitions, Stamford Museum and Nature Center, Stamford, CT, chasethedinosaur@gmail.com
Abstract.

The faunal changes that occurred in the few million years before the Cretaceous-Paleogene extinction are of much interest to vertebrate paleontologists. Western North America preserves arguably the best fossil record from this time, whereas terrestrial vertebrate fossils from the eastern portion of the continent are usually limited to isolated, eroded postcranial remains. Examination of fragmentary specimens from the American east, which was isolated for the majority of the Cretaceous as the landmass Appalachia, is therefore important for better understanding dinosaur diversity at the end of the Mesozoic. Here, I report on two theropod teeth from the Mount Laurel Formation, a lower-middle Maastrichtian unit from northeastern North America. One of these preserves in fine-detail the structure of the outer enamel and resembles the dentition of the tyrannosauroid *Dryptosaurus aquilunguis* among latest Cretaceous forms in being heavily mediolaterally compressed and showing many moderately developed enamel crenulations. Along with previously reported tyrannosauroid material from the Mt. Laurel and overlying Cretaceous units, this fossil supports the presence of non-tyrannosaurid tyrannosauroids in the Campanian-Maastrichtian of eastern North America. The other tooth is assignable to a dromaeosaurid and represents both the youngest occurrence of a non-avian maniraptoran in eastern North America and the first from the Maastrichtian reported east of the Mississipi. This tooth, which belonged to a medium-sized dromaeosaurid based on size comparisons with the teeth of taxa for which skeletons are known, increases the diversity of the Maastrichtian dinosaur fauna of Appalachia. Along with previously reported dromaeosaurid teeth, the Mt. Laurel specimen supports the presence of mid-sized to large dromaeosaurids in eastern North America throughout the Cretaceous. This indicates that dromaeosaurids
approaching or exceeding 3 meters in length were more common in the Late Cretaceous than
previously thought.

Keywords: Dinosaur; Appalachia; Cretaceous; Fauna; Tyrannosaur; Teeth

**Introduction.**

The extinction of the non-avian dinosaurs at the end of the Mesozoic Era is a topic that
has continued to intrigue vertebrate paleontologists (e.g., Alvarez et al., 1980; Sloan et al., 1986;
Sarjeant and Currie, 2001; Le Loeuff 2012, Brusatte et al., 2012, 2015; Sakamoto et al., 2016).
However, a poor global terrestrial record from the Maastrichtian has hindered attempts to assess
the diversity dynamics of important groups like the Dinosauria during this period (e.g., Le
Loeuff, 2012; Brusatte et al., 2015). Western North America preserves arguably the most well-
characterized vertebrate record from the last 20 million years of the Mesozoic Era (Brusatte et
al., 2015), whereas that from the eastern portion of the continent is far more obscure. During the
majority of the Late Cretaceous, eastern and western North America were separated, the former
existing as a rectangular landmass called Appalachia. Appalachian dinosaur faunas included
intermediate-grade tyrannosauroids (Carr et al., 2005; Brusatte et al., 2011), basal hadrosaurids
and derived non-hadrosaurid hadrosauroids (Langston, 1960; Prieto-Márquez et al., 2006; Prieto-
Márquez et al., 2016), nodosaurids (Gallagher, 1993; Burns and Ebersole, 2016), and
ornithomimosaurs (Miller, 1967; Schwimmer et al., 1993; Weishampel and Young, 1996;
Schwimmer et al., 2015; Brownstein, 2018a).

Despite the amount of knowledge of Cretaceous faunal change to be gleaned from the
fossil record of Appalachia, the assemblages of this landmass have remained fundamentally
understudied since the mid-19th century (e.g., Weishampel & Young, 1996; Gallagher, 1997;
Weishampel, 2006; Brownstein, 2018a). The scarcity of terrestrial sedimentary units known from
the eastern half of the United States has also contributed to the obscurity of Appalachian faunas
compared to western North American ones (Weishampel and Young, 1996; Gallagher, 1997;
Carr et al., 2005; Weishampel, 2006; Brusatte et al., 2011). Only in the past few years have
indications of faunal changes in the latest Cretaceous (late Campanian-Maastrichtian) of the
American east come, and all from isolated, fragmentary finds. Although a ceratopsian tooth from
the uppermost Maastrichtian of Mississippi (Farke and Phillips, 2017) and possible
lambeosaurine bones from the upper Maastrichtian of New Jersey (Gallagher, 1993) have
revealed that faunal exchanges probably occurred between Appalachia and Laramidia following
the regression of the Western Interior Seaway in the latest Campanian-earliest Maastrichtian, the
timing of these events remains poorly constrained. Further sampling of enigmatic assemblages
from the Maastrichtian, such as those of the eastern United States, is therefore important for
understanding faunal change in latest Mesozoic North America.

In the Campanian-Maastrichtian of New Jersey, a set of formations corresponds to a
period of transgressions and regressions of the Atlantic Ocean (e.g., Gallagher, 1993; Sugarman
et al., 1995; Miller et al., 2004; Gallagher et al., 2014). The majority of these Cretaceous units
are known for producing marine vertebrate and invertebrate fossils (Gallagher, 1993), although
some, such as the Woodbury and New Egypt formations, are notable for producing some of the
first partial dinosaur skeletons from the Americas (e.g., Leidy, 1858; Cope, 1866; Gallagher,
1993, Weishampel and Young, 1996; Gallagher, 1997). One of the most fossiliferous of these
formations is the Mount Laurel Formation, which is either uppermost Campanian or lowermost
Maastrichtian (Miller et al., 2004) and in New Jersey has produced the remains of several groups
of dinosaurs, including hadrosaurs, tyrannosaurs, and ornithomimosaus (Gallagher, 1993;
Because of the sheer diversity of the community represented in the Mt. Laurel, the formation serves as a window into Campanian-Maastrichtian eastern North American faunas. However, the terrestrial fossils it produces are often eroded postcranial fragments (Gallagher, 2014).

Here, I describe some theropod teeth from the Mt. Laurel Formation of New Jersey. These include a large tooth assignable to a 6—8 m tyrannosauroid and a smaller, heavily recurved one assignable to a 3—4 m dromaeosaurid. These teeth are among the most diagnostic records of theropods from the Mt. Laurel Formation, allowing for a more precise understanding of the faunal composition and ecology of the eastern seaboard during the Maastrichtian, a globally under-sampled time period (Le Loeuff, 2012; Brusatte et al., 2012).

Results.

Geological setting.

Both theropod teeth described here were collected from sediments of the Mount Laurel Formation (Gallagher, 1993; pers. obs.), a marine deposit that represents a regression of the Atlantic Ocean during the Late Cretaceous period and is the oldest unit included in the Monmouth Group (Gallagher, 1993; Miller et al., 2004). The tyrannosauroid tooth described here, NJSNM GP 12456, was recovered from Big Brook (Fig. 1A), a highly fossiliferous locality famous for producing an extensive marine fauna (Gallagher, 1993; Weishampel and Young, 1996). At Big Brook, the stratigraphic column is exposed along the banks, with the Wenonah Formation grading into the Mt. Laurel such that the border between the two are indistinguishable (Gallagher, 1993). The contact between the Mt. Laurel and the overlying Navesink Formation is an unconformity (Miller et al., 2004; Gallagher et al., 2014). The Mt. Laurel Formation appears as gray to dark brown, pebbly quartz sands. The Big Brook tyrannosauroid tooth (Fig. 1E—H) is
unusual among the terrestrial vertebrate teeth collected from the site in possessing a well-
preserved enamel surface. Whereas other terrestrial vertebrate fossils from Big Brook are known
for being heavily water-worn and lacking morphological details, NJSM GP 12456 preserves both
its outermost enamel layer and many of its denticles.

NJSM GP 22949, the dromaeosaurid tooth, was recovered from Mt. Laurel deposits in
Burlington County, New Jersey (Fig. 1A). In this area, which makes up a portion of the
southwestern-most range of the Monmouth Group, the sands of the Mt. Laurel are more
glaucnitic than farther north and are intermixed with iron compounds (Gallagher, 1993). The
thickness of this unit is also far greater to the southwest of its range (e.g., Gallagher, 1993).

Tyrannosauroidea

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Tyrannosauroidea Osborn 1905

Tyrannosauroidea indet.

Material.

New Jersey State Museum collections (NJSM) GP 14256, the partial tooth of a large theropod
dinosaur (Fig. 1E—H).

Locality and Horizon.

Mt. Laurel Formation sediments at Big Brook, Monmouth County, New Jersey, latest
Campanian to early Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.
NJSM GP 14256 (Fig. 1E—H) closely resembles the dentition of tyrannosaurid theropods in several respects. The tooth resembles those of adult tyrannosaurs in its size, which is closely comparable to tyrannosaur crowns known from both western and eastern North America (Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et al., 2011; Williamson and Brusatte, 2014). In addition to its size, the Mt. Laurel tooth resembles those of tyrannosaurs to the exclusion of other theropods known from Late Cretaceous North America in possessing a combination of packed denticles (2–2.5/mm) on its distal carina (15+ mm), the presence of denticles along both carinae, its slight, rather than pronounced, curvature, the presence of numerous transverse undulations (density = 2/mm) on its main surface, the presence of slightly biconvex denticle outlines for denticles all along the tooth (Fig. 1J), and its smooth but slightly irregular surface texture (Fig 1E—H)(Currie et al., 1990; Brochu, 2003; Samman et al., 2005; Smith, 2005; Brusatte et al., 2011; Williamson and Brusatte, 2014).

However, despite the size of the Mt. Laurel tooth, NJSM GP 14256 is notably unlike the teeth of tyrannosaurids, for which incrassate teeth are a synapomorphy (e.g., Williamson and Brusatte, 2014; Brusatte and Carr, 2016). Instead, NJSM GP 14256 shows is highly mediolaterally compressed and possesses a lens-shaped basal cross-section, indicative it came from a tyrannosaurid outside Tyrannosauridae. Among large Late Cretaceous tyrannosaurs, only *Dryptosaurus aquilunguis* from the Maastrichtian New Egypt Formation of New Jersey is known to possess a combination of high mediolateral compression and tyrannosaurid-like features of the denticles and tooth surface (e.g., Brusatte et al., 2011). NJSM GP 14256 is also comparable with the mediolaterally compressed teeth of *Dryptosaurus aquilunguis* in its dimensions, curvature, and enamel crenulations (Brusatte et al., 2011; pers. obs. of YPM PU 22208). Given the Mt.
Laurel tooth’s very close spatiotemporal proximity to the holotype of *Dryptosaurus*, I suggest the

tooth belongs to a closely related form.

Given the number of measurements unable to be taken from this tooth, I did not include it

in a morphometric analysis. However, phylogenetic analysis of the tooth within the dataset of

Hendrickx and Mateus (2014) found NJSM GP 14256 to be the sister taxon of *Tyrannosaurus

*rex* in a clade united by four characters. These are characters 94 (biconvex apical denticles

present on distal carinae of lateral teeth), 100 (subequal number of denticles apically than at mid-
crown portion of distal carinae on lateral teeth), 103 (interdenticular space between mid-crown
denticles on distal carinae of lateral teeth broad), and 105 (interdenticular sulci between mid-
crown denticles on distal carinae of lateral teeth present, long, and well-developed) (Hendrickx

and Mateus, 2014). The clade comprised of NJSM GP 14256 and other derived tyrannosaurs

(*Alioramus, Tyrannosaurus, “Raptorex”*) is united by the presence of a sub-symmetric crown

with a centrally-positioned distal carina in distal view (char. 83). Characters uniting the
tyrannosauroid clade include 3, 5, 19, 27, 37, 38, 41, and 48 in the list of Hendrickx and Mateus

(2014). The strict consensus tree (tree length = 688, consistency index = 0.340, retention index =

0.561) is shown in Fig. 1B.

**Description.**

NJSM GP 14256 (Fig. 1) is the apical half of the tooth of a theropod dinosaur.

Measurements of the specimen may be found in Table 1. The tooth is well-preserved for a
terrestrial fossil collected from one of the marine deposits of the Cretaceous Atlantic Coastal

Plain, preserving details of the outer enamel layer and dentine morphology. Unfortunately, the

basal half of the crown and the entirety of the root of the tooth are not preserved. This is
probably due to erosion, as the tooth is broken transversely and heavily rounded at its preserved base (Fig. 1E—F).

The tooth displays the ziphodont condition in being labiolingually compressed and only slightly recurved. The preserved mesial carina is slightly convex, whereas the distal carina is vertical along its entire run. The labial and lingual portions of the enamel are well-preserved (Fig. 1G), bearing transverse undulations that develop out of the distal margin of the tooth to become bands (Brusatte et al. 2007). In NJSM GP 14256, these undulations (= marginal bands) are relatively strongly developed, although they are less prominent than in carcharodontosaurids (e.g., Sereno et al., 1996; Brusatte et al., 2007). The labial and lingual surfaces of the tooth are slightly convex, as in most other theropod dinosaurs (Hendrickx et al., 2015a). The apex of the tooth bears a slight wear facet on its lingual surface. The tooth is lenticular in basal cross-section.

The distal carina preserves many denticles (Fig. 1E—F, H), which are small, dense (6/mm), and apicobasally straightened. The denticles are interspersed with diminutive interdenticular sulci (Currie et al., 1990). These are encompassed by the apical ends of the denticles. These denticles maintain a similar density along the entirety of the distal carina. However, their density may have changed along the missing portion of the tooth. The mesial carina preserves a few denticles, although these are too eroded.

| Specimen     | CH    | CBL | CWB | AL | CA | DB | DC | DA |
|--------------|-------|-----|-----|----|----|----|----|----|
| NJSM GP 12456 | 15 (est. 25) | 8.99 | 4.90 | N/A | N/A | 2 | 2 | 2.5 |
| NJSM GP 22949 | 15.5  | 8.0  | 2.0  | 18.00 | 55.5 | 6 | 5 | 5  |

Table 1. Measurements of teeth described in this study (in/per mm).
for much morphological description. These denticles appear to be similar in size to those on the
distal carina.

Dromaeosaur tooth.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria von Huene 1921

Maniraptora Gauthier 1986

Dromaeosauridae Matthew & Brown 1922

Saurornitholestinae Sues 1978

cf. Saurornitholestinae indet.

Material.

NJSM GP 22949, well-preserved, complete isolated tooth.

Locality and Horizon.

Mt. Laurel Formation sediments in Burlington County, New Jersey, latest Campanian to early
Maastrichtian (Gallagher, 1993; Miller et al., 2004; Gallagher et al., 2014).

Identification.

NJSM GP 22949 is identified as the lateral tooth of a dromaeosaurid theropod based on
the following combination of features: (1) its extreme apicobasal curvature created by its
concave distal carina and distally offset apex, (2) the presence of apically hooked distal denticles,
(3) the absence of mesiodistal constriction along the crown base, and (4) distal denticles that
decrease in size towards the apex of the tooth (Fig. 3A—E)(Currie et al., 1990; Turner et al.,
2012; Larson and Currie, 2013; Williamson and Brusatte, 2014). NJSM GP 22949 is smaller
than the majority of Appalachian theropod teeth assigned to tyrannosauroids, in which crown
heights surpass 50 mm (Schwimmer et al., 1993; Carr et al., 2005; Brusatte et al., 2011; Denton et al., 2011; Schwimmer et al., 2015). However, the tooth is notably larger than most North American dromaeosaurid teeth, which are often less than 10 mm in height and mostly measure around 5 mm in that dimension (Ostrom, 1969; Currie et al., 1990; Currie and Varricchio, 2004; Larson and Currie, 2013; Williamson and Brusatte, 2014; Wick et al., 2015). *Dakotaraptor*, which possessed crowns up to ~25 mm high, represents the exception among Maastrichtian dromaeosaurids, the teeth of which usually are below 10 mm in height (Larson and Currie, 2013; DePalma et al., 2015). Instead, the Mt. Laurel dromaeosaurid tooth is more comparable to the teeth of the 3—4 meter *Deinonychus* and an indeterminate specimen from the Tar Heel Formation of North Carolina in its dimensions (Ostrom, 1969; Brownstein, 2018b).

NJSM GP 22949 is also distinguished from Appalachian tyrannosaurids in lacking subquadrangular distocentral denticles (Hendrickx et al., 2015). The first discriminant analysis on the Mt. Laurel dromaeosaurid tooth supports this hypothesis by placing the specimen within the convex hull formed by the teeth of *Velociraptor* and not in the convex hull formed by the teeth of tyrannosaurs or troodontids (Fig. 4A).

NJSM GP 22949 is notable for being similar to the teeth of western North American saurornitholestine dromaeosaurids (Fig. 3A—E, G)(Larson and Currie, 2013) and somewhat unlike those previously discovered from the American east (Kiernan and Schwimmer, 2004; Schwimmer et al., 2015; Brownstein, 2018a). Teeth assigned to *Saurornitholestes* have been described from the Cretaceous of the southeastern United States (Kiernan and Schwimmer, 2004; Schwimmer et al., 2015). These teeth are extremely small (< 6 mm), far less recurved than NJSM GP 22949, and have proportionally large denticles that are more strongly apically hooked (e.g., fig. 1 in Kiernan and Schwimmer, 2004). One tooth from Alabama measuring 4.9 mm in crown
height and preserving 7 distal denticles and 8 mesial denticles per mm is less recurved than
NJSM GP 22949 and far less elongate in labial and lingual views (see Kiernan and Schwimmer, 2004). Some saurornitholestine teeth from South Carolina (Schwimmer et al., 2015) also lack the ‘slender’ condition in NJSM GP 22949, where the mesiodistal width of the heavily recurved tooth crown is much smaller than the crown height. Teeth from the Ellisdale site of New Jersey include dromaeosaurid crowns (Denton et al., 2011; Brownstein, 2018c). However, large crowns from Ellisdale are not ‘slender’ like NJSM GP 22949, are larger in size, and bear distal denticles that are considerably more apically hooked than the Mt. Laurel tooth and western saurornitholestines (Brownstein, 2018c). A dromaeosaurid tooth from North Carolina is slightly larger than NJSM GP 22949, but is less recurved and far less slender (Brownstein, 2018b).

When compared to dromaeosaurid teeth from outside eastern North America, NJSM GP 22949 most closely resembles the teeth of western North American saurornitholestine dromaeosaurids. Despite the fact that NJSM GP 22949 was placed in the convex hull formed by the teeth of Velociraptor in the first discriminant analysis conducted, the tooth is unlike those of the western North American velociraptorine Acheroraptor temertyorum (Evans et al., 2013) or the Mongolian Velociraptor mongoliensis (Turner et al., 2012; Fig. 3F) in lacking strongly developed striations along its crown surface, in being more strongly recurved, and in being far more slender (lower CBL/CH value)(Fig. 2A—B, F)(Smith et al., 2005; Evans et al., 2013). In contrast to Dromaeosaurus albertensis, and ‘dromaeosaurine’ teeth from western North America, the mesial carina in NJSM GP 22949 is not twisted onto the mesiolingual face of the crown, the distal denticles are apically hooked, and the tooth is more strongly recurved (Fig. 3H—I; Turner et al., 2012; Larson and Currie, 2013). The Mt. Laurel tooth is far less robust and has far less developed carinae than the teeth of Utahraptor (Fig. 2H). The Mt. Laurel tooth is
also smaller, much more strongly recurved, and possesses denticles more apically hooked than
those of the giant Maastrichtian dromaeosaurid *Dakotaraptor steini* (DePalma et al., 2015).

NJSM GP 22949 lacks the ‘figure-8’ basal cross-section seen in the teeth of *Deinonychus*
(Ostrom, 1969; Brownstein, 2018b; pers. obs.). Although the strongly recurved maxillary teeth
of *Deinonychus* (Ostrom, 1969; Turner et al., 2012; pers. obs.) are somewhat comparable with
NJSM GP 22949, the differing basal cross-sections among these specimens and the slightly
asymmetrical morphology of the teeth in *Deinonychus* distinguish *D. antirrhopus* and the Mt.
Laurel form. The discriminant analysis of the Larson and Currie (2013) dataset supports
saurornitholestine affinities for NJSM GP 22949, classifying the tooth as a saurornitholestine
crown (Supplementary Information).

NJSM GP 22949 resembles the teeth of western North American Maastrichtian
saurornitholestines in having a slender, tall outline in labial and lingual views (the “Lancian”
saurornitholestine morphotype of Larson and Currie, 2013). The tooth is closely comparable with
the crowns of the juvenile saurornitholestine ‘*Bambiraptor feinbergi,*’ which are extremely
recurved and slender and possess apically-hooked denticles (Fig. 3G). A discriminant analysis of
the Late Cretaceous western North American paravian tooth dataset of Larson and Currie (2013)
found NJSM GP 22949 to nest within the convex hulls formed by four tooth morphotypes
(Saurornitholestinae, Dromaeosaurinae, *Zapsalis*, and *Atrociraptor*). NJSM GP 22949 is also
quantifiably unlike YPM VPPU.021397, the large dromaeosaurid tooth from the Campanian of
North Carolina (Brownstein, 2018b), plotting far from the southeastern North American
specimen in both morphometric analysis in which these teeth were included (Fig. 4). Thus,
NJSM GP 22949 is most comparable to the crowns of a saurornitholestine-like dromaeosaurid.
Saurornitholestines are small-bodied dromaeosaurids (Turner et al., 2012), and so NJSM GP
291 NJSM GP 22949 is important for indicating members of this group may have achieved relatively large body
292 sizes for dromaeosaurs.

293 Description.

294 NJSM GP 22949 is the complete crown of a dromaeosaurid dinosaur. Measurements of
295 this specimen are in Table 1. This tooth is heavily recurved, displaying the ziphodont condition.
296 The crown possesses an ovoid basal cross-section. In distal view, the middle portion of tooth is
297 convex labially, although the crown becomes labiolingually straightened towards its apex. The
298 labial and lingual surfaces are flattened, and the lack of a root attached to this crown indicates it
299 was shed. Although both the mesial and distal carinae are preserved, the mesial denticles have
300 been mostly eroded away, and precise denticle counts for the mesial carina are unable to be
301 taken. Some portions of the tooth crown are cracked, and the outer enamel layer is poorly
302 preserved towards the distal end of the specimen. Small portions of the middle of the crown are
303 missing. The distal profile of NJSM GP 22949 is strongly concave. The preserved portions of the
304 outer enamel layer are smooth, although at the apex several slightly developed ridges appear.
305 These ridges could represent features of the original morphology of the tooth or be damage from
306 feeding or taphonomic processes. The distal carina preserves a large number of apically hooked
307 denticles that become smaller towards the apex of the crown. These denticles are separated by
308 interdenticular sulci that, along with the serrations, project slightly onto the tooth surface.
309 Unfortunately, the shape and density of the mesial denticles could not be determined, as the
310 mesial carina is heavily eroded in NJSM GP 22949.

311 Discussion.

312 The two theropod teeth described here add to one of the most complete Maastrichtian
313 faunas from eastern North America. The dromaeosaurid tooth NJSM GP 22949 is
biogeographically significant for being the first occurrence of this clade in the Mount Laurel Formation and more generally Maastrichtian of eastern North America. Until now, tyrannosauroids and ornithomimosauruses were the only known theropods from the late Campanian-Maastrichtian of this area (Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997; Brusatte et al., 2011; Brusatte et al., 2012; Gallagher et al., 2014), with the latest records of dromaeosaurids in the American east hailing from mid-Campanian units in the Carolinas (Schwimmer et al., 2015; Brownstein, 2018b) and the Ellisdale site of New Jersey (Denton et al., 2011). Although NJSM GP 22949 is most comparable to the crowns of mid-sized to largish dromaeosaurids like *Deinonychus antirrhopus* and *Dakotaraptor steini* (Ostrom, 1969; DePalma et al., 2015) and to small tyrannosauroids (Denton et al., 2011; Williamson and Brusatte, 2014; Schwimmer et al., 2015) in its dimensions, it is most closely allied with dromaeosaurids in the morphometric analyses conducted (Fig. 4) and in many key features of its morphology.

The tyrannosauroid tooth NJSM GP 14256 supports the presence of *Dryptosaurus*-like tyrannosauroids in the early Maastrichtian of New Jersey. Isolated teeth and postcranial material from the Mount Laurel were previously assigned to *Dryptosaurus* sp. based on little more than their geographic proximity to the site where the holotype of this taxon was recovered (Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997), but no detailed description of late Campanian to early Maastrichtian tyrannosauroids from New Jersey has appeared in the literature. The well-preserved nature of NJSM GP 14256 thus allows for the formal recognition of the presence of non-tyrannosauroid tyrannosauroids in the latest Campanian to earliest Maastrichtian of the Atlantic Coastal Plain. Furthermore, the excellent condition of the outer enamel layer of NJSM GP 12456 allows for further documentation of the dental anatomy of Appalachian tyrannosauroids, the isolated teeth of which are often found highly abraded among...
stream deposits (e.g., Weishampel & Young, 1996). The presence of non-tyrannosaurid
tyrannosaurids in the Mt. Laurel Formation is expected given the presence of *Dryptosaurus*
aquilunguis and non-tyrannosaurid tyrannosaurs of similar phylogenetic position in both the
middle-late Maastrichtian Navesink and New Egypt formations (Gallagher, 1993; Brusatte et al.,
2011) and early Campanian Marshalltown Formation (Denton et al., 2011). However, that NJSM
GP 14256, originally discovered in 1984, is only described now attests to the understudied nature
of these deposits.

The late recognition of dromaeosaurids in the Maastrichtian sediments of New Jersey is
notable, given that the dinosaurs of the Mt. Laurel and other Cretaceous units in the Atlantic
Coastal Plain have been studied for over a century and a half (e.g., Leidy, 1858; Cope, 1866;
Gallagher, 1993; Weishampel & Young, 1996; Gallagher, 1997). Teeth from locations like the
Ellisdale site of the Marshalltown Formation of New Jersey originally assigned to tyrannosaurs
have more recently been reclassified as the crowns of dromaeosaurids (Gallagher et al., 1986;
Gallagher, 1993, 1997; Denton et al., 2011), so it is entirely possible that the lack of diversity in
dinosaur faunas from the Maastrichtian of the Atlantic Coastal Plain reflects systematic
misidentification of these isolated fossils. Only further work on Appalachian fossils will allow
for more comprehensive revision of the identification of fossils from this area.

During the Cretaceous, terrestrial faunas became more regionalized as the breakup of
supercontinents like Gondwana and Laurasia and the inundation of smaller landmasses like
North America and Europe occurred (e.g., Russell, 1995; Sereno et al., 1996; Csiki et al., 2010;
Sampson et al., 2010; Csiki-Sava et al., 2015). In particular, the faunas of Appalachia and
Laramidia, which became isolated from each other as the Western Interior Seaway flooded the
middle of North America (e.g., Russell, 1995; Roberts and Kirschbaum, 1997; Schwimmer,
2002; Sampson et al., 2010), have been recognized as highly distinctive (e.g., Gallagher, 1993; Weishampel and Young, 1996; Gallagher, 1997; Sampson et al., 2010; Denton et al., 2011; Schwimmer et al., 2015). In the past thirty years, a handful of discoveries from the eastern margin of North America have indicated some faunal interchange occurred between Laramidian and Appalachian dinosaur communities during the latest Maastrichtian. These include the tooth of a ceratopsid from the latest Maastrichtian of Mississippi and the fragmentary forelimb material of possible lambeosaurines from the Maastrichtian of New Jersey and earliest Maastrichtian of Nunavut, Canada (Gallagher, 1995; Gallagher, 1997; Farke and Phillips, 2017). At the same time, Appalachian faunas continued to harbor endemic forms like intermediate tyrannosaurs, represented by *Dryptosaurus aquilunguis* and comparable forms through the Campanian-Maastrichtian transition in the Atlantic Coastal Plain (Gallagher, 1993; Brusatte et al., 2011; this paper). *Faunal interchange in the last 10 million years of the Mesozoic seems to have occurred throughout the northern hemisphere. Phylogenetic evidence strongly posits that the presence of *Tyrannosaurus rex* in the Maastrichtian of the western United States and Canada represents a dispersal of Asian tyrannosaurs into the Americas (Brusatte et al., 2010; Brusatte and Carr, 2016). A dispersal event between Asian and North American faunas during the Maastrichtian may have occurred over Beringia (Fiorillo, 2008), given the similarity of Maastrichtian polar faunas from Russia, Alaska, and lower latitudes in the United States and Canada (e.g., Weishampel et al., 2004; Gangloff, 2012; Godefroit et al., 2012; Le Loeuff, 2012). Along with previous discoveries, the tyrannosaurid tooth described here supports the ‘refugium’ model for eastern North America, wherein taxa more closely allied with middle Cretaceous forms (e.g., non-tyrannosaurid tyrannosaurs like *Dryptosaurus* and *Appalachiosaurus*) (Carr et
al., 2005; Brusatte et al., 2011; Brusatte and Carr, 2016) persisted in relative isolation as more derived forms evolved in Laurasia.

Conclusions.

Two theropod teeth from the Campanian-Maastrichtian Mount Laurel Formation of New Jersey are described in detail. The dromaeosaurid tooth, which plots with western North American saurornitholestine teeth in principle components and discriminant analyses, is the youngest record of a non-avian maniraptoran from eastern North America and the first from the latest Campanian-Maastrichtian of the American east. This tooth provides another record of a mid-sized to large dromaeosaurid in the Cretaceous of eastern North America. However, this tooth is more allied with those of saurornitholestines and velociraptorines than with *Deinonychus*, dromaeosaurines, or largish dromaeosaurid teeth previously described from Appalachia, tentatively suggesting that several types of dromaeosaurids might have grown to relatively large sizes in the Cretaceous of the eastern United States and indicating mid-sized to largish dromaeosaurids were a usual component of Appalachian faunas. The tyrannosaurid tooth is the first specimen to suggest the presence of *Dryptosaurus aquilunguis* or a closely related tyrannosaurid in the Mt. Laurel ecosystem, further supporting the refugium model for Appalachian vertebrate evolution.

Methods.

Measurements and nomenclature.

Measurements of both teeth were taken in accordance with the methodology of Smith et al. (2005) and Larson and Currie (2013). The dimensions of the Mt. Laurel teeth were determined using digital calipers. I follow the nomenclature of Hendrickx et al. (2015) when describing the two teeth on which this paper focuses.
In order to provide support for the assignment of the dromaeosaurid tooth to a specific group of theropod dinosaurs, I included it in principle components and discriminant analyses conducted in the program PAST v. 3.18 (Hammer et al., 2001). In order to assess the morphological similarity of the Mt. Laurel teeth to theropod clades present in the Cretaceous of the northern hemisphere, I used a modified version (Brownstein, 2018b) of the dataset of Smith et al. (2005) that includes tooth data on tyrannosauroids, troodontids, and dromaeosaurids. A principle components analysis was run on this dataset, which included data on fifteen measurements: crown height (CH), crown base length (CBL), crown base width (CBW), apicobasal length (length of the tooth along the longest apicobasal axis), and serration density per 5mm for the basal (DB), mid-crown (DC), and apical (DA) distal carina. An additional principle components analysis (PCA) was conducted using the dataset of Larson and Currie (2013) in order to better assess the similarity of the Mt. Laurel dromaeosaurid specimen to other North American paravian teeth. This principle components analysis assessed for five measurements: CH, CBL, CBW, and the mesial (MD) and distal (DD) denticles per millimeter. The summary statistics and loadings from the results of the PCAs conducted are included in the Supplementary Information.

To further assess the affinities of the Mt. Laurel dromaeosaurid tooth, I performed a discriminant analysis on the tooth datasets of Smith et al. (2005, modified in Brownstein, 2018b) and Larson and Currie (2013). This analysis creates a morphospace by maximally separating objects sorted into pre-determined groups. This analysis was also run in PAST v. 3.18 (Hammer et al., 2001), and the loadings and confusion matrices can be found in the supplementary information.
Phylogenetic analysis.

To provide additional support for the referral of the incomplete tyrannosauroid tooth to that family, I coded the specimen for the phylogenetic matrix of Hendrickx and Mateus (2014), a dataset of theropod dentition that includes 64 taxa/specimens coded for 141 characters. The matrix was entered into the phylogenetics program TNT 1.5 (Goloboff and Catalano, 2016) for a phylogenetic analysis. The matrix was first analyzed using the “New Technology Search,” with default parameters for ratchet, tree drift, tree fuse, and sectorial search. A total of 10 trees of length 688 were retained. These topologies were then subjected to traditional (TBR) branch swapping, which allows for a more extensive exploration of each tree island. This found over >99.9% most parsimonious topologies of 688. These were summarized in a strict consensus topology.

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Availability of data and material.

All data is available in the Supplementary Information.

Competing interests.

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Dear editor of Royal Society Open Science,

I would like to resubmit to you my manuscript “New records of theropods from the latest Cretaceous of New Jersey and the Maastrichtian Appalachian fauna” for consideration at your journal.

In revising my work, I’ve paid special attention to the stylistic issues noted by the reviewers. Detailed responses may be found below. I hope the manuscript is now suitable for publication, and thank you for your reviews.

Regards,

Chase Brownstein
Research Associate,
Collections & Exhibitions, Stamford Museum & Nature Center
Stamford, Connecticut, United States
Responses to Reviewers:

Reviewer 1

First and foremost— the phylogenetic analysis of teeth. You must use the super matrix of Hendrickx and Mateo, not just the tooth matrix. Please recode and rerun the analysis. Also, you should add Dryptosaurus and potentially one other tyrannosaurid to the matrix so that you might get some resolution as to the phylogenetic affinities of your tooth. Without this there is little that can be said except it is a tyrannosauroid tooth.

Although I appreciate this comment, I want to note that the matrix of Hendrickx and Mateus I use in the paper was recommended by Dr. Hendrickx in a previous review of this manuscript. Also, beyond general phylogenetic placement, the conclusions to be drawn about the evolutionary relations of teeth from this type of analysis are really tenuous. The reviewer is correct in saying that little else besides the tooth’s tyrannosauroid affinities can be deduced from this tree. Therefore, adding new taxa to the matrix wouldn’t provide any strong new phylogenetic conclusions. As the other reviewers have not raised issues with this, I’ve chosen to keep the phylogeny as is.

Put some or all of the Discriminant Analysis results in the paper, not the SM. We need to see the data.

Done. I’ve made the relevant corrects.

The last sentence of the abstract does not make sense. I suggest deleting it, but you can try to modify it.

Done. I’ve deleted this sentence.

Reviewer: 3

Comments to the Author(s)

This revision of the original paper is much better present and the interpretations are supported. I think it is nearly ready for publication. I made minor corrections to the MS on the PDF. Please be careful with the use of the clade names. Tyrannosaurids = members of Tyrannosauridae. I noted these throughout. Also, put the description before the identification of each tooth section.

Done. I’ve made the suggested edits. One edit I did not choose to comply with was the switching of the Description and Identification sections. A previous reviewer had me order the paper that way, and switching them does not drastically change the manuscript or increase clarity.

Reviewer: 4

I suggest publication with minor revision; in addition to the specific comments below, I think the author should more clearly couch the article in terms of the refugium versus exchange models. In the introduction and conclusion, he leans heavily on the exchange model and that needs to be balanced, in both places, by a skeptical assessment of the case for the exchange model. An explicit statement of the evidence in favor of the refugium hypothesis must also be included in the abstract and the title must be adjusted accordingly.

Done. I’ve more clearly stated that these are the two models. I’ve also made the other suggested corrections.

The author may know my identity: Thomas D. Carr