Peer Community In Paleontology

Not-so-simple turtle ecomorphology

Jordan Mallon based on peer reviews by *Heather F. Smith* and *Donald Brinkman*

Serjoscha W. Evers, Christian Foth, Walter G. Joyce, Guilherme Hermanson (2024) Simple shell measurements do not consistently predict habitat in turtles: a reply to Lichtig and Lucas (2017). bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Paleontology. https://doi.org/10.1101/2024.03.25.586561

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Published: 18 December 2024

I am a non-avian dinosaur palaeontologist by trade with a particular interest in their palaeoecology. This can be an endless source of both fascination and frustration. Fascination, because non-avian dinosaurs are quite unlike anything alive today, warranting some use of creative license when imagining them as living animals. Frustration, because the lack of good, extant ecological analogues frequently makes reconstruction of their ancient ecologies an almost insurmountable challenge.

The Canadian Museum of Nature where I work has a good collection of Late Cretaceous turtles. I took an interest in these some years ago because it struck me that, despite the quality of our collection, relatively few people come to study them. I thought, "Someone should work on these. Why not me?" I figured studying a new fossil group would present a fun change of pace and perhaps a more straightforward object of palaeoecological reconstruction. After all, fossil turtles are a lot like living turtles, so how hard can it be? Right?

In 2018, I took a special interest in one recently prepared fossil turtle, which I determined to be a new species of Basilemys (Mallon and Brinkman, 2018). Basilemys held my interest because, although it is a relatively common form, there has been some debate concerning the palaeohabitat of this animal and its closest relatives, the nanhsiungchelyids. Some have argued for an aquatic habitat for these animals; others, for a terrestrial one. It seems that where one comes down on the issue depends on which aspect of ecomorphology is emphasized. If it is on the flat carapace, nanhsiungchelyids must have been aquatic; if it is on the stout feet, terrestrial. This is how I came to appreciate the numerous ecomorphological proxies (e.g., skull shape, shell shape, limb proportions) that are used in turtle palaeoecology and how incongruent they can sometimes be. So much for easy answers!

The present study by Evers et al. is a response to an original piece of research by Lichtig and Lucas (2017), who claimed to be able to use simple shell measurements (carapacial doming and relative plastral width) to accurately deduce/infer the habitats of living turtles and, by extension, fossil ones. In short, they found that terrestrial turtles tend to have more domed carapaces and wider plastra, yielding some unconventional

palaeoecological reconstructions of particular stem turtles. Evers et al. take issue with several aspects of this study, including issues of faulty data entry, inappropriate removal of extant taxa from the model, and insufficient accounting for phylogenetic non-independence. By correcting for these overights, they find that the model of Lichtig and Lucas (2017) performs more poorly than advertised and that the palaeoecological classification it produces should be questioned. "The map is not the territory", as Alfred Korzybski put it, and this latest study by Evers et al. serves as an important reminder of that lesson.

Still, even if Lichtig and Lucas's model is overly simplistic, it is true that aquatic turtles, on average, have lower carapaces and narrower plastra, and that they have relatively lower skulls and longer toes. Surely, there is merit in each of these anatomical proxies, even if no single one predicts ecology with total accuracy. I would love to see a model that combines them all. Until then, Evers et al. have inched us closer to knowing what turtle morphology can (and cannot) tell us about habitat.

Thanks to D. Brinkman and H. Smith for their helpful reviews of the manuscript.

References:

Evers, S. W., Foth, C., Joyce, W. G., and Hermanson, G. (2024). Simple shell measurements do not consistently predict habitat in turtles: A reply to Lichtig and Lucas (2017). bioRxiv, 586561, ver. 3 peer-reviewed by PCI Paleo. https://doi.org/10.1101/2024.03.25.586561

Lichtig, A. J., and Lucas, S. G. (2017). A simple method for inferring habitats of extinct turtles. Palaeoworld, 26(3), 581–588. https://doi.org/10.1016/j.palwor.2017.02.001

Mallon, J. C., and Brinkman, D. B. (2018). *Basilemys morrinensis*, a new species of nanhsiungchelyid turtle from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. Journal of Vertebrate Paleontology, 38(2), e1431922. https://doi.org/10.1080/02724634.2018.1431922

Reviews

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2024.03.25.586561
Version of the preprint: 1

Authors' reply, 05 December 2024

Dear Dr. Mallon,

Attached, please find our point-by-point revisions to our manuscript. I apologize that this took so long.

With best regards on behalf of all authors,

Serjoscha Evers

A worthy manuscript in need of minor tweaks

This is a timely and well-written preprint that both reviewers see much merit in. However, Dr. Smith raises a few key points worthy of careful consideration, particularly with regard to the differential effect of the newly added flat-shelled outliers and the possibility that the baenid and adocid data originally given by Lichtig and Lucas were also inadvertently transposed. The possibility that the entirety of their fossil dataset is recorded inaccurately should really be examined. Dr. Smith also provides some other minor comments worth considering. I will be happy to recommend the preprint pending these minor changes.

by Jordan Mallon, 07 Jun 2024 17:15

Response: We thank the editor for this assessment. We have taken the reviewers' comments on board, as explained in detail below. The largest changes of our manuscript are summarized here:

- Based on comments by Heather Smith, we explored statistically the effect of excluding Malacochersus tornieri, Homopus boulengeri and Terrapene coahuila. Although we do not agree that these should be excluded, this is a worthwhile exercise, especially as the results show that there is still no discrimination strength in the dataset, given the broad overlap of aquatic and terrestrial turtles along the doming gradient

- Based on comments by Heather Smith, we expanded our introduction to speak more broadly about the topic of palaeoecological inference in turtles, the role that habitat ecology plays for turtle evolution, and the general idea that shell shape relates to hydrodynamics, which has, of course, been formulated before the Lichtig and Lucas (2017) paper.

- Based on comments by Heather Smith, we explore alternative habitat categorizations in a new, second figure. This figure shows that same data as panels C and D of Figure 1, but the species means are colour-coded by hand-webbing as a finer proxy for levels of aquaticness. We discuss how these alternatives of scoring habitat ecology seem to have no impact on out general results that the simple measurements proposed by Lichtig and Lucas (2017) cannot distinguish habitat ecologies among turtles.

- Based on comments by Heather Smith, we now use a 3D model of a particular Basilemys specimen as the basis for our measurements. The new measurements refine the height measurement, which is difficult to measure in lateral images. We also included another Basilemys fossil that we found on MorphoSource and that seemed worth including. Thus, we had re-run the analyses with the new measurements and adjust our figures, but this had no effect on our results or interpretations.

Review by Donald Brinkman, 20 May 2024 21:11

This paper is a critique of the attempt by Lichtig and Lucas (2017) to demonstrate a relationships between shell shape, especially doming, and aspects of their ecology. The questions of relationship of shell shape and ecology has long been recognized as a problem because there seems to be a pattern for terrestrial turtles to have high-domed shells, but there are notable exceptions that cannot be easily explained. Lichtig and Lucas had attempted to quantify the relationship, and their results appeared to be significant. However, Evers et al identify a number of issues with the Lichtig and Lucas paper, both in the original data set and in the methods of analysis. When corrected, the results do not allow paleoecology to be predicted from shell shape. The problems with the original data set identified by Evers et al are clear and their approach to providing corrected data is clear and can be reproduced by other authors. The statistical methods used are sound. I have no recommendations for modifications of the manuscript.

Response: We thank you for assessing our MS, and are of course happy to see that you like it as it is.

Review by Heather F. Smith, 01 Jun 2024 23:14

Thank you for inviting me to review this manuscript by Evers et al. It provides an important contribution to the field by correcting the scientific record, rectifying erroneous conclusions put forth by a previous study (Lichtig & Lucas, 2018). I reviewed not only this paper, but the original article to which this study serves as a reply, and I agree with the conclusions of the current authors that the original study contains numerous errors and resultingly unsubstantiated conclusions.

Response: We are pleased to see that you agree with the conclusions of our study.

It occurs to me that maybe there is another opportunity here to discuss the utility of making a dichotomous (arguably oversimplified) categorization of aquatic vs terrestrial habitus in turtles. As the authors demonstrate, there are several aquatic "morphs", many of which correspond to varying degrees of obligate "aquaticness". While many box turtles may be more aquatic than terrestrial, they rarely swim and can flourish on (wet) land.

Response: This is, of course, a very good point to be made and we have now incorporated this into our text by stating: "The underlying observation is one that has long been observed: aquatic turtles on average have flatter shells than terrestrial turtles, whereby flatness is commonly interpreted as a hydrodynamic adaptation whilst a high domed shell morphology can aid in self-righting (e.g., Romer 1967; Claude et al. 2003; Domokos & Várkonyi 2008; Rivera 2008; Benson et al. 2011; Stayton 2011; Polly et al. 2016; Williams & Stayton 2019; Stayton 2019; Ferreira et al. 2024). Although there are of course gradients of "aquaticness" among turtles (e.g., with many testudinids never entering a body of water, many chelonioids and trionychids only leaving the water to lay they eggs, but some turtles, such as the wood turtle Glyptemys insculpta readily spending time in water or on land [Ernst and Barbour 1989]) that could be further anatomized, the principal distinction between terrestrial and aquatic species is a meaningful categorization, for several reasons. First, one of the most important functional aspects of aquatic lifestyles is a habitual submersion in water (e.g., Fabbri et al. 2022b), which can occur for different reasons, including foraging or seeking protection. Aquatic animals face functional challenges that are different from functional challenges imposed on animals that never submerge (e.g., Joyce & Gauthier 2004, Fabbri et al. 2022b). Evidence for this among turtles comes, for instance, from differences in hand structure in aquatic bottom walking chelydroids and terrestrially walking tortoises (Joyce & Gauthier 2004). For the purpose of shell geometry, there is a clear expectation formulated in Lichtig and Lucas (2017), but also in other studies (e.g., Stayton et al. 2018), that shell geometry is influenced by hydrodynamic adaptations, which should universally apply to turtles that enter the water and universally be absent to those that do not. Secondly, the clear definition and distinction of variables is beneficial to analyses of ecomorphology (e.g., Fabbri et al. 2022b), and the binary distinction of turtles that never enter the water (i.e., terrestrial turtles) and turtles that do (i.e., aquatic turtles) provides a clearly testable habitat hypothesis that is not confounded by the varying degrees of aquaticness. Lastly, the principal categorization into aquatic and terrestrial turtles is one that has been used frequently in ecomorphological studies (e.g., Claude et al. 2003; Benson et al. 2011; Stayton 2011; Wise & Stayton 2017; Stayton et al. 2018), and even in those that also use finer degrees of classifying aquatic taxa (e.g., Joyce & Gauthier 2004; Foth et al. 2017; Hermanson et al. 2022; Evers et al. 2022). As such, this categorization is useful for literature comparisons of other studies focused on shell geometry but also those that study other anatomical systems influenced by aquatic/terrestrial adaptations, such as limbs (e.g., Joyce & Gauthier 2004)."

In addition, we explore the potential of alternative, finer habitat divisions in our new (discussion) figure 2. For this, we use the hand-webbing proxy first used by Foth et al. (2017). We discuss how this has no impact on the interpretation of patterns:

"Using finer habitat ecologies does not lead to a gradational pattern of doming according to habitat ecology: Our Figure 2 shows species mean data for the recorded shell ratios, whereby species are colour-coded according to their intensity of hand-webbing, which is a morphological proxy for their swimming capabilities (e.g., Foth et al. 2019; Dziomber et al. 2020). Although we do not provide formal statistical analyses for this, the webbing-groups show large overlap especially along the doming axis. Our results do not mean that there is no habitat information in turtle shell shape, but that the simple measurements proposed by Lichtig and Lucas (2017) do not work as sufficient discriminators between the two principal habitat ecologies of turtles."

How are the impactful the primary outliers, especially Malacochersus, Homopus, and Terrapene coahuila, to the revised analyses? The reason I'm curious is that Malacochersus, in particular, is extremely unusual with a shell full of fontanelles, and I can concede understanding the inclination of Lichtig & Lucas to omit it. Perhaps there is even a statistical argument for doing so. I'm not arguing that it necessarily should be omitted, but I would be curious to know how its presence (and those of the other "outliers") impacts the analysis.

Response: This is a good point. We tested this by running additional analyses (under phylogenetic flexible

discriminant methodology) that exclude these three "outlier" species. However, the statistical results from these analyses also suggest that the simple shell measurements cannot distinguish the broad habitat categories. Indeed, using coronal coming, the median success rate for correct identification of terrestrial turtles is 3.6%, and for sagittal doming it is 7.4%. As before, nearly all turtles are predicted to be aquatic, even if they are terrestrial. This shows that the method does not even work when the strongest morphological "outliers" are excluded, due to the substantial overlap of shell morphological in terms of primary habitat division. We worked these new analyses and results into the manuscript.

In looking at Table 1 in Lichtig & Lucas, it appears to me that the column headings are switched for all taxa for: 1) Plastron width and Carapace width; 2) Height and Length. Thus, it is not only the values for Basilemys that are backwards (as the authors note), but also the data for the adocids and baenids that were included in the Lichtig & Lucas sample. For example, the plastron in Scabremys is decidedly not wider than the carapace, nor is its shell taller than it is long. Since the current authors do not include Adocus or baenids in their analyses, this Lichtig & Lucas error doesn't affect the current analyses, but it might be worth pointing out in order to further correct the record.

Response: Thank you for these additional comments. It is true that the entire table of Lichtig & Lucas has to be incorrect, because all species show impossible combinations of measurements. However, we do not believe that a "simple" switch of columns as suggested by Dr. Smith does the trick of getting the data correct. At least for Basilemys, for which we can repeat the measurements, the plastral width is actually larger than the shell height, but rearranging the data columns, as suggested by Dr. Smith, does not provide that result. Thus, we do not feel comfortable to speculate on how to rearrange this erroneous table. Instead, we provide corrected measurement data for the turtles that are actually relevant for the study question at hand. Adocus, Denazinemys, Scabremys and Thescelus are an eclectic mix of turtle material that are – unlike Basilemys as a terrestrial but flat turtle and unlike stem turtles as the taxa of interest to infer habitat for – not really relevant to the main story line. We believe that the particular taxon choice in Lichtig & Lucas was likely guided by whatever specimens they had available at the time. Our original text already stated that the tables and supplements contain illogical values for a number of turtles. We strengthened this by changing the beginning of the Materials & Methods section to say the following (underlined text is new): "The tables and supplementary data of Lichtig and Lucas (2017) contain illogical values for a number of turtles. For instance, the plastron widths and carapace lengths of all taxa given in their table 1 exceed the values for carapace width and carapace length, respectively – which is anatomically impossible for the former and not realized among any known extant or fossil turtle for the latter. This is likely a result of data having been entered into the wrong column, but the aforementioned columns do not seem to have simply been mislabeled, because simply rearranging of the data columns also do not lead to plausible results. For example, (...)"

A 3D model of Basilemys morrinensis is available on Morphosource should the authors wish to use it rather than calculating dimensions based on the figures from Mallon & Brinkman (2018).

https://www.morphosource.org/index.php/Detail/MediaDetail/Show/media_le_id/31637)

Response: Thanks, we were not aware of this at the time we wrote the first version of the manuscript. We updated our measurements according to the model and updated the Materials & Methods text accordingly. The model allows a much more precise height measurement, which refines the ratio for doming. Browsing MorphoSource, we also found another well-preserved shell of Basilemys sp. from the DMNS, which we included as a fourth novel Basilemys measurement. As a result, we updated our plots and analyses with the new measurement data for both of these specimens. This had no impact on the interpretation of our data.

The first paragraph of the Results indicates that there are general patterns of higher doming in terrestrial versus aquatic turtles, even if the statistical findings are not significant and should not be used predictively. I think this point is worthy of discussion, if only to avoid throwing away the proverbial "baby with the bath water".

Response: Thanks for this. In the discussion, we added "This is not only because several extant aquatic and terrestrial turtle species exist that show doming that is atypical for the majority of their ecological guild,

as our analyses excluding these species show. More importantly, this is because there is a large region of morphological overlap along the gradient of doming. (…) Our results do not mean that there is no habitat information in turtle shell shape, but that the simple measurements proposed by Lichtig and Lucas (2017) do not work as sufficient discriminators between the two principal habitat ecologies of turtles."

Minor points:

The Introduction is quite succinct. It addresses the primary purpose of the paper, which is to test and ultimately rebut the Lichtig & Lucas (2018) paper. However, I think there is a potential opportunity here to expand the discussion of shell shape and its relation to aquatic versus terrestrial habitus beyond the Lichtig & Lucas study.

Response: We indeed had a very short introduction initially, because our primary aim was to address the issues we found in the Lichtig & Lucas (2017) paper. However, we agree that a broader framing of the principal topic is warranted. Thus, we expanded the introduction by a first paragraph that talks about the importance of palaeoecology for turtle evolution specifically, citing many case studies that have demonstrated some effect of habitat ecology on various aspects of turtle evolutionary history. Secondly, we introduce the general pattern of shell geometries of turtles more widely, framing the attempt of Lichtig & Lucas (2017) in the context of what is already known about ecologically-determined shell geometries. Both these additions warrant the inclusion of many novel citations. The new text reads as follows (novel text bits underlined):

"Inferring the palaeoecology of fossil species is of central importance for the field of palaeobiology, as knowing the ecological attributes of organisms (e.g., its habitat or diet) allows researchers to test if or how evolutionary patterns in the origin of lineages and body plans are related to ecology. For turtles, habitat ecology has been discussed to be important as drivers of their biogeographic distribution (e.g., Joyce et al. 2016; Ferreira et al. 2018), body size evolution (Farina et al. 2023), ecomorphological diversification (e.g., Evers et al. 2022; Hermanson et al. 2022), body shape and proportions (e.g., Hermanson & Evers 2024), dietary adaptations, morphological and functional innovations related to locomotion (e.g., Joyce & Gauthier 2004; Evers et al. 2019), and also the origin of the shell as the most characteristic trait of turtles (e.g., Rieppel & Reisz 1999; Rieppel 2013; Lyson et al. 2016; Schoch et al. 2019). However, the habitat ecology of fossil turtles can be difficult to know, for example when allochthonous fossil deposition may be invoked for turtles found in aquatic depositional environments (e.g.; Odontochelys semitestacea: Li et al. 2008; Joyce 2015; thalassochelydians in Solnhofen lagerstätten deposits: Anquetin et al. 2017; Joyce et al. 2021). Researchers frequently try to synthesize simple anatomical observations that reliably (i.e., accurately and precisely) correspond to (habitat) ecology among extant turtles, proposing that these can be used to ecologically classify extinct turtles (e.g., Joyce & Gauthier 2004; Dudgeon et al. 2021). Lichtig and Lucas (2017) recently proposed a method that allows inferring the habitat palaeoecology (i.e., aquatic versus terrestrial) of fossil turtles based on simple shell measurements. The underlying observation is one that has long been known: aquatic turtles seem to have flatter shells than terrestrial turtles, whereby flatness is commonly interpreted as a hydrodynamic adaptation whilst high domed morphology can aid in self-righting (e.g., Romer 1967; Claude et al. 2003; Domokos & Várkonyi 2008; Rivera 2008; Benson et al. 2011; Stayton 2011; Polly et al. 2016; Williams & Stayton 2019; Stayton 2019; Ferreira et al. 2024). (…)"

P6, second paragraph: Suggest changing "pFDA allows to test if a predictor can…" to "pFDA allows the test of whether a predictor can…"

Response: okay, changed.

P7, second sentence: Suggest changing "as was already done by…" to "following" or "as in".

Response: okay, changed.

P7, final sentence: Suggest changing "This is caused by…" to something more precise such as "This pattern is caused by…"

Response: okay, changed.

P9, last sentence, "Variation between.." should be "Variation among…". Between = 2, among = more than 2.

Response: okay, changed.

P11, suggest changing “no further support” to “no longer support”.

Response: okay, changed.

P11, last sentence: I was a bit surprised to see Naomichelys listed as having a narrow plastron. I tend to think of their plastral as being relatively wide (see Joyce et al., 2014, fig 8). Perhaps it is comparatively narrow in relation to the particularly broad carapace of this taxon? Also, the reference here to Rollot et al. 2022 appears to be a mis-citation to an unrelated paper.

Response: This is definitely worth to think about, thank you for raising the subject. We agree that “relatively narrow plastra” is a term that can be interpreted differently by different people. In order to be a bit more specific, we exchanged “relatively narrow plastra” with “relatively narrow posterior plastral lobes”. Rollot et al. 2022 is the last paracryptodiran phylogeny performed in a more global context, and it finds helochelydrids as paracryptodiran stem turtles. This is different from earlier helochelydrid work, like the Joyce et al. (2014) descriptive paper, which was agnostic with regard to ‘solemydid’ relationships more globally. To not confuse the citation with one that is linked to Naomichelys in terms of descriptions, we added the Joyce et al. (2014) citation, but leave the Rollot et al. (2022) included and modified the text somewhat: “Naomichelys speciosa (a helochelydrid stem turtle: e.g., Joyce et al. 2014; see phylogeny of Rollot et al. 2022)”

P12, suggest changing “as already said by…” to “as already described by…” or “already indicated by…”

Response: okay, changed.

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Decision by Jordan Mallon, posted 07 June 2024, validated 11 June 2024

A worthy manuscript in need of minor tweaks

This is a timely and well-written preprint that both reviewers see much merit in. However, Dr. Smith raises a few key points worthy of careful consideration, particularly with regard to the differential effect of the newly added flat-shelled outliers and the possibility that the baenid and adocid data originally given by Lichtig and Lucas were also inadvertently transposed. The possibility that the entirety of their fossil dataset is recorded inaccurately should really be examined. Dr. Smith also provides some other minor comments worth considering. I will be happy to recommend the preprint pending these minor changes.

Reviewed by Donald Brinkman, 20 May 2024

Title and abstract

- Does the title clearly reflect the content of the article? [ ] Yes,
- Does the abstract present the main findings of the study? [ ] Yes,

Introduction

- Are the research questions/hypotheses/predictions clearly presented? [ ] Yes,
- Does the introduction build on relevant research in the field? [ ] Yes, [

Materials and methods

- Are the methods and analyses sufficiently detailed to allow replication by other researchers? [ ] Yes,
- Are the methods and statistical analyses appropriate and well described? [ ] Yes

Results

- In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [ ] Yes

- Are the results described and interpreted correctly? [ ] Yes,

Discussion

- Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [ ] Yes,
- Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [ ] Yes,

This paper is a critique of the attempt by Lichtig and Lucas (2017) to demonstrate a relationships between shell shape, especially doming, and aspects of their ecology. The questions of relationship of shell shape and ecology has long been recognized as a problem because there seems to be a pattern for terrestrial turtles to have high-domed shells, but there are notable exceptions that cannot be easily explained. Lichtig and Lucas had attempted to quantify the relationship, and their results appeared to be significant. However, Evers et al identify a number of issues with the Lichtig and Lucas paper, both in the original data set and in the methods of analysis. When corrected, the results do not allow paleoecology to be predicted from shell shape. The problems with the original data set identified by Evers et al are clear and their approach to providing corrected data is clear and can be reproduced by other authors. The statistical methods used are sound. I have no recommendations for modifications of the manuscript.

Reviewed by Heather F. Smith, 01 June 2024

Thank you for inviting me to review this manuscript by Evers et al. It provides an important contribution to the field by correcting the scientific record, rectifying erroneous conclusions put forth by a previous study (Lichtig & Lucas, 2018). I reviewed not only this paper, but the original article to which this study serves as a reply, and I agree with the conclusions of the current authors that the original study contains numerous errors and resultingly unsubstantiated conclusions.

It occurs to me that maybe there is another opportunity here to discuss the utility of making a dichotomous (arguably oversimplified) categorization of aquatic vs terrestrial habitus in turtles. As the authors demonstrate, there are several aquatic "morphs", many of which correspond to varying degrees of obligate "aquaticness". While many box turtles may be more aquatic than terrestrial, they rarely swim and can flourish on (wet) land.

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Minor points:

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Sincerely,

Heather Smith

Download the review