nature portfolio

Peer Review File

Early gigantic lamniform marks the onset of mega-body size in modern shark evolution

Corresponding Author: Dr Mohamad Bazzi

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

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
Main comments:
The manuscript by Bazzi et al. reports the vertebrae of the oldest known “giant” lamniform shark from an Aptian deposit in Australia. Additionally, the relationship between centrum diameter and total length across living lamniforms is tested more broadly on the fossils, estimating a total length of 5-7 m. The key implication of the paper’s findings is that gigantism in lamniform sharks first evolved earlier than generally thought – originating in the Early Cretaceous rather than later on.
I enjoyed reading this paper. Its methods are well described and explained, the rationale behind the work is clear, and the paper’s “narrative” fits together very nicely. I commend the authors for this interesting and well done work. The supplementary file provides all the necessary extra details, and there is good discussion about the use of proxies and extrapolations from living to extinct sharks to estimate body size. I particularly appreciate how much work has been done to ensure reproducibility of the study; and the authors have done a great job there.
My only concern is the vertebral count analysis. The result is well explained and fits in well with the rest of the paper, but the analysis is based on a rather tiny sample size of just four white sharks. I would suggest that the authors try to increase the sample size for the poisson regression, if possible, or at least briefly explain the confidence of the results despite the sample size. In addition, would it be worth considering multiple species in such an analysis given that multiple different species may be used as proxies for predicting extinct shark sizes depending on the researcher or hypothesis being tested?
As such, beyond the above comments on one single analysis, I only have some minor suggestions for the revision. You can find my comments below by line number and I wish the authors the best in addressing them. I hope these are helpful and I look forward to seeing this manuscript published shortly.
Many thanks,
Jack Cooper (Swansea University)

Specific comments (by line number):
L54: Functional specialization has a specific definition in ecology – namely species with extreme trait values (e.g., the largest body sizes). Naturally, that doesn’t necessarily apply to all of the living lamniforms; and so I’d suggest altering to something like “ecological disparity” or something similar. Thanks.
L262: What is the value of the adjusted R2 here? Please add.
L361: Please also cite Cooper et al. 2023, which looked at broader relationships between tooth height and width to body size across a range of living shark species. Thanks.
L373-375: Do you have specific references for the information about tooth files between O. ferox and C. carcharias? If so, please cite. Thanks.
L457: Please additionally cite more recent literature that has also concluded around 6 m as the maximum size of white sharks. Examples include Randall 1987, De Maddalena et al. 2003, Castro 2012 and Ebert et al. 2021. Thanks.
L470: Is that meant to be “fed” rather than “feed”? Thanks.

Many thanks for the invitation to review this manuscript. I wish the authors well and hope these comments will be helpful!
Please find references below if needed:
Castro JI, 2012. A summary of observations on the maximum size attained by the white shark, Carcharodon carcharias. In Global Perspectives on the Biology and Life History of the White Shark; Domeier ML, Ed.; CRC Press: Boca Raton, FL, USA; pp. 85–90.

Cooper JA, Griffin JN, Kindlimann R & Pimiento C, 2023. Are shark teeth proxies for functional traits? A framework to infer ecology from the fossil record. Journal of Fish Biology, 103, 798-814.
De Maddalena A, Glaizot O & Oliver G, 2003. On the great white shark, Carcharodon carcharias (Linnaeus, 1758), preserved in the Museum of Zoology in Lausanne. Marine Life, 13, 53-59.
Ebert DA, Dando M & Fowler S, 2021. Sharks of the world: a complete guide. Princeton University Press.
Randall JE, 1987. Refutation of lengths of 11.3, 9.0, and 6.4 m attributed to the white shark, Carcharodon carcharias. California Fish and Game, 73, 163-168.

Reviewer #2

(Remarks to the Author)
In this paper the authors report the evolution of body size among the iconic mackerel sharks (Lamniformes) with the record of vertebrae form the Cretaceous species which pushes back the evolution of body size in this groups. The authors gathered a large data set to perform regression models using the vertebrae to infer body size of the fossil specimens. I consider the study important to understand how body size evolved in this shark lineage. My main concern is the phylogeny used to estimate the body size. There are a few points which I think are necessary to cover before its publication (see below).

Introduction

Overall is quite succinct and does not introduce properly the reader to the implications of understanding body size evolution in Lamniformes. The first paragraph of the discussion could be moved here to add more general context.

L59-61 This might be limiting, although acknowledging the several studies using teeth to estimate body size has led to interesting hypotheses regarding the ancestral state (e.g., Shimada, K., Becker, M. A., & Griffiths, M. L. (2021). Body, jaw, and dentition lengths of macrophagous lamniform sharks, and body size evolution in Lamniformes with special reference to ‘off-the-scale’gigantism of the megatooth shark, Otodus megalodon. Historical Biology, 33(11), 2543-2559.) Not to forget that a previous study about body size estimation in a now confirmed Lamniform shark (Ptychodus) is available. Jambura, P. L., & Kriwet, J. (2020). Articulated remains of the extinct shark Ptychodus (Elasmobranchii, Ptychodontidae) from the Upper Cretaceous of Spain provide insights into gigantism, growth rate and life history of ptychodontid sharks. PLoS One, 15(4), e0231544.

Methods
From the supplementary file the first section describes well the differences between the vertebrae of the specimen compared to other species. However, there are no images associated with the text immediately, since it's part of the supplementary information I do not see any limitation to include figures there which help to emphasize the observations by the authors.

The phylogeny used takes Pseudocarcharias as a sister species of Alopias vulpinus. Although I do admit that the monophyletic grouping of all the Alopias species has been elusive in most studies, some have found at least some consensus with A pelagicus and A vulpunis as sister species (Kousteni et al, 2021) using whole mitochondrial genome, and even a study found all Alopias species monophyletic (Cerdeñosa et al, 2014). From the tree in the supplementary figure 5 this arrangement is not similar as previous studies. Could this be the source of discrepancies between the support of the models tested in the manuscript? It would be worth placing the posterior probability from the MCC tree used in the study as well as considering alternative topologies in this regard.

Kousteni, V., Mazzoleni, S., Vasileiadou, K., & Rovatsos, M. (2021). Complete mitochondrial DNA genome of nine species of sharks and rays and their phylogenetic placement among modern elasmobranchs. Genes, 12(3), 324.

Cardeñosa, D., Hyde, J., & Caballero, S. (2014). Genetic diversity and population structure of the pelagic thresher shark (Alopias pelagicus) in the Pacific Ocean: evidence for two evolutionarily significant units. PloS one, 9(10), e110193.

L87 "milimeter"

L95-96 Can you specify how close to each other?

L133 Define BM here, I assume is body mass, but it's not defined in previous lines

L160-161 Only TL once it was defined and BM from the previous comment

L188-193 From these models I can see why to exclude Alopias in two of the models, but why exclude Cetorhinus? Perhaps explaining a bit the rationale behind these models can help

Results

L276-283 While I agree that a model will fit better without these two outliers, it is part of the whole data and the most complete phylogenetically speaking.

L289-291 The same applies here. I don't see an argument to exclude one species here just because it might be an outlier.

Perhaps considering pre-caudal length or fork length can add a clearer picture of the estimation since the extreme caudal fin of Alopias would be adjusted.

Discussion

L347-359 This section could serve well as part of the introduction as context.

L369 It is also the case in squaliforms, more specifically in Isistius and Dalatias.

Reviewer #3

(Remarks to the Author)
This is an interesting paper and highlights the early appearance of large lamniforms. This is a simple concept and essentially boild down to methods of predicting whole animal size based on some exceptionally large vertebrae. Whilst this is a useful paper on the changes in marine ecosystems, as it is based on very incomplete material and as a result the paper is largely on the methodology of tabulating shark sizes. This makes the paper difficult to read and it is not easy to find the impoerant conclusions, as they are not made very clear at an early point.
In summary, I think that this is clearly material that is impotant and needs publishing, but I have some serious reservations on the style of the writing making it rather hard to follow, and also whether this is the correct journal for pointing out some very large vertebrae and with the conclusions (although almost certainly correct) are based on a lot of assumptions.

I thing that there is a lot of emphasis on analysis but not very much discussion on the methods, especially whether total or fork length was to be used, and the relationship between length and weight.
Also it is no clear why Ptychodus was excluded; it is arguably no further from the "lamniform bauplan" than Cetorhinus.

Also it is mentioned that there is an indirect link from centra size and teeth, but even then there is a minimum size that teeth would indicate, so teeth are useful if only indirectly.

As it is, the paper (correctly) indicates the first huge (length, but i would argue estimated 1000kg would be better as a limit) sharks appeared in the mid Cretaceous. That is not new information, only these vertebrae are exceptionally large. This rather misses the point of an indication of shark size over time. Clearly there is a dramatinc size inclrease from the Valanginian to Cenomanian. A plot of this would be extremely useful, even if there is a vast error bar. From there until the late Paleocene is seems predatory sharks of many clades seem to reach, but not exceed, a similar total length. Why is this the case at least until the Neogene?

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
The revision by Bazzi et al. is much improved from an already well-done manuscript. I believe the comments of myself and the other reviewers have been sufficiently addressed and so I think this paper can be accepted for publication as it is.

Many congratulations to the authors. I look forward to seeing their paper published very soon.

All the best,
Jack Cooper

Reviewer #2

(Remarks to the Author)
After the review I can tell the authors have done an excellent work. They have addressed all my comments and concerns regarding the phylogeny's topology and possible results from it. The figure showing the possible discrepancy between the analyses due to the phylogeny's topology illustrates it well. The new structure with the introduction adding more context to the subject helps the reader to get a general understanding of it. Therefore I recommend to publish the manuscript as it is.

Reviewer #3

(Remarks to the Author)
I still like this as a paper and it clearly shows that large predatory sharks (5 m+) appeared in the Aptian, rather than the Middle Albian as previously written. However this is not too surprising- there are teeth of Cretodus known from the Aptian of France and (I think) Uk and even though potentially as large as the specimen here, still pretty big. Study of an unprepared specimen from the Lebanese Cenomanian would be needed to sort out tooth-vertebra size. Also, pre-Albian Cretaceous shark faunas are exceptionally poorly known with only a handful of sites globally known to have a reasonable fauna, and so the sampling errors are likely to ve vast due to the small amount ot available material.
The record of this very large species is an interesting point, but other than being a "that's interesting" point, does not add very much, and I really don't think this is the right journal for it.

The paper also feels extremely unbalanced with the majority moving no direct reference to the fossil specimens under consideration, but instead being a methodology for measuring sharks based on modern species. If anything, this is the more significant part of the paper, but again I do not think this is the correct journal and a Palaeontological methods journal may be better.

Response to Reviewers

Reviewer #1

Main comments:

The manuscript by Bazzi et al. reports the vertebrae of the oldest known “giant” lamniform shark from an Aptian deposit in Australia. Additionally, the relationship between centrum diameter and total length across living lamniforms is tested more broadly on the fossils, estimating a total length of 5-7 m. The key implication of the paper’s findings is that gigantism in lamniform sharks first evolved earlier than generally thought – originating in the Early Cretaceous rather than later on.

I enjoyed reading this paper. Its methods are well described and explained, the rationale behind the work is clear, and the paper’s “narrative” fits together very nicely. I commend the authors for this interesting and well done work. The supplementary file provides all the necessary extra details, and there is good discussion about the use of proxies and extrapolations from living to extinct sharks to estimate body size. I particularly appreciate how much work has been done to ensure reproducibility of the study; and the authors have done a great job there.

My only concern is the vertebral count analysis. The result is well explained and fits in well with the rest of the paper, but the analysis is based on a rather tiny sample size of just four white sharks. I would suggest that the authors try to increase the sample size for the poisson regression, if possible, or at least briefly explain the confidence of the results despite the sample size. In addition, would it be worth considering multiple species in such an analysis given that multiple different species may be used as proxies for predicting extinct shark sizes depending on the researcher or hypothesis being tested?

As such, beyond the above comments on one single analysis, I only have some minor suggestions for the revision. You can find my comments below by line number and I wish the authors the best in addressing them. I hope these are helpful and I look forward to seeing this manuscript published shortly.

Many thanks,

Jack Cooper (Swansea University)

We are grateful to Reviewer #1 for endorsing the analytical rigour and impact of our results. We also agree that the ‘vertebral count analysis’ could be improved by expanding the sample size. Accordingly, we have sought out additional data to address the valid concern raised by Reviewer #1. In the revised version we know include the vertebral counts from other lamniform species: Shortfin Mako shark (3 individuals), Common thresher (2 individuals), and Porbeagle shark (3 individuals). These were compiled from Natanson *et al*. 2018 and are provided as a separate supplementary excel sheet.

L54: Functional specialization has a specific definition in ecology – namely species with extreme trait values (e.g., the largest body sizes). Naturally, that doesn’t necessarily apply to all of the living lamniforms; and so I’d suggest altering to something like “ecological disparity” or something similar. Thanks.

Amended and now reads (see line 40-42): “Lamniformes (Mackerel sharks) is one of the most ecologically disparate modern selachian groups, with 15 extant species utilizing a variety of benthic to pelagic lifestyles, and inhabiting the intertidal to neritic (>200–1,000 m) and oceanic deep-water zones (>1,000 m)[1].”

L262: What is the value of the adjusted R2 here? Please add.

Amended (see lines 104-107)

“We therefore fitted an augmented TL model integrating all of the *C. carcharias* data (Supplementary Fig. 3); this confirmed statistically significant negative allometry between log-transformed (log-) CD and log-TL (β_1= 0.86 ± 0.02, R^2 = 0.94, $F_{1,127}$ = 2158, $p < 0.001$, N = 129) with high model accuracy (RSE = 0.03, PPE = 4.07%).”

L361: Please also cite Cooper et al. 2023, which looked at broader relationships between tooth height and width to body size across a range of living shark species. Thanks.

Thanks for bringing this paper to our attention. It’s now been added to the reference list.

L373-375: Do you have specific references for the information about tooth files between O. ferox and C. carcharias? If so, please cite. Thanks.

Amended (see line 183-185). The information comes from Compagno 2001.

L457: Please additionally cite more recent literature that has also concluded around 6 m as the maximum size of white sharks. Examples include Randall 1987, De Maddalena et al. 2003, Castro 2012 and Ebert et al. 2021. Thanks.

Thanks for providing additional citations on the body size *of C. carcharias*. The discussion section has changed slightly from the previous version, and we now draw parallels with *C. carcharias* based on dietary ecology. (see lines 254-256).

L470: Is that meant to be “fed” rather than “feed”? Thanks.

Text amended.

Reviewer #2

In this paper the authors report the evolution of body size among the iconic mackerel sharks (Lamniformes) with the record of vertebrae form the Cretaceous species which pushes back the evolution of body size in this groups. The authors gathered a large data set to perform regression models using the vertebrae to infer body size of the fossil specimens. I consider the study important to understand how body size evolved in this shark lineage. My main concern is the phylogeny used to estimate the body size. There are a few points which I think are necessary to cover before its publication (see below).

We thank Reviewer #2 for their endorsement of our work and for providing constructive feedback.

Introduction

Overall is quite succinct and does not introduce properly the reader to the implications of understanding body size evolution in Lamniformes. The first paragraph of the discussion could be moved here to add more general context.

We appreciate Reviewer #2’s comments and agree that the previous version required further development. In the revised manuscript, we have substantially improved the introduction by providing clearer context—both regarding the material under study and the broader evolutionary and ecological significance of understanding body size evolution in lamniform sharks.

L59-61 This might be limiting, although acknowledging the several studies using teeth to estimate body size has led to interesting hypotheses regarding the ancestral state (e.g., Shimada, K., Becker, M. A., & Griffiths, M. L. (2021). Body, jaw, and dentition lengths of macrophagous lamniform sharks, and body size evolution in Lamniformes with special reference to ‘off-the-scale’gigantism of the megatooth shark, Otodus megalodon. Historical Biology, 33(11), 2543-2559.) Not to forget that a previous study about body size estimation in a now confirmed Lamniform shark (Ptychodus) is available. Jambura, P. L., & Kriwet, J. (2020). Articulated remains of the extinct shark Ptychodus (Elasmobranchii, Ptychodontidae) from the Upper Cretaceous of Spain provide insights into gigantism, growth rate and life history of ptychodontid sharks. PLoS One, 15(4), e0231544.

We thank Reviewer #2 for their suggestion to include Jambura et al. (2020) in our discussion. However, we respectfully note several concerns with their interpretation: (1) they propose that a set of vertebrae from the Toolebuc Formation (Queensland) closely resemble those in their study, yet the Toolebuc Formation lacks any evidence of *Ptychodus* teeth—unsurprising given that the genus had not yet evolved during the early Late Albian. In contrast, the formation contains two species of highly abundant anacoracids; (2) the placoid scales of the Spanish specimen described by Jambura et al. appear more similar to those of anacoracids from the Toolebuc Formation than to verified *Ptychodus* material from the Smoky Hill Chalk; (3) *Ptychodus* vertebrae that are found associated with teeth consistently exhibit both concentric and radial ('parallel') lamellae. While Jambura and Kriwet assert the presence of both structures in their specimen, their figure 2D clearly shows only concentric lamellae, which are perforated by radial tubes or rods, rather than true radial lamellae. In summary, the evidence for a ptychodontid affinity appears weak, and the observed features are more consistent with an anacoracid identification. Additionally, the size of the specimen may have been overestimated, as anacoracids are known to possess vertebrae with relatively large diameters.

Methods

From the supplementary file the first section describes well the differences between the vertebrae of the specimen compared to other species. However, there are no images associated with the text immediately, since it's part of the supplementary information I do not see any limitation to include figures there which help to emphasize the observations by the authors.

We acknowledge Reviewer #2's concern; however, due to limitations on the number of figures permitted in the main text, we have prioritized those that directly support the primary analytical findings of our study. That said, we have included illustrations of the cardabiodontid fossil specimens alongside selected main text figures and provide further details and additional visual material in the supplementary file.

The phylogeny used takes Pseudocarcharias as a sister species of Alopias vulpinus. Although I do admit that the monophyletic grouping of all the Alopias species has been elusive in most studies, some have found at least some consensus with A pelagicus and A vulpunis as sister species (Kousteni et al, 2021) using whole mitochondrial genome, and even a study found all Alopias species monophyletic (Cerdeñosa et al, 2014). From the tree in the supplementary figure 5 this arrangement is not similar as previous studies. Could this be the source of discrepancies between the support of the models tested in the manuscript? It would be worth placing the posterior probability from the MCC tree used in the study as well as considering alternative topologies in this regard.

In response to Reviewer #2's suggestion, we have now included a sensitivity analysis assuming *Alopias* to be monophyletic. We would like to clarify, however, that the phylogenetic generalized least squares (PGLS) models were not used to predict body size in fossil taxa, due to the uncertain phylogenetic placement of extinct species. As such, this analysis was exploratory in nature and not intended as the primary basis for fossil body size estimations. We have added the following statement to the main text to clarify this point.

See lines (405-408) "To test the effects of variable lamniform phylogenetic relationships (e.g., [88,92–94]) we modified our existing tree, making *Alopias* monophyletic (sensu Sorensen *et al*.[94]). This alternate topology was generated by importing the initial tree file into Mesquite v. 3.81[95] and manually altering the phylogenetic arrangement."

L87 "milimeter"

Amended.

L95-96 Can you specify how close to each other?

This part of the text has been amended (see lines: 224-230)

"Unfortunately, the disarticulated and isolated condition of NTM P922-29, NTM P922-32, NTM P922-33, NTM P922-37, and NTM P9382 makes their association (if any) and original positioning along the vertebral column difficult to establish. Nonetheless, our TL predictions assumed that each dorsal centrum was derived from the region of maximum body girth. We therefore view them as conservative, and suspect that the Darwin Formation cardabiodontid might have attained even larger body sizes than those proposed here."

L133 Define BM here, I assume is body mass, but it's not defined in previous lines

Amended.

L160-161 Only TL once it was defined and BM from the previous comment

We have now provided the abbreviations for total length and body mass in correct order.

L188-193 From these models I can see why to exclude Alopias in two of the models, but why exclude Cetorhinus? Perhaps explaining a bit the rationale behind these models can help

This is now explained in the main text (see lines 199-203)

"Interestingly, our TL predictions from the *Cetorhinus maximus* dataset (Fig. 3A) concurred with those produced by lamnids, despite stark differences in growth trajectory and body size between these taxa (Table 1). Nonetheless, contrasting levels of vertebral calcification[51], atypical development[52], and the specialized filter-feeding lifestyle of *C. maximus*[1] prompt us to reject TL predictions based on this species."

Results

L276-283 While I agree that a model will fit better without these two outliers, it is part of the whole data and the most complete phylogenetically speaking.

The inclusion of *Alopias* species poses challenges when estimating total length (TL) in non-*Alopias* taxa due to their apomorphic trait of an extremely elongated caudal fin. This distinct morphology significantly alters the centrum diameter–total length (CD–TL) relationship, making it difficult to justify their inclusion in comparative analyses with other macrophagous lamniforms (extant and extinct).

L289-291 The same applies here. I don't see an argument to exclude one species here just because it might be an outlier. Perhaps considering pre-caudal length or fork length can add a clearer picture of the estimation since the extreme caudal fin of Alopias would be adjusted.

This study focused on total length and while fork length and precaudal length could be explored in more detail, it currently falls outside the scope of the article. We acknowledge that this could be an interesting avenue for research in the future.

Discussion

L347-359 This section could serve well as part of the introduction as context.

We have substantially revised the Introduction and hope that the updated version provides sufficient context.

L369 It is also the case in squaliforms, more specifically in Isistius and Dalatias.

We thank the reviewer for bringing this to our attention.

Reviewer 3

Reviewer #3 (Remarks to the Author):

This is an interesting paper and highlights the early appearance of large lamniforms. This is a simple concept and essentially boild down to methods of predicting whole animal size based on some exceptionally large vertebrae. Whilst this is a useful paper on the changes in marine ecosystems, as it is based on very incomplete material and as a result the paper is largely on the methodology of tabulating shark sizes. This makes the paper difficult to read and it is not easy to find the impoerant conclusions, as they are not made very clear at an early point.

In summary, I think that this is clearly material that is impotant and needs publishing, but I have some serious reservations on the style of the writing making it rather hard to follow, and also whether this is the correct journal for pointing out some very large vertebrae and with the conclusions (although almost certainly correct) are based on a lot of assumptions.

We thank Reviewer #3 for recognizing the significance of our study and for highlighting that our conclusions are well-supported by both a substantial dataset and a rigorous analytical framework. In our revised manuscript, we have made a concerted effort to improve the clarity of the narrative while preserving the necessary technical detail. That said, we are uncertain about the broader concerns the reviewer may have had. We respectfully disagree with the assertion that our study is based on "a lot of assumptions," particularly since no specific examples were provided to clarify this point.

I thing that there is a lot of emphasis on analysis but not very much discussion on the methods, especially whether total or fork length was to be used, and the relationship between length and weight.

It is our objective as part of this study to explain the method and data used in detail to eliminate any ambiguity in how we derived our main findings. This study focused on total length which is the single most used body length measutment used in fossil shark literature. Body weight featured comparably less because such data was limited to oen species (i.e., C. carcharias). However, it is not clear what the Reviewer #3 is asking for with respect to body-length versus weight.

Also it is no clear why Ptychodus was excluded; it is arguably no further from the "lamniform bauplan" than Cetorhinus.

We did not include *Ptychodus* in our Mesozoic dataset, as it represents a highly specialized lineage. Including *Ptychodus* would likely skew body length estimates for non-*Ptychodus* taxa—such as the cardabiodontid described in our study—by disproportionately lowering the inferred values.

Also it is mentioned that there is an indirect link from centra size and teeth, but even then there is a minimum size that teeth would indicate, so teeth are useful if only indirectly.

We respectfully ask the Reviewer to clarify their comment, as its current wording is unclear and we are unsure what specific action is required in response.

As it is, the paper (correctly) indicates the first huge (length, but i would argue estimated 1000kg would be better as a limit) sharks appeared in the mid Cretaceous. That is not new information, only these vertebrae are exceptionally large. This rather misses the point of an indication of shark size over time. Clearly there is a dramatinc size inclrease from the Valanginian to Cenomanian. A plot of this would be extremely useful, even if there is a vast error bar. From there until the late Paleocene is seems predatory sharks of many clades seem to reach, but not exceed, a similar total length. Why is this the case at least until the Neogene?

We again thank the Reviewer for acknowledging the robustness of our study. However, the remark regarding the use of "1000 kg as a limit" is unclear, and we kindly ask the Reviewer to clarify their intention.

The Reviewer also requests a plot illustrating the transition in body size from the Valanginian to the Cenomanian. We interpret this as referring to total length (TL) estimates based on teeth, as there is, to our knowledge, no continuous record of vertebral centra spanning all of these stages.