Simple shell measurements do not consistently predict habitat in turtles: a reply to Lichtig and Lucas (2017)

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Abstract

Inferring palaeoecology for fossils is a key interest of palaeobiology. For groups with extant representatives, correlations of aspects of body shape with ecology can provide important insights to understanding extinct members of lineages. The origin and ancestral ecology of turtles is debated and various shell or limb proportions have been reported to correlate with habitat ecology among extant turtles, such that they may be informative for inferring the ecology of fossil turtles, including early shelled stem turtles. One recently described method proposes that simple shell measurements that effectively quantify shell doming and plastron width can differentiate habitat classes among extant turtles in linear discriminant analysis, whereby aquatic turtles have low domed shells with narrow plastra. The respective study proposes unorthodox habitat predictions for key fossil turtles, including aquatic lifestyles for the early turtle *Proganochelys quenstedtii* and the meiolaniform *Meiolania platyceps*, and terrestrial habits for the early turtle *Proterochersis robusta*. Here, we show that these published results are the consequence of questionable methodological choices such as omission of species data which do not conform to a preconceived shell shape-ecology association. When these choices are reversed, species measurements for fossils are corrected, and phylogenetic flexible discriminant analysis applied, habitat cannot be correctly predicted for extant turtles based on these simple shell measurements. This invalidates the method as well as the proposed palaeohabitats for fossils.

Key words: turtles, phylogenetic comparative methods, ecomorphology, shell, palaeoecology

Introduction

Lichtig and Lucas (2017) recently proposed a method that allows inferring the habitat palaeoecology of fossil turtles based on simple shell measurements. For this purpose, Lichtig and Lucas (2017) used biplots and discriminant analysis of measurements obtained from extant turtles, in particular sagittal doming (i.e., carapace length to shell height ratio) versus plastral width (i.e., carapace width to plastron width ratio), to establish that shell ratios can discriminate between aquatic and terrestrial turtles. Cursory examination of the figured plot (their figure 3), however, reveals some oddities. For instance, the fossil stem-trionychian *Basilemys gaffneyi* plots as one of the highest-domed turtles, although this species is known for its flat shell morphology (Sullivan et al. 2013). This casts doubt on the primary data of Lichtig and Lucas (2017).

We, here, show that the published dataset of Lichtig and Lucas (2017) has errors, that their statistical analysis exhibits fundamental flaws, and that a corrected phylogenetic statistical analysis of their data cannot support the conclusion of these authors, namely that simple shell measurements can accurately and reliably predict the ecology of living and fossil turtles.

Material and Methods

Illogical fossil measurements in the original data

The tables and supplementary data of Lichtig and Lucas (2017) contain illogical values for a number of turtles. For instance, the measurements provided for the fossil turtle *Basilemys gaffneyi* suggest that its plastron width exceeds the width of the carapace and that its shell height is greater than the carapace length (their table 1). This is likely a result of data having been entered into the wrong column. However, even if the values provided are arranged into a sequence that makes sense for the morphology of *Basilemys gaffneyi* (USNM 11084; i.e., carapace length > carapace width > plastron width > shell height; see Sullivan & Lucas 2015), the datapoint falls at an average doming value for turtles, which contradicts expectations for the species. To produce more accurate values for the genus *Basilemys*, we computed new ratio estimates based on a figured specimen of the species *Basilemys morrinensis* (Mallon & Brinkman 2018). This specimen (CMN 57059) is likely somewhat compressed dorsoventrally,

but the original description states explicitly that the low shell profile of this specimen is consistent with other, relatively uncrushed *Basilemys* shells (Mallon & Brinkman 2018). We also added measurement for a specimen of *Basilemys variolosa* (CMN 8516) based on figures by Langston (1956). This specimen is also likely somewhat compressed, but has also been reported to be relatively undistorted (Mallon and Brinkman, 2018). As a third specimen, we added AMNH FARB 5448, a specimen listed as *Basilemys* sp. by the AMNH but which has been referred to *Basilemys variolosa* (e.g., Brinkman 2003). The specimen includes a near perfectly preserved 3D shell with no apparent taphonomic flattening. The shell is available as a 3D file produced with surface scanning by the AMNH, and provided on the online repository MorphoSource, from which we downloaded it (https://www.morphosource.org/concern/media/000611825).

Other fossil measurement data of Lichtig and Lucas (2017) exhibit similar, non-replicable ratio values, including those for *Proterochersis robusta* (SMNS 17561) and *Proganochelys quenstedtii* (based on multiple specimens). Indeed, some of the values provided in table 1 of Lichtig and Lucas (2017) mismatch those from the supplements (e.g., *Proterochersis robusta* carapace length-height ratio is listed as 1.82 in the table 1 but as 1.39 in the supplements and figure 3). Neither the ratios from table 1 nor the ones in the supplements could be reproduced by us when using the same data sources as listed in Lichtig and Lucas (2017). Thus, we repeated the measurements of Lichtig and Lucas (2017) for *Proterochersis robusta* on the same data source (images in Szczygielski & Sulej 2016) as well as on a 3D model of this specimen (SMNS 17561; Dziomber et al. 2020; available at: https://www.morphosource.org/concern/media/000116495) to produce measurements that reflect the dimensions of the actual specimen (see Table 1). For all analyses below, we used our measurements based on the 3D specimen. We also retrieved alternative measurements for *Proganochelys quenstedtii* (Table 1) based on a 3D model of SMNS 16980 (Dziomber et al. 2020; available at: https://www.morphosource.org/concern/media/000116494). We could, however, verify the shell ratios of Lichtig and Lucas (2017) for *Meiolania platyceps* based on figures in Gaffney (1996; a reconstruction based on AM:F 57984 and 18775), and differences between our and their values for this species are within the range of expected measurement error when basing ratios on published figures.

We added our novel measurements to the supplementary data of Lichtig and Lucas (2017), but we did not cross-check any of the measurements for extant species, as these appear plausible. For plots and analyses, we deleted other fossil turtles with implausible values from the dataset (i.e., *Adocus bossi*, *Denazinemys nodosa*, *Scabemys ornata*, *Thescelus hemispherica*), as we were both unable to re-arrange the values into a meaningful order, but also unable to obtain new measurements. Thus, our dataset includes only five fossil species, for which one species (*Basilemys variolosa*) is represented by two specimens. To graphically show how measurement corrections for fossils result in different placements in the shell doming vs. relative plastral width biplots, our datasheet retains the original values for five fossils from the supplements of Lichtig and Lucas (2017). In addition, the dataset contains the original measurements taken from 213 individuals of 94 extant species of Lichtig and Lucas (2017) (taxonomy following the TTWG 2021).

Table 1. Measurements of key ratios as provided in the supplementary data of Lichtig and Lucas (2017: LL17) and our corrected values. Note that the values for LL17 do not match their table 1 in all instances, as their supplements and tables do not agree. Also note that we use a specimen of *Basilemys morrinensis* and two specimens of *Basilemys variolosa* instead of *Basilemys gaffneyi* (see methods).

Species (specimen used for ratio; source study)	Carapace length–height ratio (sagittal doming)	Carapace width–plastron width ratio	Carapace width–height ratio (coronal doming)
Proganochelys quenstedtii (SMNS 10012 and 17204; LL17)	2.1	2.1	NA
Proganochelys quenstedtii (SMNS 16980; this study)	2.6	1.84	2.79
Proterochersis robusta (SMNS 17561; LL17)	1.39	1.94	NA
Proterochersis robusta (SMNS 17561; this study)	2.0	2.1	1.86
Meiolania platyceps (AM F:57984 and 18775; LL17)	2.0	2.54	NA
Meiolania platyceps (AM F:57984 and 18775; this study)	2.0	2.3	1.55
Basilemys gaffneyi (USNM 11084; LL17)	1.57	1.45	NA
Basilemys morrinensis (CMN 57059; this study)	3.18	1.63	2.39
Basilemys variolosa (CMN 8516; this study)	4.34	1.55	4.2
Basilemys variolosa (AMNH FARB 5448; this study)	3.86	1.62	2.82

Unjustified exclusion of datapoints

Lichtig and Lucas (2017) mention that they discarded several extant terrestrial taxa with relatively flat shells from their plots and analyses because they interpreted them as “outliers” (Lichtig & Lucas 2017: p. 4). As the affected species (i.e., *Malacochersus tornieri*, the pancake

tortoise, and *Homopus boulengeri*, Boulenger's cape tortoise) are valid biological observations of shell shape, we re-inserted them into the dataset. We also assigned habitat ecologies to *Rhinoclemmys areolata* (i.e., terrestrial) and *Rhinoclemmys funerea* (i.e., aquatic) (Ernst & Barbour 1989), which were previously scored as "not assigned" for their ecologies. We furthermore corrected the habitat preference of *Malacochersus tornieri* from "aquatic" to "terrestrial". Using this corrected dataset, we reproduced versions of the original plot of Lichtig and Lucas (2017: their figure 3) based on specimen-level data as well as species means. We additionally created a plot that uses coronal doming (i.e., carapace width divided by carapace height) as an alternative doming variable, as this is the more typical measure of doming used in the turtle literature (e.g., Benson et al. 2011; Dziomber et al. 2020).

Comparison of our sagittal doming plots with the figure 3 of Lichtig and Lucas (2017) suggests that at least one aquatic turtle species is absent from their plot although it is part of the supplementary file that forms their data basis. As only about 100 data points can be discerned from their plot, we presume it shows species means for taxa with multiple measurements, whereas their figure caption suggests that the data correspond to specimens, of which there should be 225 according to their supplements (250 according to their figure caption). Nonetheless, one aquatic turtle seems to have been omitted from the plot completely. Specifically, the mean species values for the aquatic box turtle (*Terrapene coahuila*) are 1.29 for the carapace length to height ratio and 2.1 for the carapace width to plastron width ratio, but no aquatic datapoint is found at these coordinates. Indeed, as this data point should be located within the area of the graph only occupied by terrestrial species, we suspect that it was omitted as yet another "outlier". This is not reported as such, although the values for *Terrapene coahuila* are discussed as "odd" and "inaccurate" (Lichtig & Lucas 2017: p. 6).

Re-analysis of corrected original data

Lichtig and Lucas (2017) performed a linear discriminant analysis to test if extant species can be correctly classified as "aquatic" or "terrestrial" based on their shell measurements. However, as noted above, they removed numerous "outliers" from their analysis (i.e., turtles that do not conform to an "aquatic species have low domed shells" association). Besides the fact that these

species should not have been removed from analysis, we note that the appropriate statistical treatment of species data are phylogenetic comparative methods due to phylogenetic autocorrelation (Felsenstein, 1985). Here, we performed phylogenetic flexible discriminant analysis (pFDA; Motani & Schmitz 2011) on the relationship of sagittal as well as coronal doming and relative plastral width using our measurement-corrected version of the Lichtig and Lucas (2017) dataset. This was done in R statistical environment (R Core Team 2021).

pFDA allows to test if a predictor (here, the relationship of shell measurement ratios) can correctly discriminate between known ecologies of a training dataset. Thus, the training dataset only includes extant species. If the training dataset is successful in discriminating between ecologies, pFDA can further be used to predict unknown ecologies based on the predictor (Motani & Schmitz 2011, Close & Rayfield 2012; Angielczyk & Schmitz 2014; Choiniere et al. 2021; Fabbri et al., 2022; Hand et al. 2023; Leavey et al. 2023; Lowi-Merri et al. 2023; see Foth et al. 2019, Stayton 2019, and Hermanson et al. 2022 for turtle examples), such as palaeoecology from fossil shell measurements. The analysis thus basically tests if simple shell ratio measurements can indeed be used to predict habitat ecology of turtle species.

Phylogenetic comparative methods require a time scaled phylogeny. We used trees from Thomson *et al.* (2021), who provided a posterior sample of 100 trees from their Bayesian node-dating analysis of molecular sequence data, which represent different time-scaled trees of the same topology. We used the “bind.tip” function of the ape v.5.0 package (Paradis & Schliep 2019) and the “date_nodes” function of Claddis 0.6.3 (Lloyd 2016) to add the five fossil species using a minimum branch length argument of 1 Ma (Laurin 2004) and published stratigraphic ages of the fossils. Hereby, *Proterochersis robusta* is used as the earliest branching testudinatan from our sample, following phylogenetic studies that include the latest anatomical insights from *Proterochersis robusta* (Szczygielski & Sulej, 2016, 2019). *Proganochelys quenstedtii* and *Meiolania platyceps* were added as successively more crownwardly placed stem turtles, following the consensus topology across multiple studies (e.g., Sterli et al. 2015; Joyce et al. 2016; Joyce 2017; Evers & Benson 2019). The species of *Basilemys* were added as sister taxa onto the stem of *Trionychia*, following the generally accepted position of these turtles (e.g., Brinkman 1998; Joyce et al. 2016). As phylogenetic comparative methods use one specimen per

species, we selected the well-preserved AMNH FARB 5448 to represent *Basilemys variolosa*. For extant species, we used species means as was already done by Lichtig and Lucas (2017). We performed 100 pFDA replicates based on the posterior sample of 100 trees from Thomson *et al.* (2021). This procedure allowed us to obtain a distribution of posterior probabilities (PPs) of predicted habitats for the fossils. In all cases, all categories were assigned equal prior probability, as this decreases posterior misidentification rates (Motani & Schmitz 2011). The robustness of the predictions was analyzed based on a two-factor rationale, inspecting (i) the success rates of predicting known ecological categories for extant turtles, whereby we label success of >75% as good and >90% as very good; and the (ii) the median PPs of each predicted habitat, whereby a PP > 75% is considered high and PP>90% very high. This is conservative, as any PP > 50% indicates the presence of an estimated trait. In addition, for the prediction of fossils, we counted the number of times each taxon was predicted as having a specific habitat (e.g., Fabbri et al. 2022), whereby high numbers indicate consistent predictions regardless of the posterior probability. All supplementary data and R scripts are provided in GitHub (https://github.com/G-Hermanson/Reply_shell_measurements_LL2017).

Results

Changes in morphospace occupation

Biplots of shell doming vs. relative plastron width using the corrected dataset of Lichtig and Lucas (2017) show that terrestrial turtles, on average, have high domed shells and relatively broad plastra, whereas aquatic turtles, in general, show the opposite relationship. This is true regardless of whether shell doming is measured sagittally (i.e., as carapace length–height ratio; Fig. 1A, C) as was done by Lichtig and Lucas (2017), or by the more commonly used coronal doming (i.e., carapace width–height ratio; Fig. 1B, D). Overall, extant and fossil species have similar distributions in all plots, indicating that the choice of how to measure doming has little impact at least on the graphical distribution of data points. The area of ecological overlap has nearly the same extent along the doming axes in the plots that use species means (Fig. 1C–D) and in the plots using specimen-level data (Fig. 1A–B), although the species mean data causes a lesser density of high-domed aquatic turtles. This is caused by only a few species, such as *Cuora*

amboinensis, for which the measured specimens have a relatively large range of doming values.

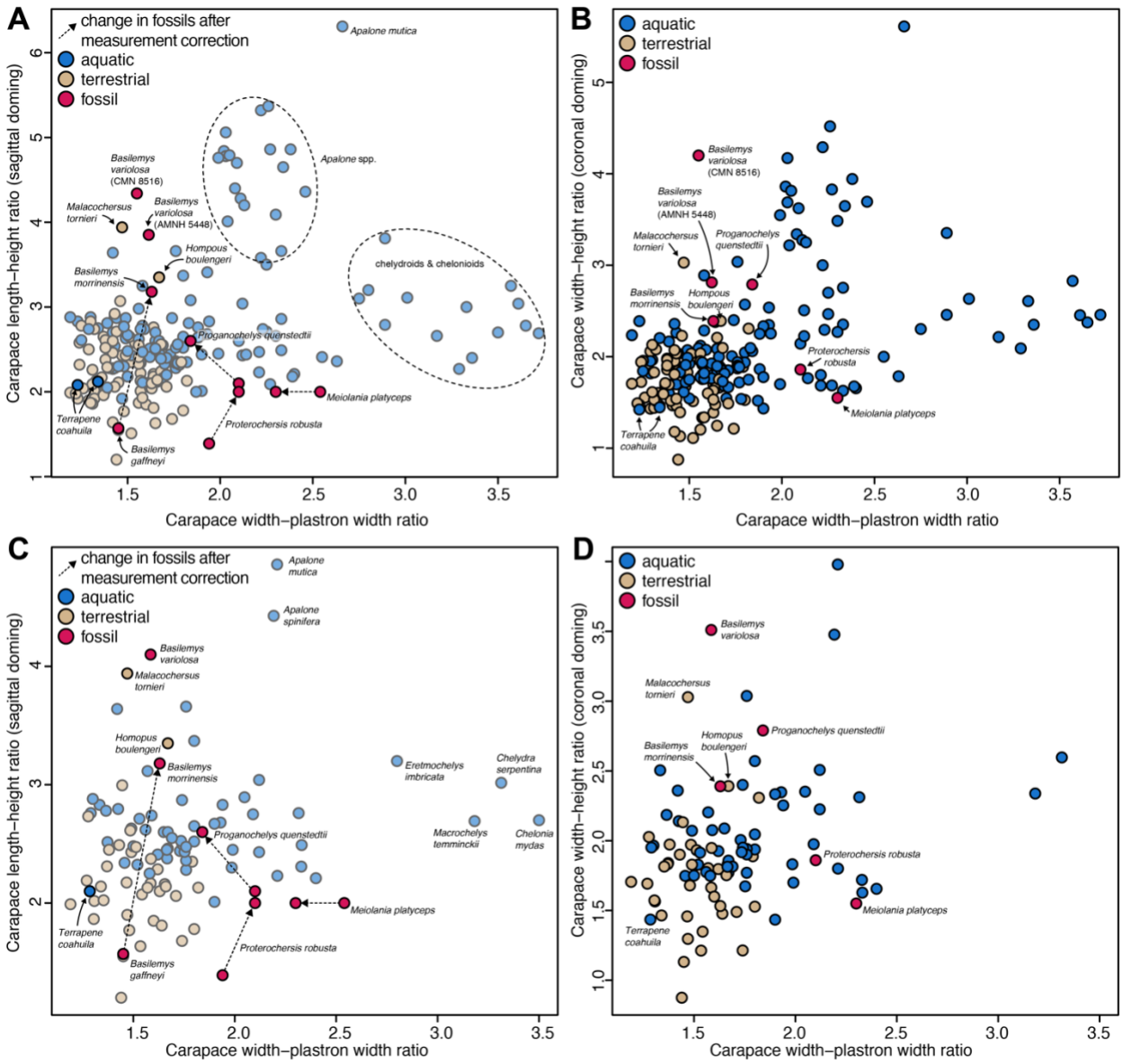

Figure 1. Plots of shell doming against relative plastral width. **A**, using sagittal doming, as in Lichtig and Lucas (2017), on the specimen level. **B**, using coronal doming, on the specimen level. **C**, using sagittal doming, as in Lichtig and Lucas (2017), but using species means for species with multiple individuals. **D**, using coronal doming, using species means. Note that most datapoints in A and C are shown as transparent, to highlight the positions of fossils and previously omitted extant taxa. Fossil datapoint pairs represent original (i.e., uncorrected) values provide by Lichtig and Lucas (2017) and corrected versions of the same species or closely related species in the case of *Basilemys* (see methods), for which the arrow shows the shortest possible change in morphospace. A version of this plot with numbers that correspond to species, and a key can be found in Supplementary Figure 1.

The ecological distribution of data points in all of our corrected plots is consistent with the general pattern reported by Lichtig and Lucas (2017). However, our plots show a graphically much larger area of overlap between ecological groups of turtles (Fig. 1A, C). This is mostly attributable to the fact that the revised dataset includes all explicitly or non-explicitly removed outliers, including the terrestrial *Malacochersus tornieri* and *Homopus boulengeri*, which plot among aquatic turtles, or the aquatic *Terrapene coahuila*, which plots among terrestrial turtles. Despite the large overlap of ecologies, some regions of the morphospace are exclusively occupied by aquatic turtles. For example, species of the trionychid softshell genus *Apalone* strongly expand the morphospace along high values of the doming axis (i.e., extremely low shell morphologies). The morphospace expansion of aquatic turtles toward low relative plastron widths is caused by chelydrids (i.e., *Macrochelys temminckii* and *Chelydra serpentina*) and chelonioids (i.e., *Chelonia mydas* and *Eretmochelys imbricata*) (Fig. 1).

Correction of measurements for the fossils we retained from the original study (Lichtig & Lucas 2017) also changes their positions among the data population for the sagittal doming plots (Fig. 1A, C). *Proterochersis robusta* moves from a position close to predominantly terrestrial species into an area of the plot where exclusively aquatic taxa are found, caused by its low relative plastron width. *Proganochelys quenstedtii* moves along the doming axis into a region of the plot with intermediate levels of doming. Although predominantly surrounded by aquatic turtles, *Proganochelys quenstedtii* plots at the edge of the area of greatest ecological overlap. *Meiolania platyceps* plots in a position along the relative plastral width axis that is otherwise only populated by aquatic turtles, consistent with Lichtig and Lucas (2017). Our datapoints for *Basilemys morrinensis* and *Basilemys variolosa* plot in complete opposite ends of the doming axis of the plot than the *Basilemys gaffneyi* datapoint of Lichtig and Lucas (2017), highlighting the errors associated with the *Basilemys gaffneyi* measurement provided in Lichtig and Lucas (2017). Variation between the three novel *Basilemys* specimens included could represent individual or taxonomic or taphonomic differences in relative doming. Nevertheless, given the good preservation state of these fossils, our datapoints indicate the low doming shape of the carapace that has also been reported for the genus in general (e.g., Langston 1956;

Sullivan et al. 2013; Mallon & Brinkman 2018). Although this region of the plot is predominantly populated by aquatic turtles, it also includes terrestrial tortoises with relatively low domed shells (i.e., *Malacochersus tornieri* and *Homopus boulengeri*), which had been omitted by Lichtig and Lucas (2017).

Analysis of linear shell measurements

The data point distributions in our biplots (Fig. 1) should, in our view, not be seen as hypothesis tests of the ecologies of these turtles, which can only be done if the discriminating strength of the relationships depicted are tested with phylogenetic comparative methods. Our respective phylogenetic Flexible Discriminant Analysis indicates that the two ecological categories (i.e., aquatic and terrestrial) cannot be differentiated based on the relationships of sagittal or coronal doming and relative plastral width. Although success rates for predicting aquatic ecology are high (for sagittal doming a median value of 95.6% across 100 trees; for coronal doming consistently 95.6% across 100 trees), this is contrasted by zero-success rates for predicting terrestrial ecology for sagittal doming (median of 0% across 100 trees) as well as for coronal doming (consistently 0 across 100 trees). This amounts to an overall median success rate for predicting the correct ecology of 63.0% for sagittal doming and 63.0% for coronal doming, but also means that every turtle is predicted to be aquatic, which is not very helpful. This is confirmed by all five fossil species being predicted to be aquatic, with high posterior probabilities for both sagittal doming (*Proganochelys quenstedtii* PP_{median}= 99.1%; *Proterochersis robusta* PP_{median} = 99.0%; *Meiolania platyceps* PP_{median} = 79.3%; *Basilemys morrinensis* PP_{median} = 78.7%; *Basilemys variolosa* PP_{median}= 84.3% across 100 trees) and coronal doming (*Proganochelys quenstedtii* PP_{median}= 99.6%; *Proterochersis robusta* PP_{median} = 99.5%; *Meiolania platyceps* PP_{median} = 80.8%; *Basilemys morrinensis* PP_{median} = 77.1%; *Basilemys variolosa* PP_{median}= 80.1% across 100 trees). Given that the data cannot discriminate between extant aquatic and terrestrial species, the high posterior probabilities for fossil predictions are rendered meaningless, and it must be concluded that the shell measurements used in this study cannot predict ecology in turtles, whereby it does not matter if shell doming is quantified along the long axis or transverse width of the turtle carapace.

Discussion

When examining the Lichtig and Lucas (2017) dataset, we found numerous reproducibility issues. Correcting fossil species measurements, correcting some ecological classifications (e.g., *Malachersus tornieri* was corrected to be terrestrial), including all datapoints (aquatic turtles with high-domed carapaces such as *Terrapene coahuila* were reinserted), and using adequate phylogenetic discriminant analysis returns strongly different results that no further support the central claims of the Lichtig and Lucas (2017) study. Based on our results, the simple carapace measurements proposed by Lichtig and Lucas (2017) are insufficient to characterize or infer ecology of turtles. This is because several extant aquatic and terrestrial turtle species exist that show doming that is atypical for the majority of their ecological guild. In addition, this is because there is a large region of morphological overlap along the gradient of doming.

Although *Proganochelys quenstedtii* plots in an area of the morphospace that is predominantly occupied by aquatic turtles, this should not be misinterpreted as evidence for an aquatic ecology of this fossil species, as was done by Lichtig and Lucas (2017). Contrary to Lichtig and Lucas (2017), *Proterochersis robusta* has no shell dimensions that are uniquely found in terrestrial turtles. The shell shape of *Basilemys* spp. is consistent with aquatic turtles or flat terrestrial turtles, contrary to Lichtig and Lucas (2017) who portray the species as one of the highest domed turtles. *Meiolania platyceps* has shell doming values that are within the range of greatest overlap between aquatic and terrestrial species, but it has a narrow plastron that today is largely observed among aquatic chelydrids and chelonioids, leading Lichtig and Lucas (2017) to the unusual interpretation that *Meiolania platyceps* was an aquatic turtle (contra, e.g., Sterli 2015).

An interesting observation from our data is that all stem turtles included in the dataset (i.e., *Proganochelys quenstedtii*, *Proterochersis robusta*, *Meiolania platyceps*) have relatively narrow plastra, although they are most commonly interpreted to be terrestrial (e.g., Joyce 2017). This seems to be the case also in early stem turtles not included in the dataset, such as *Kayentachelys aprix* (a mesochelydian stem turtle: e.g., Sterli & Joyce 2007), *Naomichelys speciosa* (a helochelydrid stem turtle: e.g., Rollot et al. 2022), and *Mongolochelys efremovi* (a

sichuanchelyid stem turtle: e.g., Joyce et al. 2016). These species have carapace width to plastron width ratios of 1.86, 2.11, 1.94, respectively, such that they would fall further to the right on the relative plastron width axis than the majority of datapoints in our Figure 1. Thus, it is possible that narrow plastra are plesiomorphic for stem turtles. The evolution of narrow plastra should be researched more, especially because the phylogenetic uncertainty surrounding the stem lineages of americhelydians (i.e., chelonioids+chelydroids) and cryptodires more widely (e.g., Zhou & Rabi 2015) means that it is currently not clear if the narrow plastra of some aquatic cryptodires are symplesiomorphic retentions or independent acquisitions of this trait. For example, an independent origin of narrow plastra could have taken place under different selection pressures, whereas the retaining of the feature could mean that narrow plastra in aquatic cryptodires are either not functionally selected against, or an exaptation (Gould & Vrba 1982). Although this is speculative, the initial narrowness of turtle plastra may have been lost during later turtle evolution due to predation pressure of small mammals, which has also been hypothesized to cause the reduction of skull emarginations among post K/Pg baenid turtles (Lyson & Joyce 2009). As already said by Lichtig and Lucas (2017), the narrower gap between plastron and carapace in extant terrestrial turtles shields the soft tissue parts of these turtles, and this constraint may be relaxed in the bottom-walking chelydrids and marine chelonioids.

We strongly advocate researchers not to use plots that are intended to show general distribution patterns of data as a substitute to statistical hypothesis tests, or as an equally informative tool for data interpretation. Plots (biplots as here, or PCA morphospaces) can aid in formulating hypotheses, but these should be formally evaluated using appropriate methods that account for the peculiarities of the data, such as phylogenetic autocorrelation in species data (Felsenstein 1985).

Institutional abbreviations

AM, Australian Museum, Sydney, Australia.

AMNH FARB, American Museum of Natural History, Fossil Amphibians, Reptiles and Birds, New York City, New York, USA.

CMN, Canadian Museum of Nature, Ottawa, Canada.

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

USNM, United States National Museum, Washington, DC, USA.

Code Availability Statement

All R code and primary data tables required to reproduce our analyses and plots are deposited at GitHub (https://github.com/G-Hermanson/Reply_shell_measurements_LL2017).

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