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:
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> - 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
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> - 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, <u>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.</u> This is likely a result of data having been entered into the wrong column, <u>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.</u> 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_file_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 <u>not only</u> because several extant aquatic and terrestrial turtle species exist that show doming that is atypical for the majority of their ecological guild, <u>as our analyses excluding these species show</u>. <u>More importantly</u>, this is because there is a large region of morphological overlap along the gradient of doming. (…) <u>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</u>."

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.