This study investigated the relationship between shell morphology and ecology in turtles in order to evaluate if the turtle shell can be used to reliably infer the paleoecology of extinct taxa. A 3D geometric morphometric approach was used to quantify the shape of the shells in a broad sample of extant species (N=69) that represent all major turtle clades and three fossil turtles. Based on their results, the authors conclude that there is “much overlap between habitat groups”, but they detected “significant differences” between the extremes (highly specialized terrestrial and aquatic turtles). Indeed, the secondary analysis using fewer ecological categories revealed similar results with a lower misclassification rate.

Basic reporting

In my opinion, the introduction is globally sound. The material and methods section provides all necessary information on collected data and used analytical methods (but refer to specific comments below). The results are presented in a clear manner, making it easy to follow the descriptions. The discussion section could benefit by including some additional, relevant references (refer to specific comments below).

The figures are straightforward. Nevertheless, I would like to mention that some colleagues prefer to use color-blind-friendly colors (or, alternatively, to use different symbols in addition to color) to make their graphs accessible to everyone. The tables are informative. The data sampling appears reasonable. The supplementary material is ok, but I recommend to think about providing the raw data of the (semi-)landmark coordinates placed on each specimen as well as the R code. For instance, refer to other works published in PeerJ:

- Ascarrunz et al. 2019 *PeerJ* **Supplementary material** “raw landmark data in tps format”, doi: 10.7717/peerj.7476/supp-7 and “**R scripts**”, doi: 10.7717/peerj.7476/supp-8
- Mallet et al. 2019 *PeerJ* **Supplementary material** “raw data tps file”, doi: 10.7717/peerj.7647/supp-9 and “**R code used for the analysis**”, doi: 10.7717/peerj.7647/supp-10

Experimental design

The present study is within the scope of the journal. The methods are sound. The authors explain that they investigate the relation between shell shape and ecology, but I miss some specific hypotheses; in particular, because there are previous studies that examined this relation as well (as correctly mentioned by the authors).

Validity of the findings

The results appear valid and meaningful. We lack the raw data to be able to replicate the analyses, but the intermediate data (results from PCA etc.) are provided in the supplementary material. The paper discusses the limits of the present study. The work could benefit by including some important references (refer to specific comments below).

Specific comments

Overall, this is a very interesting and comprehensive work! I enjoyed reading the manuscript. I do have some suggestions and comments that should be addressed before acceptance.

Abstract

[30 ff] "Principal component analysis (PCA) highlights much overlap between habitat groups. Phylogenetic flexible discriminant analysis (pFDA), on the other hand, suggests differences, but only between highly specialized terrestrial turtles, highly specialized aquatic turtles, […]."

In my opinion, the differences between the extremes are also evident in the PCA. Thus, I would not state "on the other hand". I would recommend to just leave the "on the other hand" out.

Introduction

[56] "The resulting bones of the carapace of a typical turtle are called […]."

Not sure if it is very informative to name the individual bones (at least in its current form) without giving any further information, such as a figure or some other detail, to explain why this is important for the present study.

[78] "Given that correlations appear to exist between shell shape and ecology […]."

Here or maybe at the end of the introduction, I would have expected some precise hypotheses (based on functional assumptions for example). What exactly do you expect from your study?

[123 ff] "The correlations observed among extant turtles are then applied to the Triassic turtles […]."

It's a bit misleading that the Late Jurassic *Plesiochelys bigleri* is not mentioned here.

Material and Methods

[190] […] inguinal buttress (landmarks 6 and 7) […] (Fig. 1)

I am wondering if landmarks 6 and 7 (visible in Fig. 1E) should be shown in Fig. 1C as well? Furthermore, I have the impression that landmark 1 is not positioned exactly in Fig. 1A. Do you mind checking this?

[193] […] twelve semi-landmark curves […] (curves C1 and C2) […]

I suggest to name the curves in figure 1 (as it is done in figure 2). It would then be easier to follow the description in the text.

[193] […] twelve semi-landmark curves […] (curves C1 and C2) […]

Fig. 3, Tab. 1

The reader can imagine that the ecological category numbers ("Ecol 0-4" in table 1 and "Cat0-4" in Table 3) correspond to the webbing types (A-E) displayed in figure 3, but it would be useful to indicate the numbers in figure 3 as well to avoid any misunderstandings. Furthermore, I would avoid writing "Cat" in table 3 because you do not use "Cat" in table 1. It's unnecessary and may confuse some readers.

[235 ff] […] The PCA was computed using the function PlotTangentSpace *in the software package* Geomorph *[…] and the R software and language […]"*

Please consider revising the sentence. *Geomorph* is a package in R.

Results

[275] […] For SET1 (Fig. 6A) […]

Fossils are indicated as diamonds in the legend of figure 6, but shown as stars in some PCA graphs. Please correct that.

[278] […] (negative PCs) […]

Since you're describing PC1 here, I suggest to write "negative PC1 scores" instead in order to be precise. Dito for the other PCA descriptions (SET1-4).

[279] […] categorized by the presence of flippers (4) are scattered […]

I suppose you mean "category 4". I strongly recommend to make this homogenous throughout the whole (!) manuscript (including the tables and images). Refer also to my previous comment on line 193, Fig. 3 and Table 1.

[331] This is perhaps a result of the tear-drop-shaped shells of these taxa.

In my opinion, this sentence should not be part of the results section, but of the discussion section.

Discussion

[408 ff] "Discussion"

The authors should have a look at the following references. In my opinion, they are important to be considered in the present work:

Rivera (2008) Ecomorphological variation in shell shape of the freshwater turtle *Pseudemys concinna* inhabiting different aquatic flow regimes. *Integrative and Comparative Biology*. doi:10.1093/icb/icn088

>> (…) the **carapace and plastron show significant morphological differences** between habitats characterized by slow-flowing (i.e., lentic) and fast-flowing (i.e., lotic) water. (…) Of the two shell components (carapace and plastron), the **carapace shows greater divergence between habitats** (…)

Stayton (2011) Biomechanics on the half shell: functional performance influences patterns of morphological variation in the emydid turtle carapace. *Zoology*. doi: 10.1016/j.zool.2011.03.002

>> **Aquatic turtle shells differ in shape** from terrestrial turtle shells and are characterized by lower frontal areas and presumably lower drag. **Terrestrial turtle shells are stronger** than those of aquatic turtles; **many-to-one mapping of morphology to function** does not entirely mitigate a functional trade-off between mechanical strength and hydrodynamic performance. (…) Given that the shells of terrestrial turtles perform fewer functions than those of aquatic turtles (terrestrial shells are not under selective pressure to improve hydrodynamic performance) (…)

[422] […] possible to recognized two […]

Typo: "recognize" (without the "d")

[492 f] […] of the same primary dataset of shell (SET1) of extant and fossil turtles.

Do you mean “dataset of shell morphology” or maybe “shells”?