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RESEARCH ARTICLE

Turtle body size evolution is determined by lineage-specific specializations rather than global trends

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Abstract

Organisms display a considerable variety of body sizes and shapes, and macroevolutionary investigations help to understand the evolutionary dynamics behind such variations. Turtles (Testudinata) show great body size disparity, especially when their rich fossil record is accounted for. We explored body size evolution in turtles, testing which factors might influence the observed patterns and evaluating the existence of long-term directional trends. We constructed the most comprehensive body size dataset for the group to date, tested for correlation with paleotemperature, estimated ancestral body sizes, and performed macroevolutionary model-fitting analyses. We found no evidence for directional body size evolution, even when using very flexible models, thereby rejecting the occurrence of Cope's rule. We also found no significant effect of paleotemperature on overall through-time body size patterns. In contrast, we found a significant influence of habitat preference on turtle body size. Freshwater turtles display a rather homogeneous body size distribution through time. In contrast, terrestrial and marine turtles show more pronounced variation, with terrestrial forms being restricted to larger body sizes, up to the origin of testudinids in the Cenozoic, and marine turtles undergoing a reduction in body size disparity after the extinctions of many groups in the mid-Cenozoic. Our results, therefore, suggest that long-term, generalized patterns are probably explained by factors specific to certain groups and related at least partly to habitat use.

KEYWORDS
ancestral states estimation, Cope's rule, evolutionary models, Testudinata

TAXONOMY CLASSIFICATION
Evolutionary ecology

1 | INTRODUCTION

Organisms have evolved a remarkable disparity of body plans, sizes, and functions (Smith et al., 2016), and the relationship between phenotypic evolution and species diversification is a widely discussed subject in evolutionary biology (e.g., Cooney & Thomas, 2021; Stanley, 1973). Body size in particular has been shown to affect several traits in organisms, especially life history (Brown et al., 1993;

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White et al., 2022), metabolic rates (Blanckenhorn, 2000; Clauss et al., 2007; D'Amico et al., 2001), and ecology (Brown & Maurer, 1986; Smith et al., 2018; White et al., 2007). For such reasons, the topic has always intrigued researchers, and its role in microevolution (i.e., natural and artificial selection) and macroevolution (e.g., acquisition of new traits or production of ecological opportunities) has been extensively debated (Blanckenhorn, 2000; Maurer et al., 1992; Peters, 1983; Schmidt-Nielsen & Knut, 1984; Stanley, 1973).

The evolution of body size is commonly explained in the light of different hypotheses that attempt to elucidate patterns of disparity, such as Cope's rule (or Deperet's rule; Stanley, 1973), a hypothesized tendency lineages to evolve toward larger body sizes (Cope, 1896). Although directional trends of increasing body size have been identified in a few groups, including medium- to large-bodied mammals (Alroy, 1998) and pterosaurs (Benson et al., 2014), non-directional patterns are present in many other groups (Benson et al., 2018; Godoy et al., 2019; Laurin, 2004; Moen, 2006). The generalization of hypothesized evolution toward large body sizes has also been questioned, because there is no apparent need for selection to produce ever larger sizes in most lineages (Gould, 1988).

In spite of the presence of hypotheses to explain evolutionary variation of body size in ectothermic vertebrates, few groups have been studied in a comprehensive manner (but see Gearty & Payne, 2020; Godoy et al., 2019; Heim et al., 2015; Smith et al., 2016), with most studies focusing on groups of overall higher metabolic rates, such as mammals and dinosaurs, including birds (Benson et al., 2014, 2018; Cooper & Purvis, 2010; Cullen et al., 2020; Gearty et al., 2018; Kubo et al., 2019; Raia & Meiri, 2011). Turtles, in particular, have a rich fossil record and relatively stable phylogenetic relations, which provide a reliable framework for macroevolutionary studies. The presence of fossils is particularly important because the inclusion of deep-time data can have a large effect on the outcomes of macroevolutionary analyses.

Turtles include 357 living species (Rhodin et al., 2021), but the fossil record of crown-group Testudines, and that of the more inclusive group Testudinata, reveals a much richer history (Gaffney et al., 2006; Joyce et al., 2013). The early evolution of the turtle stem-lineage is thought to have occurred in terrestrial habitats (Joyce, 2017; Joyce & Gauthier, 2004; Lautenschlager et al., 2018; Scheyer et al., 2022; Scheyer & Sander, 2007), but aquatic habits evolved toward the crown group, and represents the ancestral condition for Testudines (Joyce, 2017; Joyce & Gauthier, 2004; Sterli et al., 2018). Therefore, possibly reflecting the different habitats occupied through time (although not only for that reason), the group shows considerable morphological disparity in their limbs, skull, carapace shape, and body size (Benson et al., 2011; Dickson & Pierce, 2019; Foth et al., 2017; Hermanson et al., 2022; Jaffe et al., 2011; Joyce & Gauthier, 2004; Lautenschlager et al., 2018; Vlachos & Rabi, 2018).

Considering the relatively low extant diversity of turtles, particularly when compared to mammals, birds, or squamates, the body size disparity of the group is striking. The smallest living testudine, *Homopus signatus*, has an adult carapace length of about 100 mm, and the largest one, *Dermochelys coriacea*, reaches more than 2200 mm (Rhodin et al., 2021). Furthermore, fossils display an even broader range of body sizes, including the South American *Stupendemys geographicus*, with a carapace length of more than 2800 mm (Cadena et al., 2020). This emphasizes the importance of including the available fossil diversity when characterizing patterns of body size evolution in Testudinata (and see Finarelli & Flynn, 2006; Fritz et al., 2013), which has been largely disregarded in most previous attempts (Eastman et al., 2011; Jaffe et al., 2011; Moen, 2006; Uyeda & Harmon, 2014).

Using data from living species only, previous studies presented several hypotheses to explain the observed body size variation of turtles. For example, it has been suggested that such variation is intrinsically related to habitat, with marine species and island tortoises usually possessing larger sizes than freshwater and mainland taxa (Jaffe et al., 2011). This resembles the large body size attained by marine mammals (e.g., Gearty et al., 2018) and, in some aspects, the "island rule" seen in some mammals, reptiles, and birds (Lomolino, 2005). However, Uyeda and Harmon (2014) analyzed turtle body size using unconstrained evolutionary models and suggested that the scenario for turtle optimal body size is more complex than simple differences in habitats, with multiple macroevolutionary body size shifts along the tree. Furthermore, analysis of tortoise (Testudinidae) body size, including fossils, did not find support for the island effect (Vlachos & Rabi, 2018). Moen (2006) tested for evolutionary trends in extant cryptodires, but found no support for directional body size evolution. Moreover, it is not currently clear how temperature influenced long-term body size patterns in turtles, with ongoing discussion about the group following overall rules such as a latitudinal gradient, with larger body sizes seen in colder regions (Angielczyk et al., 2015; Ashton & Feldman, 2003). Yet, except for Vlachos and Rabi (2018) and Sterli et al. (2018), these hypotheses have yet to be tested in a framework including both extinct and extant taxa. In this study, we compiled the largest body size dataset ever assembled for Testudinata, which was used to investigate the tempo and mode of body size evolution in the group, as well as test for possible biotic and abiotic drivers.

2 | METHODS

2.1 | Body size data

Straight-line maximum dorsal carapace length (SCL) was used as a proxy for turtle body size (Jaffe et al., 2011). Aiming to maximize sampling, we also used linear regressions to estimate SCL from the ventral skull length (measured from the rostral tip of the premaxillae to the caudal tip of the occipital condyle) for some specimens lacking carapace. About 7.5% of the SCL data in our dataset was estimated from the ventral skull length. Measurements were collected from photographs (personal archive or the literature), using software ImageJ (Schneider et al., 2012). The final dataset includes body

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size data for 795 taxa, considerably more than in previous studies (e.g., Angielczyk et al., 2015 = 245 taxa; Jaffe et al., 2011 = 226 taxa; Moen, 2006 = 201 taxa; Vlachos & Rabi, 2018 = 59 taxa). In addition, we also collected habitat preference and chronostratigraphic information for these same taxa using the literature and the Paleobiology Database (PBDB).

2.2 | Supertree construction and time calibration

To account for major uncertainties within the phylogenetic relations of the main groups of Testudinata, two informal supertrees were manually assembled using Mesquite version 3.61 (Maddison & Maddison, 2018). These were based on two phylogenetic hypotheses, Evers et al. (2019) and Sterli et al. (2018), hereafter referred to as "Ev19" and "St18," respectively. The most significant differences between the two supertrees are the positions of Protostegidae and Thalassochelyidia (sensu Joyce et al., 2021). Protostegids are stem-Chelonioidea and Thalassochelyidia are stem-Pleurodira in "Ev19," whereas both groups belong to the turtle stem-lineage in "St18" (in which they are originally represented only by *Santanachelys gaffneyi* and *Solnhofia parsoni*, respectively). Less inclusive groups were positioned based on several additional hypotheses (Table A1). Both supertrees include four outgroup taxa (*Eunotosaurus africanus*, *Eorhynchochelys sinensis*, *Pappochelys rosinae*, and *Odontochelys semitestacea*), which were used for calibration purposes. Each supertree includes a total of 846 taxa, 659 of which are shared with our body size dataset.

Both supertrees were time-scaled using Bayesian inference under a fossilized birth death process (Heath et al., 2014; Stadler, 2010), performed with MrBayes version 3.2.7 (Ronquist et al., 2012). We used R (version 4.0.2; R Core Team, 2021) package *paleotree* (Bapst, 2012) to create a MrBayes command for time-calibration analyses. The function *createMrBayesTipDatingNexus()* allows the use of "empty" morphological matrices in clock-less tip-dating analyses (Bapst, 2012; Gearty & Payne, 2020; Godoy et al., 2019). The two supertrees ("Ev19" and "St18") were entered as topological constraints (i.e., for two separate time-scaling analyses) and data on occurrence times (= tip ages) were obtained from the primary literature and supplemented by the PBDB. We used uniform constraints on the tip ages, and the tree age prior was set as a uniform distribution defined between the Kungurian and Roadian stages of the Permian (283.5 and 268.8 million years ago, Ma), as this would represent a maximum possible age for the origin of the group. All other priors were unaltered from the default setting of the *createMrBayesTipDatingNexus()* function, which were guided by the best practices of Matzke and Wright (2016; see Gearty & Payne, 2020 for more details). Two MCMC runs, with four chains each, were set for 20,000,000 generations, with 25% of the trees discarded as burn-in. Convergence of both runs was verified when values of potential scale reduction factors approached 1.0 and average standard deviation of split frequencies was below 0.01. For both supertrees, we used either the maximum clade credibility (MCC) tree or a set of 10 randomly selected trees from the post-burn-in posterior to perform subsequent analyses.

2.3 | Characterizing body size patterns in Testudinata

The entire body size dataset of 795 taxa was used to construct body size through-time plots. Welch's two sample *t*-tests (Welch, 1947) were used to assess significant changes across different time intervals (i.e., Triassic, Jurassic, Early Cretaceous, Late Cretaceous, Paleogene, Neogene, and Quaternary), focusing on mean body size and disparity, using the standard deviation as a metric of body size disparity. To assess the influence of ecology on the body size distribution, habitat preference information (i.e., terrestrial, freshwater, and marine) was also incorporated into the body size through-time plots. To further test the influence of ecology, we used analysis of variance (ANOVA), performed with R function *aov()*, as well as the RRPP approach (randomizing residuals in a permutation procedure; Adams & Collyer, 2018), which accounts for phylogenetic dependency (i.e., "phylogenetic ANOVA"), performed with the *lm.rrpp()* function, from the R package *RRPP* (Collyer & Adams, 2018, 2019), and using the MCC tree of each supertree ("Ev19" and "St18").

We also tested for the presence of phylogenetic signal in the body size data using the R function *phyloSignal()* (Keck et al., 2016), using 10 randomly selected trees from the posterior distribution of trees of both supertrees. We used 1000 replicates and estimated Pagel's lambda (λ) as our metric of phylogenetic signal given that this index is robust when using trees with poorly resolved branch length information (Molina-Venegas & Rodríguez, 2017; Münkemüller et al., 2012).

To further characterize body size evolution within Testudinata, we used maximum likelihood to estimate ancestral body sizes under Brownian motion (BM), using the *fastAnc()* function of the R package *phytools* (Revell, 2012). Inferred ancestral sates were performed with both the complete supertrees (i.e., using the MCCT trees with all 659 taxa, including fossils and extant species) and a subtree with only extant taxa (i.e., dataset reduced to 312 taxa).

2.4 | Testing for the presence of Cope's rule

To test if Cope's rule played an important role in turtle body size evolution, we fitted different evolutionary models to our body size data in both supertrees. To account for temporal and phylogenetic uncertainties, 10 time-scaled versions of each alternative supertree ("Ev19" and "St18") were used.

We fitted four uniform phenotypic models to our data, starting with the uniform BM model, in which body size undergoes an unconstrained, single-rate random walk along phylogenetic lineages, resulting in diffusive evolutionary expansion (Felsenstein, 1973, 1985; Freckleton & Harvey, 2006). This pattern is consistent with several possible causes, including genetic drift or wandering adaptive

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optima (Felsenstein, 2003), between which genetic drift seems a less likely explanation at macroevolutionary scales. The model has two parameters: sigma squared (σ^2), which indicates evolutionary rate, and the root state of the trait at time zero, sometimes represented by *X(0)* (Felsenstein, 1973).

We also fitted three other uniform models: (1) the "mean_trend" (or "drift") model, which is a modification of the BM model that incorporates a parameter (μ) describing an uniform directional trend along all branches of the phylogeny (Pagel, 2002); (2) the EB model (also known as "ACDC model"; Blomberg et al., 2003), in which lineages experience a burst of rapid increase in trait variation in the beginning of their evolutionary history, followed by a deceleration (Harmon et al., 2010); (3) the Ornstein–Uhlenbeck (OU) model, which incorporates attraction of trait values (represented by the α parameter) toward an optimum (θ) (Butler & King, 2004; Hansen, 1997). In the case of the OU model fitted here, the parameters (α and θ) were not allowed to vary along the tree.

We also fitted 13 non-uniform trend-like models to our data. Unlike uniform "mean_trend" model, these multi-regime models allow the μ parameter—the amount of directional change in a trait through time (Hunt & Carrano, 2010; Pagel, 2002)—to vary along the tree in temporal or node shifts ("time-shift model" and "node-shift model," respectively). We fitted "time-shift" models (which allow shifts in all branches after a determined point in time) allowing the number of shifts to vary from one to three; and "node-shift" models (which allow shifts in some branches) allowing the number of shifts to vary from 1 to 10, resulting in a total of 13 multi-trend models (3 "time-shift" and 10 "node-shift" models). In this study, both uniform trend and multi-trend models were fitted as a representation of the Cope's rule, given that it is described as a multi-lineage directional trend toward larger sizes (Cope, 1887, 1896; Stanley, 1973). Moreover, among mammals, the foundational example of Cope's rule, directional body size evolution is only present in some lineages (e.g., Alroy, 1999), more consistent with a "node-shift" model, with multiple independent origins of directional evolution.

Akaike's information criterion for finite sample sizes (AICc) was used for the selection of the best fit (Akaike, 1974). Model-fitting analyses were performed using R package *geiger* (Harmon et al., 2008) and the scripts made available by Benson et al. (2018) for fitting the multi-trend models, using the R packages *mnormt* (Azzalini & Genz, 2022), *ape* (Paradis & Schliep, 2019), *geiger* (Harmon et al., 2008), *phytools* (Revell, 2012), *phangorn* (Schliep, 2011), and *surface* (Ingram & Mahler, 2013).

2.5 | Influence of paleotemperature

We used regressions to test for the possible influence of global paleotemperature on turtle body size (795 taxa). As a proxy for paleotemperature, we compiled $\delta^{18}O$ data (lower $\delta^{18}O$ values indicate higher environmental temperature) from two different sources. First, we used tropical isotopic data collected in tropical regions by Prokoph et al. (2008), who assembled isotopic information from marine organisms, extending from Precambrian to recent. Furthermore, we also used global paleotemperature data from Zachos et al. (2008), which compiled information about isotopic ratios in foraminifer shells from the Maastrichtian to the recent. We tested for correlation between both temperature curves and our body size indices, including maximum, minimum, and mean body size, as well as body size disparity (= standard deviation).

Correlation between body size data and paleotemperature was initially assessed using ordinary least squares. In addition, to avoid potential issues created by temporal autocorrelation, we used generalized least squares with a first-order autoregressive model incorporated (tsGLS; Fox & Weisberg, 2018), using the R package *nlme* (Pinheiro et al., 2022). The data were divided into time intervals, using approximately equal-length (~9 million years) stratigraphic time bins (from Mannion et al., 2015). For each time bin, we calculated body size indices (disparity [= standard deviation], maximum, minimum, and mean body size) and weighted mean $\delta^{18}O$ values using R package *disparity* (Guillerme, 2018).

The figures presented by this study were made using the R packages *palaeoverse* (Jones et al., 2023) and *deeptime* (Gearty, 2023).

3 | RESULTS

3.1 | Inferred ancestral states

Inferred ancestral states based on both supertrees ("Ev19" or "St18"; Figure A3 and Figure 1) show similar results. For this reason, the description below is based solely on "St18" (Figure 1).

When fossil taxa are included in the analysis, ancestral size estimates for most major (= more diverse) turtle subgroups (e.g., Testudines, Pleurodira, Chelidae, Pelomedusidae, Cryptodira, Trionychidae, and Testudinidae) were broadly similar to one another, with SCL values between 500 and 230 mm (Figure 1c). Similar ancestral values are also seen among stem-turtles, with paracryptodires remaining within approximately this body size range throughout their evolution and meiolaniids increasing their body size over time, from an ancestral body size estimated in 645 mm (Figure 1). Among pleurodires, several extinct branches splitting before the origin of Podocnemididae show smaller body sizes (between 100 and 250 mm; Figure 1a,c), although the estimated ancestral body size for Podocnemididae is larger (between 300 and 500 mm; Figure 1c). Within Cryptodira, crown-groups Testudinidae, Geoemydidae, and Emydidae have similar ancestral body sizes (about 250 mm; Figure 1c). Chelonioidea show ancestral body sizes above 500 mm, and Kinosternidae was one of the few main clades with an estimated ancestral body size close to (or slightly above) 200 mm.

The inclusion of fossils affects ancestral body size estimate for most major lineages (compare square symbols [ignoring fossils] to circles [including fossils] in Figure 1c). No specific directional influence is noted when paleontological data are included. For some groups (e.g., Chelidae, Podocnemididae, Emydidae, Geoemydidae), the inclusion of extinct taxa results in a slight increase in estimated

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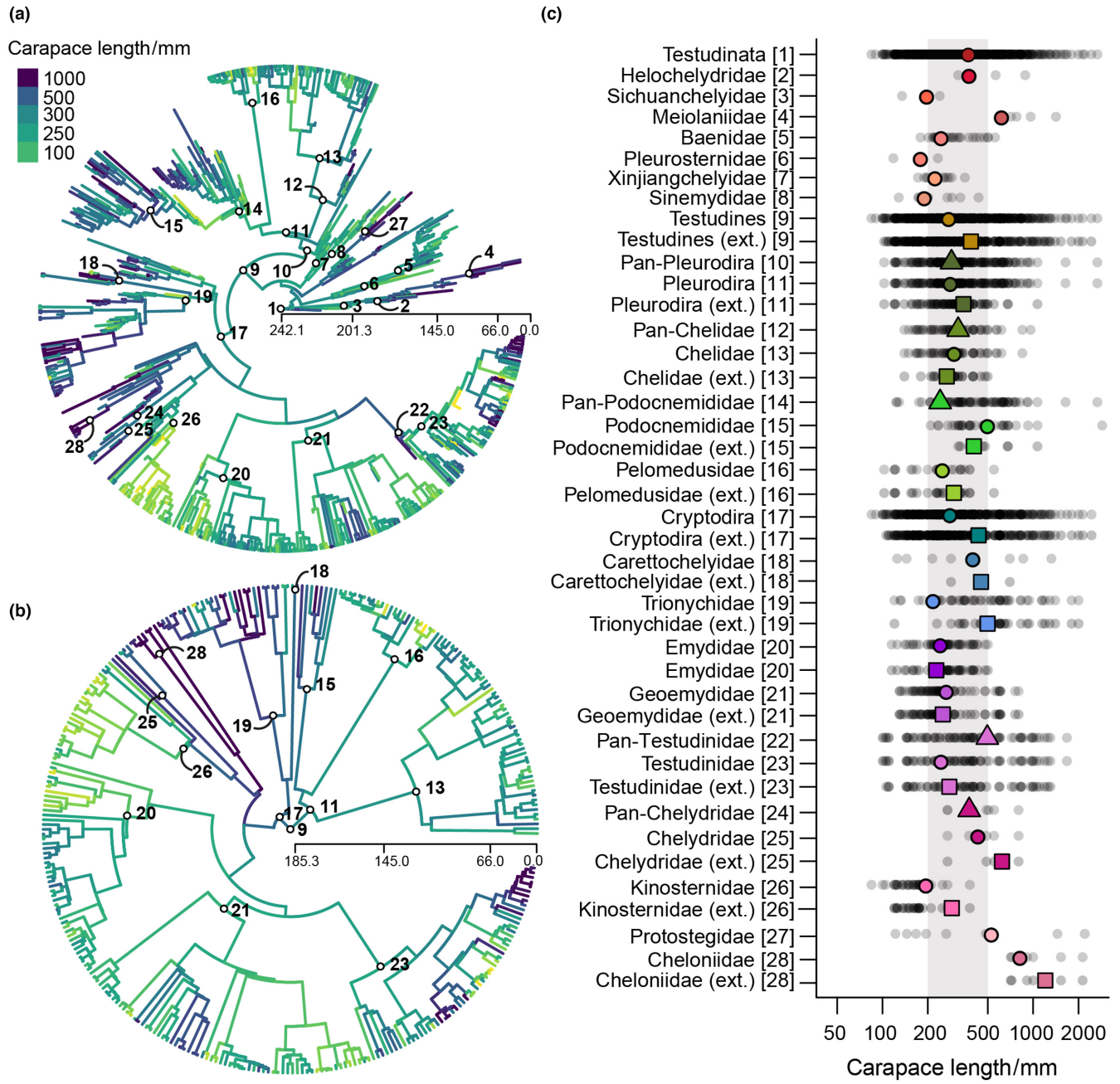

FIGURE 1 Ancestral body sizes ($\log_{10}$ maximum dorsal carapace length in millimeters) mapped onto Testudinata phylogeny ("St18"), with (a) complete tree and (b) extant-only subtree. Ancestral body size for different taxonomic groups (c); small gray dots indicate all taxa within that lineage; colored triangles represent the ancestral estimates of stem-groups; circles represent ancestral estimates of the crown groups; and squares represent ancestral estimates of the crown groups without the fossil taxa. Gray area indicates sizes between 200 and 500 mm. The numbers indicate the same groups in a–c.

body sizes, whereas for others (e.g., Pelomedusidae, Trionychidae, Testudinidae, Chelydridae, Kinosternidae, Cheloniidae), a decrease is observed. The magnitude of this effect varies; the largest changes were seen in the nodes circumscribing Cryptodira, Trionychidae, Chelydridae, Kinosternidae, and Cheloniidae (Figure 1). It is worth noting that even a slight increase in fossil sampling changed the estimates in relation to previous studies. For instance, the ancestral body size for Pan-Testudinidae—based on 78 taxa (53 living and 25 extinct)—is 496.3 mm. Larger than the 370 mm estimated by Vlachos and Rabi (2018), which included 59 taxa (23 living and 36 extinct). Moreover, our ancestral body size estimate for Testudines (345 mm) is smaller than that estimated by Sterli et al. (2018; 359 mm), whereas our Testudinata ancestral body size is much smaller (396 mm, in comparison to 570 mm estimated by Sterli et al., 2018). More importantly, however, some similar patterns are observed between our results and those by Sterli et al. (2018), such

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as the body size increase seen in Podocnemididae and the decrease seen in Kinosternidae.

3.2 | Model fitting

The AICc scores for all the evolutionary models fitted to the turtle trees and body size data show an overwhelmingly stronger support (i.e., lower AICc values) for the uniform OU model, even when compared to the non-uniform multi-trend models. Consistently, this stronger support for the OU model was found when using both "Ev19" and "St18" topologies (Table 1). These results rule out the presence of trend-like processes (either uniform or multi-trend) in the body size evolution of Testudinata, at least when the entire tree is considered.

3.3 | Correlation with paleotemperature

No significant correlation was observed between global paleotemperature and mean, minimum, or maximum body size of Testudinata through time (Table A2). However, we did find a significant, but weak correlation between body size disparity (= standard deviation of body sizes) and paleotemperature (Table 2; Figure 2), with disparity increasing at lower temperatures (i.e., higher $\delta^{18}O$ values). Although significant, this correlation is relatively weak when palaeotemperature data from Prokoph et al. (2008) are used, but it becomes slightly stronger when using data from Zachos et al. (2008), which is restricted to the Late Cretaceous-Recent time interval. This may suggest that the influence of environmental temperatures on turtle body size was stronger during the Cenozoic.

3.4 | Differences among ecological habitats

Freshwater is the most common habitat occupied by turtles from the Jurassic onwards, and this category is therefore the most influential to the aggregated pattern of turtle body size variation through time. No significant changes in either disparity or mean body size of freshwater turtles occurred since the Late Cretaceous (Figure 3b,d). A significant increase in mean body size in freshwater turtles was identified between the Early (234 mm) and the Late Cretaceous (346 mm) (p-value = .001146). In general, freshwater turtles are more frequently represented among the smallest body sizes, and only rarely among the largest ones (Figure 3b).

Diversity in terrestrial turtles is low until the Paleogene, when the first tortoises (Testudinidae) appear in the fossil record (Figure 3a). The mean body size of terrestrial turtles is consistently larger than that of freshwater species through time, except during the Neogene (Figure 3d). From the Triassic to the Late Cretaceous, terrestrial turtles experienced a significant increase in mean body size (from 272 to 443 mm; p-value = .02865). However, body size disparity is low, as expected from the low number of species, and the group is mostly represented by medium- or large-bodied forms (Figure 3a).

The first marine turtles appeared at the end of the Jurassic, with body sizes like those of other groups (Figure 3c). There is a noteworthy (although not significant; p-value = .3872) increase in the mean body size of marine turtles from the Jurassic to the Early Cretaceous,

TABLE 1 Results of model-fitting analyses, depicting model parameters and AICc scores for the models fitted to our body size dataset of Testudinata (log_{10} maximum dorsal carapace length) and 10 time-calibrated trees for each of the two initial supertree topologies ("St18," based on the hypothesis of Sterli et al., 2018, and "Ev19," based on the hypothesis of Evers et al., 2019).

Supertree	St18				Ev19			
Parameter	BM	EB	OU	"Best" trend	BM	EB	OU	"Best" trend
AICc	782.09	784.11	96.69	665.15	976.62	978.64	105.28	861.80
σ^2	0.0142	0.0142	0.5833	0.0128	0.0185	0.0185	1.7895	0.432
$X(0)$	474.68	474.68	325.39	411.91	466.66	466.66	324.56	401.61
α	–	–	0.807	–	–	–	1.1089	–
μ_1	–	–	–	0.0023	–	–	–	0.0024
μ_2	–	–	–	−0.7601	–	–	–	–
μ_3	–	–	–	−0.0238	–	–	–	–
μ_4	–	–	–	−0.3237	–	–	–	–
μ_5	–	–	–	−0.7850	–	–	–	–

Note: Models: BM (Brownian Motion model), EB (Early Burst/ACDC model), OU (Ornstein–Uhlenbeck model), and "best" trend (the model with best fit [AICc scores] among the 14 trend-like models fitted [1 uniform and 13 non-uniform models], which in the case of "St18" is represented by the non-uniform trend model with 4 "time-shifts," and in the case of "Ev19" is represented by the uniform trend model). Mean values of model parameters are shown for the 10 time-calibrated trees: σ^2 (sigma squared, the Brownian variance, or rate parameter), $X(0)$ (estimated trait value [back-transformed to mm] at the root of the tree, also known as Z_0; for the OU model, this is the same as the optimum value or θ), α (alpha, the strength of attraction), and μ (the trend parameters, describing a uniform directional trend along all branches of the phylogeny, with the number of parameters varying according to the number of shifts). The mean AICc scores indicate overwhelming support (i.e., lower AICc values) to the OU model over the other models.

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TABLE 2 Results of time series generalized least squares (tsGLS) and ordinary least squares (OLS) regressions using turtle body size disparity and paleotemperature data.

	tsGLS						OLS					
	Phi	p. R^2	AIC	Var.	Coef.	t-Value	p-Value	p. R^2	AIC	Var.	Coef.	t-Value	p-Value
Body size SD	0.701	−.006	−68.168	interc.	0.242	6.508	<.000	−.019	−55.638	interc.	0.261	10.152	<.000
~$\delta^{18}O$ (Prokoph)				$\delta^{18}O$	0.025	1.766	.091			$\delta^{18}O$	0.038	2.240	.036
Body size SD	−0.297	−.001	−52.563	interc.	0.248	38.476	<.000	−.002	−53.951	interc.	0.251	30.528	<.000
~$\delta^{18}O$ (Zachos)				$\delta^{18}O$	0.014	3.811	.005			$\delta^{18}O$	0.012	2.662	.028

Note: Body size disparity (standard deviation of $\log_{10}$ maximum dorsal carapace length in millimeters) and paleotemperature ($\delta^{18}O$ data as a proxy for paleotemperature from two different sources: Prokoph et al., 2008; Zachos et al., 2008) data were divided into time bins (24 time-bins when the Prokoph et al., 2008 $\delta^{18}O$ data were used and 10 time-bins when the Zachos et al., 2008 data were used).
Abbreviations: Coef., coefficient; interc., intercept; p.R^2, Nagelkerke pseudo *R*-squared; SD, standard deviation; Var., variable.

and a small drop in the Late Cretaceous (Figure 3c,d), but the latter interval witnessed the highest variability in body sizes among marine turtles in the series (Figure 3c). After the K-Pg transition, the range of body sizes decreased substantially, although the mean remains similar. After that, from the Neogene to the Quaternary, a significant increase in mean body size (p-value = .003958), from 413 to 1036 mm, was detected for marine turtles (Figure 3c,d).

We found that ecological habitat is significantly linked to body size in turtles using ANOVA (Table 3). However, when the phylogenetic structure of the data is taken into account (using phylogenetic ANOVA; Table 3), this association is only significant for the freshwater and terrestrial ecological categories. Moreover, for all trees tested here, we found a strong phylogenetic signal in body size data ($\lambda > 0.856$; $p < .001$).

4 | DISCUSSION

4.1 | Body size patterns and ancestral estimates: The effect of including fossils

Despite previous controversies (e.g., Patterson, 1981), it has become increasingly clear that the paleontological record is crucial to answer macroevolutionary questions (Fritz et al., 2013; Louca & Pennell, 2020; Quental & Marshall, 2010). In particular, it is well documented that the inclusion of fossils affects the estimation of ancestral states and evolutionary rates (e.g., Puttick, 2016; Slater et al., 2012). Nevertheless, extinct taxa are often neglected in such analyses, having so far been included in only two macroevolution studies of turtle body size (Sterli et al., 2018; Vlachos & Rabi, 2018).

As already noted by Jaffe et al. (2011), examining the evolution of body size in the fossil record of turtles might provide new insights not revealed by previous analyses. Based on a sample of 536 extinct taxa, our study was the first comprehensive attempt in that direction, confirming the impact of including fossils on estimates of both divergence times (Figures A1 and A2) and ancestral body sizes (Figure 1 and Figure A3). The latter has been affected for most lineages assessed here, but to different degrees (Figure 1), with no directional effect on the estimates (Figure 1). This differs from the pattern seen in mammals, for which ancestors have considerably larger body sizes when estimated using fossils (e.g., Finarelli & Flynn, 2006; Finarelli & Goswami, 2013). For mammals, these results were explained by the widespread occurrence of directional evolution toward large body sizes from small ancestors (Alroy, 1999; Smith et al., 2010), a pattern not observed in turtles (see below).

4.2 | Cope's rule and directional trends of body size evolution

We found no evidence for directional patterns of body size evolution in turtles (Table 1), given that none of our trend-like models (either the uniform trend or the multi-trend models) received

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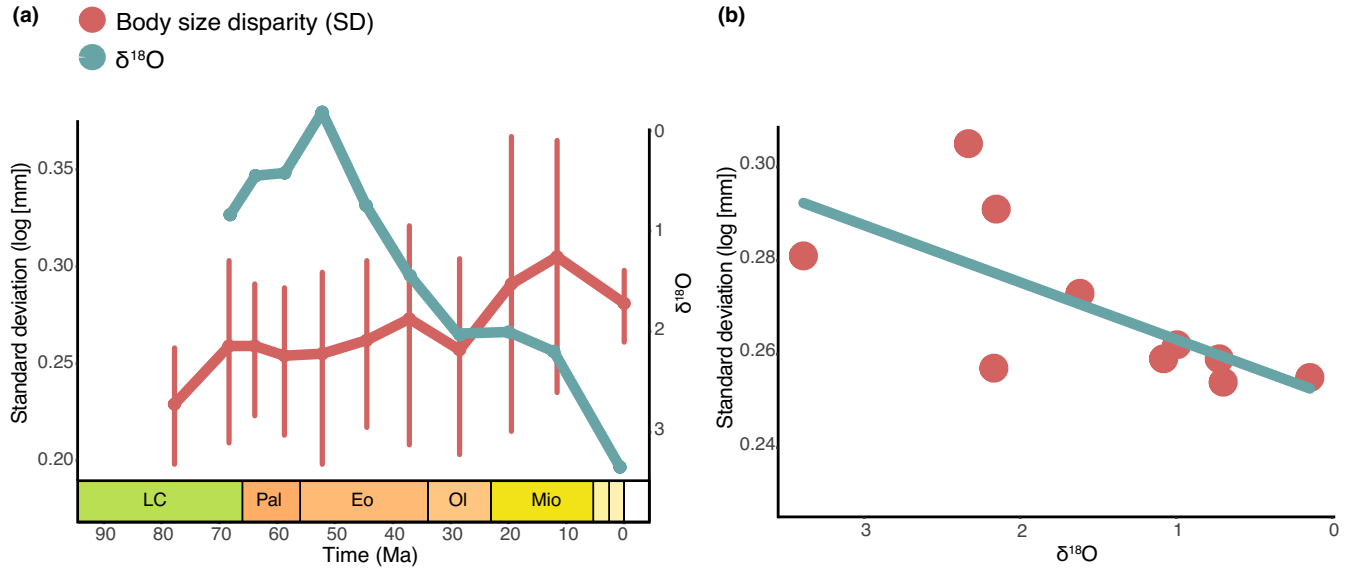

FIGURE 2 (a) Through-time patterns of Testudinata body size disparity (standard deviation of $\log_{10}$ maximum dorsal carapace length in millimeters) and paleotemperature ($\delta^{18}O$ isotopic data from Zachos et al., 2008) during the last ~70 Ma. Error bars were calculated by bootstrapping the disparity data 500 times. $\delta^{18}O$ is used as proxy for paleotemperature and is inversely proportional to temperature. (b) Linear regression (OLS) between turtle body size disparity and $\delta^{18}O$ data (regression results shown in Table 2).

more support than the uniform OU model. This result is consistent with previous investigation by Moen (2006), which also found no support for Cope's rule when analyzing extant cryptodires (even though directional evolution may be difficult to detect on extant-only datasets; Finarelli & Flynn, 2006; Schnitzler et al., 2017; Slater et al., 2012). Therefore, our results provide no support for the hypothesis that Cope's rule explain the evolution of large body sizes in Testudinata. They also add to the growing evidence that directional body size evolution is rare among vertebrates (Benson et al., 2018; Godoy et al., 2019; Huttenlocker, 2014; Sookias et al., 2012), with the exception of mammals and pterosaurs (Alroy, 1998; Benson et al., 2014), once again challenging the generality of Cope's rule.

4.3 | Influence of environmental temperature on turtle body size evolution

The relationship between abiotic factors and body size has been extensively studied, with distinct vertebrate groups being differently affected by them, especially when it comes to comparing endothermic and ectothermic organisms (Angielczyk et al., 2015; Angilletta et al., 2004; Ashton & Feldman, 2003; Mousseau, 1997; Partridge & Coyne, 1997; van der Have & de Jong, 1996; Van Voorhies, 1996). Large-scale trends such as Bergmann's rule (i.e., the tendency of having larger body sizes at higher latitudes within a species) may play an important role for within-species variation of body size in endotherms (Ashton et al., 2000; James, 1970; Zink & Remsen, 1986), and may explain patterns of maximum size during mammal evolution (Saarinen et al., 2014). Yet, results for ectothermic reptiles are less consistent (Angielczyk et al., 2015; Ashton & Feldman, 2003; Mousseau, 1997).

We evaluated the correlation between turtle body size distributions and paleotemperature variation through time. In general, no significant influence of temperature on mean, minimum, or maximum body size in the group was found (Table A2). Similar results were reported for crocodylomorphs, for which no significant correlation between paleotemperature and body size (mean, maximum, and minimum values) was found when the entire group is analyzed, even though a strong association between both variables is observed when only the crown group is considered (Godoy et al., 2019). Therefore, although our results indicate no overall influence of paleotemperature on the through-time distribution of turtle mean, maximum, and minimum body sizes, we cannot rule out an influence of environmental temperatures at smaller temporal and phylogenetic scales. Indeed, environmental temperature has been a commonly proposed explanation for body size variation in different turtle clades and species, particularly affecting disparity, diversity, or distribution of less inclusive groups (e.g., Böhme, 2003; Ferreira et al., 2018; Georgalis & Kear, 2013; Vitek, 2012).

FIGURE 3 Temporal distribution of body sizes ($\log_{10}$ maximum dorsal carapace length in millimeters) in turtles for different ecological habitats. Gray dots represent all taxa, whereas colored dots represent taxa subdivided into three ecological categories. (a) terrestrial taxa (red dots); (b) freshwater taxa (light green dots); (c) and marine taxa (light blue dots). Horizontal gray segments represent the range of occurrence of each taxon; (d) Boxplot showing body size of different ecological categories divided into time intervals. Silhouettes adapted from Jaffe et al. (2011).

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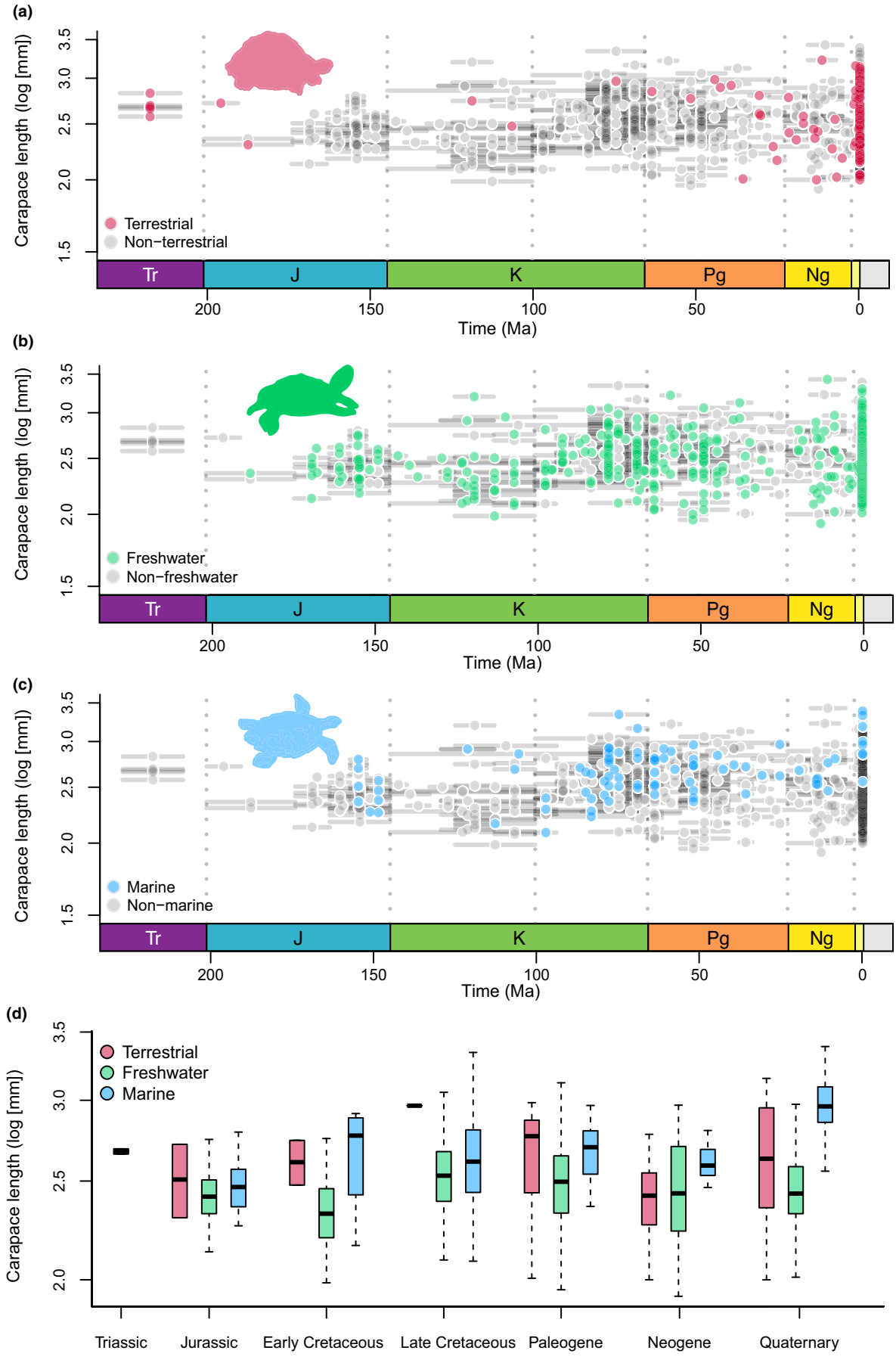

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TABLE 3 Results of ANOVA and PhyloANOVA exploring the relationship between Testudinata body size (log_{10} maximum dorsal carapace length in millimeters) and different ecological categories: terrestrial ($n = 145$), freshwater ($n = 563$), and marine ($n = 87$).

ANOVA results	df	SS	MS	*F*-value	*p*-Value
ANOVA	2	4.77	2.3868	36.55	<.0001*
PhyloANOVA	2	0.0323	0.0161295	1.8106	.109
Pairwise comparison (*p*-values)		**Marine–fresh.**	**Terrestrial–fresh.**		**Terrestrial–Marine**
ANOVA		<.0001*	<.0001*		.502
PhyloANOVA		.801	.04*		.176

Note: Pairwise comparisons between ecological categories also shown.

Abbreviations: df, degrees of freedom; MS, mean squares; SS, sum of squares.

*Significant at alpha = .05.

We did find a significant correlation between paleotemperature and turtle body size disparity (= standard deviation) during the Cenozoic, with periods of higher disparity associated with lower temperatures (or higher $\delta^{18}O$ values; Figure 2). We suggest three potential explanations for this seemingly counterintuitive result. First, low temperatures might have restricted niche availability for turtles and, consequently, driven body size specialization—toward larger or smaller body sizes—to avoid competition, as seen in some extant lineages (Cunha et al., 2020; Pritchard, 2001). Conversely, colder and dryer environments could have increased availability of coastal habitats (by sea level drops), which has been associated with higher diversification rates in turtles (Thomson et al., 2021). Higher species richness might have also led to higher disparity levels in body size. Finally, the significant correlation might be an artifact from the coincidental drop in temperature over the Cenozoic and a continuous expansion in body size in turtles. Disparity constantly increases since the origin of the group, punctuated only by small drops (e.g., in the Oligocene and present time bins, Figure 2). A slow, steady disparity increase has been also noted in cranial morphology by Foth and Joyce (2016), particularly during the Mesozoic in different lineages. That would also explain the stronger correlation with the Zachos et al. (2008) curve—restricted to Cenozoic $\delta^{18}O$ values—in relation to that using Prokoph et al. (2008), which includes the period of increasing temperatures in the Mesozoic. In any case, it seems that environmental temperature did not play a major role in determining large-scale patterns of Testudinata body size variation through time, at least not when considering the entire group.

4.4 | Body size evolution and ecological habitats

Our ANOVA results (Table 3) indicate a significant association between habitat preference and body size in turtles. This is seen in the phylogenetic ANOVA, specifically for freshwater and terrestrial habitats, indicating that evolutionary shifts of habitat correlate with directional evolutionary shifts of body size. Accordingly, through-time body size patterns for distinct habitat categories (Figure 3) can help understanding patterns observed in different turtle subgroups, which emphasizes the importance of independently examining each of the three main turtle ecologies: freshwater, terrestrial, and marine.

Since the Jurassic, most turtles have had freshwater ecologies (Figure 3b; Joyce & Gauthier, 2004), with these turtles keeping a fairly homogeneous body size disparity (= standard deviation) through time (Figure 3b). Their wide and constant disparity of body sizes might be explained by distinct evolutionary scenarios within such habitats (Jaffe et al., 2011), with different species, closely related or not, inhabiting several disparate freshwater environments (Bonin et al., 2006). For instance, different pleurodiran and cryptodiran lineages acquired resistance to estuarine or brackish water (Agha et al., 2018; Bower et al., 2016). Also, closely related taxa occupying the same areas are known to avoid competition through body size divergence, such as extant podocnemidids (Cunha et al., 2020) and trionychids (Pritchard, 2001).

Terrestrial and marine turtles, on the other hand, are represented by fewer lineages, with more restrict evolutionary histories. The earliest turtles were terrestrial, ranging from medium- to large-sized during the Mesozoic (Figure 3a–d). Meiolaniformes is the only of these stem-lineage groups to survive until recently (until the Holocene; Sterli, 2015), displaying large to gigantic body sizes, especially after the Mesozoic. Testudinids—the only extant lineage of terrestrial turtles—appeared in the fossil record during the Paleogene and remained relatively small until at least the end of that period (Figure 3c). The Eocene–Oligocene witnessed a peak of diversity, related to the origin of crown-group Testudinidae (Lourenço et al., 2012; Vlachos & Rabi, 2018), after which the group spread from Eurasia to most of the world. Therefore, the recent high variation in body size within tortoises might be also related to the expansion of occupied habitats (as in freshwater turtles), also associated with specific diversification and extinction dynamics within the group (e.g., Joos et al., 2022).

Extant marine turtles (Chelonioidea) exhibit low disparity, but remarkably large body sizes (Figure 3b), which might be related to morphological adaptations to a pelagic lifestyle, given that other groups of sea turtles (e.g., Thalassochelydia and Bothremydidae) are not as strongly associated with larger sizes and were probably not pelagic. The large size of marine turtles might also be explained by either physiological constraints (e.g., thermoregulation; Mrosovsky, 1980) or the need for higher dispersal abilities associated with migration

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(Jaffe et al., 2011). It has been previously proposed that thermoregulation and other physiological aspects (e.g., lung capacity while diving) play an important role in determining the larger body sizes of aquatic mammals and reptiles (Benson et al., 2012; Davis, 2014; Gearty et al., 2018; Gearty & Payne, 2020; Gutarra et al., 2022; Pyenson & Vermeij, 2016; Williams, 2001), by posing a minimum body size limit on these species. However, in the case of marine turtles, the fossil record shows that smaller species also existed in the past (Figure 3c,d), with *Santanachelys gaffneyi* from the Early Cretaceous of Brazil as one of the oldest and smallest sea turtles (200 mm; Hirayama, 1998). Therefore, in the case of Testudinata, perhaps the lower body size limit imposed by physiological constraints was not as strict as those inferred for other secondarily aquatic tetrapods (e.g., mammals). On the other hand, the shell and the necessity to lay eggs on land possibly pose constraints on the maximum body sizes achieved by marine turtles (Benson et al., 2012), which are, in general, smaller than other Mesozoic marine reptiles and extant cetaceans (Benson et al., 2012; Smith & Lyons, 2011).

Finally, intrinsic factors might also influence body size evolution in turtles. Sterli et al. (2018), for example, suggested that a reduction in size in Mesochelydia (the clade including all post-Triassic turtles)—which is confirmed by our ancestral state estimates (Figure 1)—could be explained by paedomorphic processes, which are also evidenced by other morphological traits. The shell might also constrain the maximum body size of turtles inhabiting terrestrial and semiaquatic environments (Golubović et al., 2017; Lyson et al., 2014). It could hamper turtles from attaining sizes as large as giant mammals and dinosaurs due to a different relation between weight and body size. Moreover, minimum body sizes in turtles are overall larger than that of the smallest lissamphibians, squamates, mammals, and birds. Endothermy could explain the smaller sizes of mammals and birds (Lovegrove, 2017), but not of lissamphibians or squamates. Hence, it is possible that the shell also imposes a lower body size limit to testudinatans.

5 | CONCLUSIONS

Turtle body sizes showed low disparity early in their evolutionary history. They reached substantial disparity only in the Early Cretaceous, concomitantly with the lowest mean body sizes. Habitat preference is only weakly linked to body size variation in turtles. Nevertheless, ecological transitions provide a partial explanation for differences in the body size distribution of turtle subgroups. Freshwater turtles show a constant range of body sizes and higher disparity through time, which might be related to the ecological diversity associated with these habitats. Body size in terrestrial turtles is explained by their ecological diversity, in addition to the higher dispersal ability in giant species. In sea turtles, upper and lower body size limits seem to be associated with physiological (e.g., thermoregulation) and morphological (e.g., the shell) constraints, as well as with adaptations to the pelagic lifestyle during the Quaternary.

We did not find support for a general trend-like process leading to larger body sizes, discarding Cope's rule as an explanation for body size evolution in turtles. Also, we did not find a significant influence of paleotemperature on mean, maximum, and minimum body size. Although we found a significant, moderate correlation between temperature and body size disparity through time, this association might be an artifact caused by a join constant increasing of disparity and continuous drop in temperatures during the Cenozoic.

AUTHOR CONTRIBUTIONS

Bruna M. Farina: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Pedro L. Godoy:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); writing – review and editing (equal). **Roger B. J. Benson:** Methodology (equal); supervision (equal); writing – review and editing (equal). **Max C. Langer:** Funding acquisition (equal); supervision (equal); writing – review and editing (equal). **Gabriel S. Ferreira:** Conceptualization (equal); data curation (equal); project administration (equal); resources (equal); supervision (equal); writing – original draft; writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

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This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://osf.io/a45hv/?view_only=ffa79065eff54a848f17168c11f3e4f6.

DATA AVAILABILITY STATEMENT

The complete dataset, supertrees, and scripts used for the analyses in this study are available on OSF: https://osf.io/a45hv/?view_only=ffa79065eff54a848f17168c11f3e4f6.

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REFERENCES

Adams, D. C., & Collyer, M. L. (2018). Phylogenetic ANOVA: Group-clade aggregation, biological challenges, and a refined permutation procedure. *Evolution*, *72*(6), 1204–1215. https://doi.org/10.1111/evo.13492

Agha, M., Ennen, J. R., Bower, D. S., Nowakowski, A. J., Sweat, S. C., & Todd, B. D. (2018). Salinity tolerances and use of saline environments by freshwater turtles: Implications of sea level rise. *Biological Reviews*, *93*(3), 1634–1648. https://doi.org/10.1111/brv.12410

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. https://doi.org/10.1109/TAC.1974.1100705

Alroy, J. (1998). Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, *280*(5364), 731–734. https://doi.org/10.1126/science.280.5364.731

Alroy, J. (1999). The fossil record of North American mammals: Evidence for a Paleocene evolutionary radiation. *Systematic Biology*, *48*(1), 107–118. https://doi.org/10.1080/106351599260472

Angielczyk, K. D., Burroughs, R. W., & Feldman, C. R. (2015). Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world's turtles. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *324*(3), 270–294. https://doi.org/10.1002/jez.b.22602

Angilletta, M. J., Jr., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, *44*(6), 498–509. https://doi.org/10.1093/icb/44.6.498

Anquetin, J., Püntener, C., & Joyce, W. G. (2017). A review of the fossil record of turtles of the clade Thalassochelydia. *Bulletin of the Peabody Museum of Natural History*, *58*(2), 317–369. https://doi.org/10.3374/014.058.0205

Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, *57*(5), 1151–1163. https://doi.org/10.1111/j.0014-3820.2003.tb00324.x

Ashton, K. G., Tracy, M. C., & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *The American Naturalist*, *156*(4), 390–415. https://doi.org/10.1086/303400

Azzalini, A., & Genz, A. (2022). *The R package 'mnormt': The multivariate normal and 't' distributions (version 2.1.1)*.

Bapst, D. W. (2012). paleotree: An R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, *3*(5), 803–807. https://doi.org/10.1111/j.2041-210X.2012.00223.x

Benson, R. B. J., Domokos, G., Várkonyi, P. L., & Reisz, R. R. (2011). Shell geometry and habitat determination in extinct and extant turtles (Reptilia: Testudinata). *Paleobiology*, *37*(4), 547–562. https://doi.org/10.1666/10052.1

Benson, R. B. J., Evans, M., & Druckenmiller, P. S. (2012). High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS One*, *7*(3), e31838. https://doi.org/10.1371/journal.pone.0031838

Benson, R. B. J., Frigot, R. A., Goswami, A., Andres, B., & Butler, R. J. (2014). Competition and constraint drove Cope's rule in the evolution of giant flying reptiles. *Nature Communications*, *5*(1), Article 1. https://doi.org/10.1038/ncomms4567

Benson, R. B. J., Hunt, G., Carrano, M. T., & Campione, N. (2018). Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology*, *61*(1), 13–48. https://doi.org/10.1111/pala.12329

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology*, *75*(4), 385–407. https://doi.org/10.1086/393620

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution; International Journal of Organic Evolution*, *57*(4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Böhme, M. (2003). The Miocene climatic optimum: Evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *195*(3), 389–401. https://doi.org/10.1016/S0031-0182(03)00367-5

Bonin, F., Devaux, B., & Dupré, A. (2006). *Turtles of the World*. A & C Black.

Bower, D. S., Scheltinga, D. M., Clulow, S., Clulow, J., Franklin, C. E., & Georges, A. (2016). Salinity tolerances of two Australian freshwater turtles, Chelodina expansa and Emydura macquarii (Testudinata: Chelidae). *Conservation Physiology*, *4*(1), cow042. https://doi.org/10.1093/conphys/cow042

Brinkman, D., Aguillon-Martinez, M. C., Hutchison, J. H., & Brown, C. (2016). *Yelmochelys rosarioae* gen. et sp. nov., a stem kinosternid (Testudines; Kinosternidae) from the Late Cretaceous of Coahuila, Mexico. *Paleo Bios*, *33*. https://doi.org/10.5070/p9331030601

Brinkman, D., Rabi, M., & Zhao, L. (2017). Lower Cretaceous fossils from China shed light on the ancestral body plan of crown softshell turtles (Trionychidae, Cryptodira). *Scientific Reports*, *7*, 6719. https://doi.org/10.1038/s41598-017-04101-0

Brown, J. H., Marquet, P. A., & Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *The American Naturalist*, *142*(4), 573–584. https://doi.org/10.1086/285558

Brown, J. H., & Maurer, B. A. (1986). Body size, ecological dominance and Cope's rule. *Nature*, *324*(6094), Article 6094. https://doi.org/10.1038/324248a0

Butler, M. A., & King, A. A. (2004). Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist*, *164*(6), 683–695. https://doi.org/10.1086/426002

Cadena, E.-A., Scheyer, T. M., Carrillo-Briceño, J. D., Sánchez, R., Aguilera-Socorro, O. A., Vanegas, A., Pardo, M., Hansen, D. M., & Sánchez-Villagra, M. R. (2020). The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Science. Advances*, *6*(7), eaay4593. https://doi.org/10.1126/sciadv.aay4593

Cadena, E., & Joyce, W. G. (2015). A Review of the Fossil Record of Turtles of the Clades Platychelyidae and Dortokidae. *Bulletin of the Peabody Museum of Natural History*, *56*(1), 3–20. https://doi.org/10.3374/014.056.0101

Claude, J., Suteethorn, V., & Tong, H. (2007). Turtles from the late Eocene – early Oligocene of the Krabi Basin (Thailand). *Bulletin de La Société Géologique de France*, *178*(4), 305–316. https://doi.org/10.2113/gssgfbull.178.4.305

Clauss, M., Schwarm, A., Ortmann, S., Streich, W. J., & Hummel, J. (2007). A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *148*(2), 249–265. https://doi.org/10.1016/j.cbpa.2007.05.024

Collyer, M. L., & Adams, D. C. (2018). *RRPP: An R package for fitting linear models to high-dimensional data using residual randomization*.

Collyer, M. L., & Adams, D. C. (2019). *RRPP: Linear model evaluation with randomized residuals in a permutation procedure*. R package version 0.4.0.

Cooney, C. R., & Thomas, G. H. (2021). Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, *5*(1), 101–110. https://doi.org/10.1038/s41559-020-01321-y

Cooper, N., & Purvis, A. (2010). Body size evolution in mammals: Complexity in tempo and mode. *The American Naturalist*, *175*(6), 727–738. https://doi.org/10.1086/652466

Cope, E. D. (1896). *The primary factors of organic evolution*. Open Court Publishing Company.

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Cope, E. D. (1887). *The origin of the fittest: Essays on evolution*. Appleton Press.

Cullen, T. M., Canale, J. I., Apesteguía, S., Smith, N. D., Hu, D., & Makovicky, P. J. (2020). Osteohistological analyses reveal diverse strategies of theropod dinosaur body-size evolution. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1939), 20202258. https://doi.org/10.1098/rspb.2020.2258

Cunha, F. L. R., Bernhard, R., & Vogt, R. C. (2020). Diet of an assemblage of four species of turtles (Podocnemis) in the Rio Uatumã, Amazonas, Brazil. *Copeia*, *108*(1), 103–115. https://doi.org/10.1643/CE-18-117

D'Amico, L. J., Davidowitz, G., & Nijhout, H. F. (2001). The developmental and physiological basis of body size evolution in an insect. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *268*(1476), 1589–1593. https://doi.org/10.1098/rspb.2001.1698

Danilov, I. G., Syromyatnikova, E. V., Skutschas, P. P., Kodrul, T. M., & Jin, J. (2013). The First 'True' Adocus (*Testudines*, *Adocidae*) from the Paleogene of Asia. *Journal of Vertebrate Paleontology*, *33*(5), 1071–1080.

Davis, R. W. (2014). A review of the multi-level adaptations for maximizing aerobic dive duration in marine mammals: From biochemistry to behavior. *Journal of Comparative Physiology B*, *184*(1), 23–53. https://doi.org/10.1007/s00360-013-0782-z

Dickson, B. V., & Pierce, S. E. (2019). Functional performance of turtle humerus shape across an ecological adaptive landscape. *Evolution*, *73*(6), 1265–1277. https://doi.org/10.1111/evo.13747

Eastman, J. M., Alfaro, M. E., Joyce, P., Hipp, A. L., & Harmon, L. J. (2011). A novel comparative method for identifying shifts in the rate of character evolution on trees. *Evolution*, *65*(12), 3578–3589. https://doi.org/10.1111/j.1558-5646.2011.01401.x

Evers, S. W., Barrett, P. M., & Benson, R. B. J. (2019). Anatomy of Rhinochelys pulchriceps (Protostegidae) and marine adaptation during the early evolution of chelonioids. *PeerJ*, *7*, e6811. https://doi.org/10.7717/peerj.6811

Evers, S. W., & Benson, R. B. J. (2018). A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group. *Palaeontology*, *62*(1), 93–134. https://doi.org/10.1111/pala.12384

Felsenstein, J. (1973). Maximum-likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics*, *25*(5), 471–492.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, *125*(1), 1–15.

Felsenstein, J. (2003). *Inferring phylogenies*. Sinauer.

Ferreira, G. S., Bronzati, M., Langer, M. C., & Sterli, J. (2018). Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira). *Royal Society Open Science*, *5*(3), 171773. https://doi.org/10.1098/rsos.171773

Finarelli, J. A., & Flynn, J. J. (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): The effects of incorporating data from the fossil record. *Systematic Biology*, *55*(2), 301–313. https://doi.org/10.1080/10635150500541698

Finarelli, J. A., & Goswami, A. (2013). Potential pitfalls of reconstructing deep time evolutionary history with only extant data, a case study using the canidae (mammalia, carnivora). *Evolution; International Journal of Organic Evolution*, *67*(12), 3678–3685. https://doi.org/10.1111/evo.12222

Foth, C., & Joyce, W. G. (2016). Slow and steady: The evolution of cranial disparity in fossil and recent turtles. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161881. https://doi.org/10.1098/rspb.2016.1881

Foth, C., Rabi, M., & Joyce, W. G. (2017). Skull shape variation in extant and extinct Testudinata and its relation to habitat and feeding ecology. *Acta Zoologica*, *98*(3), 310–325. https://doi.org/10.1111/azo.12181

Fox, J., & Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications.

Freckleton, R. P., & Harvey, P. H. (2006). Detecting non-brownian trait evolution in adaptive radiations. *PLoS Biology*, *4*(11), e373. https://doi.org/10.1371/journal.pbio.0040373

Fritz, S. A., Schnitzler, J., Eronen, J. T., Hof, C., Böhning-Gaese, K., & Graham, C. H. (2013). Diversity in time and space: Wanted dead and alive. *Trends in Ecology & Evolution*, *28*(9), 509–516. https://doi.org/10.1016/j.tree.2013.05.004

Gaffney, E. S., Tong, H., & Meylan, P. (2006). Evolution of the side-necked turtles: The families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, *300*, 1–698. https://doi.org/10.1206/0003-0090(2006)300[1:EOTSTT]2.0.CO;2

Garbin, R. C., Böhme, M., & Joyce, W. G. (2019). A new testudinoid turtle from the middle to late Eocene of Vietnam. *Peer Journal*, *7*, e6280. Portico. https://doi.org/10.7717/peerj.6280

Gearty, W. (2023). *Plotting tools for anyone working in deep time*.

Gearty, W., McClain, C. R., & Payne, J. L. (2018). Energetic tradeoffs control the size distribution of aquatic mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 4194–4199. https://doi.org/10.1073/pnas.1712629115

Gearty, W., & Payne, J. L. (2020). Physiological constraints on body size distributions in Crocodyliformes. *Evolution*, *74*(2), 245–255. https://doi.org/10.1111/evo.13901

Gentry, A. D., Ebersole, J. A., & Kiernan, C. R. (2019). *Asmodochelys parhami*, a new fossil marine turtle from the Campanian Demopolis Chalk and the stratigraphic congruence of competing marine turtle phylogenies. *Royal Society Open Science*, *6*(12), 191950. https://doi.org/10.1098/rsos.191950

Georgalis, G. L., & Kear, B. P. (2013). The fossil turtles of Greece: An overview of taxonomy and distribution. *Geobios*, *46*(4), 299–311. https://doi.org/10.1016/j.geobios.2013.05.001

Georgalis, G. L., & Joyce, W. G. (2017). A Review of the Fossil Record of Old World Turtles of the Clade Pan-Trionychidae. *Bulletin of the Peabody Museum of Natural History*, *58*(1), 115–208. https://doi.org/10.3374/014.058.0106

Godoy, P. L., Benson, R. B. J., Bronzati, M., & Butler, R. J. (2019). The multi-peak adaptive landscape of crocodylomorph body size evolution. *BMC Evolutionary Biology*, *19*(1), 167. https://doi.org/10.1186/s12862-019-1466-4

Golubović, A., Anđelković, M., Arsovski, D., Bonnet, X., & Tomović, L. (2017). Locomotor performances reflect habitat constraints in an armoured species. *Behavioral Ecology and Sociobiology*, *71*(6), 93. https://doi.org/10.1007/s00265-017-2318-0

Gould, S. J. (1988). Trends as changes in variance: A new slant on progress and directionality in evolution. *Journal of Paleontology*, *62*(3), 319–329. https://doi.org/10.1017/S0022336000059126

Guillerme, T. (2018). dispRity: A modular R package for measuring disparity. *Methods in Ecology and Evolution*, *9*(7), 1755–1763. https://doi.org/10.1111/2041-210X.13022

Gutarra, S., Stubbs, T. L., Moon, B. C., Palmer, C., & Benton, M. J. (2022). Large size in aquatic tetrapods compensates for high drag caused by extreme body proportions. *Communications Biology*, *5*(1), Article 1. https://doi.org/10.1038/s42003-022-03322-y

Hansen, T. F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, *51*(5), 1341–1351. https://doi.org/10.1111/j.1558-5646.1997.tb01457.x

Harmon, L. J., Losos, J. B., Jonathan Davies, T., Gillespie, R. G., Gittleman, J. L., Bryan Jennings, W., Kozak, K. H., McPeek, M. A., Moreno-Roark, F., Near, T. J., Purvis, A., Ricklefs, R. E., Schluter, D., Schulte Ii, J. A., Seehausen, O., Sidlauskas, B. L., Torres-Carvajal, O., Weir, J. T., & Mooers, A. Ø. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution; International Journal of Organic Evolution*, *64*(8), 2385–2396. https://doi.org/10.1111/j.1558-5646.2010.01025.x

20457758, 2023, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10201 by Université De Fribourg, Wiley Online Library on [03/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, *24*(1), 129–131. https://doi.org/10.1093/bioinformatics/btm538

Havlik, P. E., Joyce, W. G., & Böhme, M. (2014). *Allaeochelys libyca*, a New Carettochelyine Turtle from the Middle Miocene (Langhian) of Libya. *Bulletin of the Peabody Museum of Natural History*, *55*(2), 201. https://doi.org/10.3374/014.055.0207

Heath, T. A., Huelsenbeck, J. P., & Stadler, T. (2014). The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(29), E2957–E2966. https://doi.org/10.1073/pnas.1319091111

Heim, N. A., Knope, M. L., Schaal, E. K., Wang, S. C., & Payne, J. L. (2015). Cope's rule in the evolution of marine animals. *Science*, *347*(6224), 867–870. https://doi.org/10.1126/science.1260065

Hermanson, G., Benson, R. B. J., Farina, B. M., Ferreira, G. S., Langer, M. C., & Evers, S. W. (2022). Cranial ecomorphology of turtles and neck retraction as a possible trigger of ecological diversification. *Evolution*, *76*, 2566–2586. https://doi.org/10.1111/evo.14629

Hermanson, G., Iori, F. V., Evers, S. W., Langer, M. C., & Ferreira, G. S. (2020). A small podocnemidoid (*Pleurodira*, *Pelomedusoides*) from the Late Cretaceous of Brazil, and the innervation and carotid circulation of side-necked turtles. *Papers in Palaeontology*, *6*(2), 329–347. https://doi.org/10.1002/spp2.1300

Hirayama, R. (1998). Oldest known sea turtle. *Nature*, *392*(6677), Article 6677. https://doi.org/10.1038/33669

Holley, A. J., Sterli, J., & Basso, N. G. (2020). Dating the origin and diversification of *Pan-Chelidae* (Testudines, *Pleurodira*) under multiple molecular clock approaches. *Contributions to Zoology*, *89*(2), 146–174. https://doi.org/10.1163/18759866-20191419

Hunt, G., & Carrano, M. T. (2010). Models and methods for analyzing phenotypic evolution in lineages and clades. *The Paleontological Society Papers*, *16*, 245–269. https://doi.org/10.1017/S1089332600001893

Huttenlocker, A. K. (2014). Body size reductions in nonmammalian eutheriodont therapsids (Synapsida) during the end-Permian mass extinction. *PLoS One*, *9*(2), e87553. https://doi.org/10.1371/journal.pone.0087553

Ingram, T., & Mahler, D. L. (2013). SURFACE: Detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion. *Methods in Ecology and Evolution*, *4*(5), 416–425. https://doi.org/10.1111/2041-210X.12034

Jaffe, A. L., Slater, G. J., & Alfaro, M. E. (2011). The evolution of island gigantism and body size variation in tortoises and turtles. *Biology Letters*, *7*(4), 558–561. https://doi.org/10.1098/rsbl.2010.1084

James, F. C. (1970). Geographic size variation in birds and its relationship to climate. *Ecology*, *51*(3), 365–390. https://doi.org/10.2307/1935374

Jones, L. A., Gearty, W., Allen, B. J., Eichenseer, K., Dean, C. D., Galván, S., Kouvari, M., Godoy, P. L., Nicholl, C. S. C., Buffan, L., Dillon, E. M., Flannery-Sutherland, J. T., & Chiarenza, A. A. (2023). palaeoverse: A community-driven R package to support palaeobiological analysis. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.14099

Joos, J., Pimiento, C., Miles, D. B., & Müller, J. (2022). Quaternary megafauna extinctions altered body size distribution in tortoises. *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20221947. https://doi.org/10.1098/rspb.2022.1947

Joyce, W. (2017). A review of the fossil record of basal mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, *58*, 65–113. https://doi.org/10.3374/014.058.0105

Joyce, W. G., Anquetin, J., Cadena, E.-A., Claude, J., Danilov, I. G., Evers, S. W., Ferreira, G. S., Gentry, A. D., Georgalis, G. L., Lyson, T. R., Pérez-García, A., Rabi, M., Sterli, J., Vitek, N. S., & Parham, J. F. (2021). A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology*, *140*(1), 5. https://doi.org/10.1186/s13358-020-00211-x

Joyce, W. G., & Gauthier, J. A. (2004). Palaeoecology of Triassic stem turtles sheds new light on turtle origins. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *271*(1534), 1–5. https://doi.org/10.1098/rspb.2003.2523

Joyce, W. G., Parham, J. F., Lyson, T. R., Warnock, R. C. M., & Donoghue, P. C. J. (2013). A divergence dating analysis of turtles using fossil calibrations: An example of best practices. *Journal of Paleontology*, *87*(4), 612–634. https://doi.org/10.1666/12-149

Joyce, W. G. (2016). A review of the Fossil record of Turtles of the Clade *Pan-Chelydridae*. *Bulletin of the Peabody Museum of Natural History*, *57*(1), 21–56. https://doi.org/10.3374/014.057.0103

Joyce, W. G., & Anquetin, J. (2019). A review of the fossil record of Nonbaenid Turtles of the Clade *Paracryptodira*. *Bulletin of the Peabody Museum of Natural History*, *60*(2), 129. https://doi.org/10.3374/014.060.0204

Joyce, W. G., & Bourque, J. R. (2016). A review of the Fossil Record of Turtles of the Clade *Pan-Kinosternoidea*. *Bulletin of the Peabody Museum of Natural History*, *57*(1), 57–95. https://doi.org/10.3374/014.057.0104

Joyce, W. G., & Lyson, T. R. (2015). A Review of the Fossil Record of Turtles of the Clade Baenidae. *Bulletin of the Peabody Museum of Natural History*, *56*(2), 147–183. https://doi.org/10.3374/014.056.0203

Joyce, W. G., & Lyson, T. R. (2010). *Pangshura tatrotia*, a new species of pond turtle (Testudinoidea) from the Pliocene Siwaliks of Pakistan. *Journal of Systematic Palaeontology*, *8*(3), 449–458. https://doi.org/10.1080/14772019.2010.500879

Joyce, W. G., & Rollot, Y. (2020). An alternative interpretation of *Peltochelys duchastelii* as a paracryptodire. *Fossil Record*, *23*(1), 83–93. https://doi.org/10.5194/fr-23-83-2020

Joyce, W. G., Lyson, T. R., & Sertich, J. J. W. (2018). A new species of trionychid turtle from the Upper Cretaceous (Campanian) Fruitland. Formation of New Mexico, USA. *Journal of Paleontology*, *92*(6), 1107–1114. https://doi.org/10.1017/jpa.2018.30

Karl, H.-V., Groning, E., & Brauckmann, C. (2012). New materials of the giant sea turtle Allopleuron (Testudines: Chelonioidea) from the marine Late Cretaceous of Central Europe and the Palaeogene of Kazakhstan. *Studia Palaeocheloniologica*, *4*, 153–173.

Keck, F., Rimet, F., Bouchez, A., & Franc, A. (2016). phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, *6*(9), 2774–2780. https://doi.org/10.1002/ece3.2051

Kubo, T., Sakamoto, M., Meade, A., & Venditti, C. (2019). Transitions between foot postures are associated with elevated rates of body size evolution in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(7), 2618–2623. https://doi.org/10.1073/pnas.1814329116

Lapparent de Broin, F., Murelaga, X., Farrés, F., & Altimiras, J. (2014). An exceptional cheloniid turtle, *Osonachelus decorata* nov. gen., nov. sp., from the Eocene (Bartonian) of Catalonia (Spain). *Geobios*, *47*(3), 111–132. https://doi.org/10.1016/j.geobios.2014.02.002

Laurin, M. (2004). The evolution of body size, Cope's rule and the origin of amniotes. *Systematic Biology*, *53*(4), 594–622. https://doi.org/10.1080/10635150490445706

Lautenschlager, S., Ferreira, G. S., & Werneburg, I. (2018). Sensory evolution and ecology of early turtles revealed by digital endocranial reconstructions. *Frontiers in Ecology and Evolution*, *6*, 1–16. https://doi.org/10.3389/fevo.2018.00007

Lomolino, M. V. (2005). Body size evolution in insular vertebrates: Generality of the island rule. *Journal of Biogeography*, *32*(10), 1683–1699. https://doi.org/10.1111/j.1365-2699.2005.01314.x

López-Conde, O. A., Sterli, J., Alvarado-Ortega, J., & Chavarría-Arellano, M. L. (2017). A new platychelyid turtle (*Pan-Pleurodira*) from

20457758, 2023, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10201 by Université De Fribourg, Wiley Online Library on [03/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the Late. Jurassic (Kimmeridgian) of Oaxaca, Mexico. *Papers in Palaeontology*, *3*(2), 161–174. https://doi.org/10.1002/spp2.1069

Louca, S., & Pennell, M. W. (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature*, *580*(7804), Article 7804. https://doi.org/10.1038/s41586-020-2176-1

Lourenço, J. M., Claude, J., Galtier, N., & Chiari, Y. (2012). Dating cryptodiran nodes: Origin and diversification of the turtle superfamily Testudinoidea. *Molecular Phylogenetics and Evolution*, *62*(1), 496–507. https://doi.org/10.1016/j.ympev.2011.10.022

Lovegrove, B. G. (2017). A phenology of the evolution of endothermy in birds and mammals. *Biological Reviews*, *92*(2), 1213–1240. https://doi.org/10.1111/brv.12280

Lyson, T. R., Schachner, E. R., Botha-Brink, J., Scheyer, T. M., Lambertz, M., Bever, G. S., Rubidge, B. S., & de Queiroz, K. (2014). Origin of the unique ventilatory apparatus of turtles. *Nature Communications*, *5*, 5211. https://doi.org/10.1038/ncomms6211

Lyson, T. R., Sayler, J. L., & Joyce, W. G. (2019). A new baenid turtle, *Saxochelys gilberti*, gen. et sp. nov., from the uppermost cretaceous (Maastrichtian) hell creek formation: sexual dimorphism and spatial niche partitioning within the most speciose group of Late Cretaceous turtles. *Journal of Vertebrate Paleontology*, *39*(4), e1662428. https://doi.org/10.1080/02724634.2019.1662428

Maddison, W., & Maddison, D. (2018). *Mesquite*: *A modular system for evolutionary analysis* (3.61).

Mallon, J. C., & 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

Mannion, P. D., Benson, R. B. J., Carrano, M. T., Tennant, J. P., Judd, J., & Butler, R. J. (2015). Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Communications*, *6*(1), Article 1. https://doi.org/10.1038/ncomms9438

Matzke, N. J., & Wright, A. (2016). Inferring node dates from tip dates in fossil Canidae: The importance of tree priors. *Biology Letters*, *12*(8), 20160328. https://doi.org/10.1098/rsbl.2016.0328

Maurer, B. A., Brown, J. H., & Rusler, R. D. (1992). The micro and macro in body size evolution. *Evolution*, *46*(4), 939–953. https://doi.org/10.1111/j.1558-5646.1992.tb00611.x

Moen, D. S. (2006). Cope's rule in cryptodiran turtles: Do the body sizes of extant species reflect a trend of phyletic size increase? *Journal of Evolutionary Biology*, *19*(4), 1210–1221. https://doi.org/10.1111/j.1420-9101.2006.01082.x

Molina-Venegas, R., & Rodríguez, M. Á. (2017). Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC Evolutionary Biology*, *17*(1), 53. https://doi.org/10.1186/s12862-017-0898-y

Mousseau, T. A. (1997). Ectotherms follow the converse to Bergmann's rule. *Evolution*, *51*(2), 630–632. https://doi.org/10.2307/2411138

Mrosovsky, N. (1980). Thermal biology of sea turtles. *American Zoologist*, *20*(3), 531–547.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Oriozabala, C., Sterli, J., & de la Fuente, M. S. (2020). New species of the long-necked chelid Yaminuechelys from the Upper Cretaceous (Campanian–Maastrichtian) of Chubut, Argentina. *Cretaceous Research*, *106*, 104197. https://doi.org/10.1016/j.cretres.2019.104197

Pagel, M. (2002). Modelling the evolution of continuously varying characters on phylogenetic trees: The case of hominid cranial capacity. In N. MacLeod & P. L. Forey (Eds.), *Morphology, shape and phylogeny* (pp. 269–286). CRC Press.

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Parham, J. F., & Pyenson, N. D. (2010). New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. *Journal of Paleontology*, *84*(2), 231–247. https://doi.org/10.1666/09-077r.1

Partridge, L., & Coyne, J. A. (1997). Bergmann's rule in ectotherms: Is it adaptive? *Evolution*, *51*(2), 632–635. https://doi.org/10.2307/2411139

Patterson, C. (1981). Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics*, *12*, 195–223.

Pereira, A. G., Sterli, J., Moreira, F. R. R., & Schrago, C. G. (2017). Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Molecular Phylogenetics and Evolution*, *113*, 59–66. https://doi.org/10.1016/j.ympev.2017.05.008

Pérez-García, A., & Murelaga, X. (2012). *Galvechelone lopezmartinezaegen*. et sp. nov., a new cryptodiran turtle in the lower cretaceous of Europe. *Palaeontology*, *55*(5), 937–944. https://doi.org/10.1111/j.1475-4983.2012.01154.x

Pérez-García, A., de la Fuente, M. S., & Ortega, F. (2012). A new freshwater Basal Eucryptodiran Turtle from the early cretaceous of Spain. *Acta Palaeontologica Polonica*, *57*(2), 285–298. https://doi.org/10.4202/app.2011.0031

Pérez-García, A., Espílez, E., Mampel, L., & Alcalá, L. (2020). A new basal turtle represented by the two most complete skeletons of *Helochelydridae* in Europe. *Cretaceous Research*, *107*, 104291. https://doi.org/10.1016/j.cretres.2019.104291

Pérez-García, A., Vlachos, E., & Murelaga, X. (2020). A large testudinid with African affinities in the post-Messinian (lower Pliocene) record of south-eastern Spain. *Palaeontology*, *63*(3), 497–512. https://doi.org/10.1111/pala.12468

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.

Petzold, A., Vargas-Ramírez, M., Kehlmaier, C., Vamberger, M., Branch, W. R., Preez, L. D., Hofmeyr, M. D., Meyer, L., Schleicher, A., Široký, P., & Fritz, U. (2014). A revision of African helmeted terrapins (*Testudines*: *Pelomedusidae*: *Pelomedusa*), with descriptions of six new species. *Zootaxa*, *3795*(5), 523. https://doi.org/10.11646/zootaxa.3795.5.2

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACK, Heisterkamp, S., Van Willigen, B., Ranke, J., & R Core Team. (2022). *nlme*: *Linear and nonlinear mixed effects models* (3.1-160). https://CRAN.R-project.org/package=nlme

Pritchard, P. C. H. (2001). Observations on body size, sympatry, and niche divergence in softshell turtles (Trionychidae). *Chelonian Conservation and Biology*, *4*(1), 5–27.

Prokoph, A., Shields, G. A., & Veizer, J. (2008). Compilation and time-series analysis of a marine carbonate δ18O, δ13C, 87Sr/86Sr and δ34S database through Earth history. *Earth-Science Reviews*, *87*(3), 113–133. https://doi.org/10.1016/j.earscirev.2007.12.003

Puttick, M. N. (2016). Partially incorrect fossil data augment analyses of discrete trait evolution in living species. *Biology Letters*, *12*(8), 20160392. https://doi.org/10.1098/rsbl.2016.0392

Pyenson, N. D., & Vermeij, G. J. (2016). The rise of ocean giants: Maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic oceans. *Biology Letters*, *12*(7), 20160186. https://doi.org/10.1098/rsbl.2016.0186

Quental, T. B., & Marshall, C. R. (2010). Diversity dynamics: Molecular phylogenies need the fossil record. *Trends in Ecology & Evolution*, *25*(8), 434–441. https://doi.org/10.1016/j.tree.2010.05.002

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rabi, M., Zhou, C.-F., Wings, O., Ge, S., & Joyce, W. G. (2013). A new xinjiangchelyid turtle from the Middle Jurassic of Xinjiang, China and the evolution of the basipterygoid process in Mesozoic turtles. *BMC Evolutionary Biology*, *13*(1), 203. https://doi.org/10.1186/1471-2148-13-203

20457758, 2023, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10201 by Université De Fribourg, Wiley Online Library on [03/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Raia, P., & Meiri, S. (2011). The tempo and mode of evolution: Body sizes of island mammals. *Evolution; International Journal of Organic Evolution*, *65*(7), 1927–1934. https://doi.org/10.1111/j.1558-5646.2011.01263.x

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rhodin, A., Iverson, J., Bour, R., Fritz, U., Georges, A., Shaffer, H., & Dijk, P. P. (2021). *Turtles of the world: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status* (9th ed.). https://doi.org/10.3854/crm.8.checklist.atlas.v9.2021

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*(3), 539–542. https://doi.org/10.1093/sysbio/sys029

Saarinen, J. J., Boyer, A. G., Brown, J. H., Costa, D. P., Ernest, S. K. M., Evans, A. R., Fortelius, M., Gittleman, J. L., Hamilton, M. J., Harding, L. E., Lintulaakso, K., Lyons, S. K., Okie, J. G., Sibly, R. M., Stephens, P. R., Theodor, J., Uhen, M. D., & Smith, F. A. (2014). Patterns of maximum body size evolution in Cenozoic land mammals: Eco-evolutionary processes and abiotic forcing. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1784), 20132049. https://doi.org/10.1098/rspb.2013.2049

Scavezzoni, I., & Fischer, V. (2018). *Rhinochelys amaberti* Moret (1935), a protostegid turtle from the Early Cretaceous of France. *Peer J*, *6*, e4594. https://doi.org/10.7717/peerj.4594

Scheyer, T. M., Klein, N., Evers, S. W., Mautner, A.-K., & Pabst, B. (2022). First evidence of Proganochelys quenstedtii (Testudinata) from the Plateosaurus bonebeds (Norian, Late Triassic) of Frick, Canton Aargau, Switzerland. *Swiss Journal of Palaeontology*, *141*(1), 17. https://doi.org/10.1186/s13358-022-00260-4

Scheyer, T. M., & Sander, P. M. (2007). Shell bone histology indicates terrestrial palaeoecology of basal turtles. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1620), 1885–1893. https://doi.org/10.1098/rspb.2007.0499

Schliep, K. P. (2011). phangorn: Phylogenetic analysis in R. *Bioinformatics*, *27*(4), 592–593. https://doi.org/10.1093/bioinformatics/btq706

Schmidt-Nielsen, K., & Knut, S.-N. (1984). *Scaling: Why is animal size so important?* Cambridge University Press.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), Article 7. https://doi.org/10.1038/nmeth.2089

Schnitzler, J., Theis, C., Polly, P. D., & Eronen, J. T. (2017). Fossils matter – Understanding modes and rates of trait evolution in Musteloidea (Carnivora). *Evolutionary Ecology Research*, *18*(2), 187–200.

Shao, S., Li, L., Yang, Y., & Zhou, C. F. (2018). Hyperphalangy in a new sinemydid turtle from the Early Cretaceous Jehol Biota. *Peer J*, *6*, e5371. https://doi.org/10.7717/peerj.5371

Slater, G. J., Harmon, L. J., & Alfaro, M. E. (2012). Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution*, *66*(12), 3931–3944. https://doi.org/10.1111/j.1558-5646.2012.01723.x

Smith, F. A., Boyer, A. G., Brown, J. H., Costa, D. P., Dayan, T., Ernest, S. K. M., Evans, A. R., Fortelius, M., Gittleman, J. L., Hamilton, M. J., Harding, L. E., Lintulaakso, K., Lyons, S. K., McCain, C., Okie, J. G., Saarinen, J. J., Sibly, R. M., Stephens, P. R., Theodor, J., & Uhen, M. D. (2010). The evolution of maximum body size of terrestrial mammals. *Science*, *330*(6008), 1216–1219. https://doi.org/10.1126/science.1194830

Smith, F. A., Elliott Smith, R. E., Lyons, S. K., & Payne, J. L. (2018). Body size downgrading of mammals over the late Quaternary. *Science*, *360*(6386), 310–313. https://doi.org/10.1126/science.aao5987

Smith, F. A., & Lyons, S. K. (2011). How big should a mammal be? A macroecological look at mammalian body size over space and time. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2364–2378. https://doi.org/10.1098/rstb.2011.0067

Smith, F. A., Payne, J. L., Heim, N. A., Balk, M. A., Finnegan, S., Kowalewski, M., Lyons, S. K., McClain, C. R., McShea, D. W., Novack-Gottshall, P. M., Anich, P. S., & Wang, S. C. (2016). Body size evolution across the Geozoic. *Annual Review of Earth and Planetary Sciences*, *44*(1), 523–553. https://doi.org/10.1146/annurev-earth-060115-012147

Sookias, R. B., Butler, R. J., & Benson, R. B. J. (2012). Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1736), 2180–2187. https://doi.org/10.1098/rspb.2011.2441

Stadler, T. (2010). Sampling-through-time in birth–death trees. *Journal of Theoretical Biology*, *267*(3), 396–404. https://doi.org/10.1016/j.jtbi.2010.09.010

Stanley, S. M. (1973). An explanation for Cope's rule. *Evolution*, *27*(1), 1–26. https://doi.org/10.2307/2407115

Sterli, J. (2015). A review of the fossil record of Gondwanan turtles of the clade Meiolaniformes. *Bulletin of the Peabody Museum of Natural History*, *56*(1), 21–45. https://doi.org/10.3374/014.056.0102

Sterli, J., de la Fuente, M. S., & Rougier, G. W. (2018). New remains of Condorchelys antiqua (Testudinata) from the Early-Middle Jurassic of Patagonia: Anatomy, phylogeny, and paedomorphosis in the early evolution of turtles. *Journal of Vertebrate Paleontology*, *38*(4), 1–17. https://doi.org/10.1080/02724634.2018.1480112

Syromyatnikova, E. V., & Danilov, I. G. (2013). New material and phylogenetic position of *Adocus bostobensis*, a poorly known adocid turtle from the Late Cretaceous of Kazakhstan. *Proceedings of the Zoological Institute RAS*, *317*(2), 195–201. https://doi.org/10.31610/trudyzin/2013.317.2.195

Thomson, R. C., Spinks, P. Q., & Shaffer, H. B. (2021). A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(7), e2012215118. https://doi.org/10.1073/pnas.2012215118

Tong, H., & Li, L. (2019). A revision of the holotype of *Nanhsiungchelys wuchingensis*, Ye, 1966 (Testudines: Cryptodira: Trionychoidae: Nanhsiungchelyidae). *Cretaceous Research*, *95*, 151–163. https://doi.org/10.1016/j.cretres.2018.11.003

Uyeda, J. C., & Harmon, L. J. (2014). A novel Bayesian method for inferring and interpreting the dynamics of adaptive landscapes from phylogenetic comparative data. *Systematic Biology*, *63*(6), 902–918. https://doi.org/10.1093/sysbio/syu057

Valdes, N., Bourque, J. R., & Vitek, N. S. (2017). A new soft-shelled turtle (Trionychidae, *Apalone*) from the Late Miocene of north-central Florida. *Bulletin of the Florida Museum of Natural History*, *55*(6), 117–138.

van der Have, T. M., & de Jong, G. (1996). Adult size in ectotherms: Temperature effects on growth and differentiation. *Journal of Theoretical Biology*, *183*(3), 329–340. https://doi.org/10.1006/jtbi.1996.0224

Van Voorhies, W. A. (1996). Bergmann size clines: A simple explanation for their occurence in ectotherms. *Evolution; International Journal of Organic Evolution*, *50*(3), 1259–1264. https://doi.org/10.1111/j.1558-5646.1996.tb02366.x

Vitek, N. S. (2012). Giant fossil soft-shelled turtles of North America. *Palaeontologia Electronica*, *15*(16), 1–43. https://doi.org/10.26879/299

Vitek, N. S., & Joyce, W. G. (2015). A review of the fossil record of New World Turtles of the Clade *Pan-Trionychidae*. *Bulletin of the Peabody Museum of Natural History*, *56*(2), 185–244. https://doi.org/10.3374/014.056.0204

Vlachos, E., & Rabi, M. (2018). Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira:

20457758, 2023, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10201 by Université De Fribourg, Wiley Online Library on [03/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Pan-Testudinidae). *Cladistics*, *34*(6), 652–683. https://doi.org/10.1111/cla.12227

Vlachos, E. (2018). A review of the fossil record of North American Turtles of the Clade *Pan-Testudinoidea*. *Bulletin of the Peabody Museum of Natural History*, *59*(1), 3. https://doi.org/10.3374/014.059.0101

Vlachos, E., & Tsoukala, E. (2016). The diverse fossil chelonians from Milia (late Pliocene, Grevena, Greece) with a new species of *Testudo Linnaeus*, 1758 (Testudines: *Testudinidae*). *Papers in Palaeontology*, *2*(1), 71–86. https://doi.org/10.1002/spp2.1031

Weems, R. E., & Brown, K. M. (2017). More-complete remains of *Procolpochelys charlestonensis* (Oligocene, South Carolina), an occurrence of Euclastes (upper Eocene, South Carolina), and their bearing on Cenozoic pancheloniid sea turtle distribution and phylogeny. *Journal of Paleontology*, *91*(6), 1228–1243. https://doi.org/10.1017/jpa.2017.64

Welch, B. L. (1947). The generalization of 'student's' problem when several different population variances are involved. *Biometrika*, *34*(1/2), 28–35. https://doi.org/10.2307/2332510

White, C. R., Alton, L. A., Bywater, C. L., Lombardi, E. J., & Marshall, D. J. (2022). Metabolic scaling is the product of life-history optimization. *Science*, *377*(6608), 834–839. https://doi.org/10.1126/science.abm7649

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, *22*(6), 323–330. https://doi.org/10.1016/j.tree.2007.03.007

Williams, T. M. (2001). Intermittent swimming by mammals: A strategy for increasing energetic efficiency during diving. *American Zoologist*, *41*(2), 166–176. https://doi.org/10.1093/icb/41.2.166

Zachos, J. C., Dickens, G. R., & Zeebe, R. E. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, *451*(7176), Article 7176. https://doi.org/10.1038/nature06588

Zink, R. M., & Remsen, J. (1986). Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology*, *4*, 1–69.

Zvonok, E. A., & Danilov, I. G. (2017). A revision of fossil turtles from the Kiev clays (Ukraine, middle Eocene) with comments on the history of the collection of fossil vertebrates of A.S. Rogovich. *Proceedings of the Zoological Institute RAS*, *321*(4), 485–516. https://doi.org/10.31610/trudyzin/2017.321.4.485

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APPENDIX 1

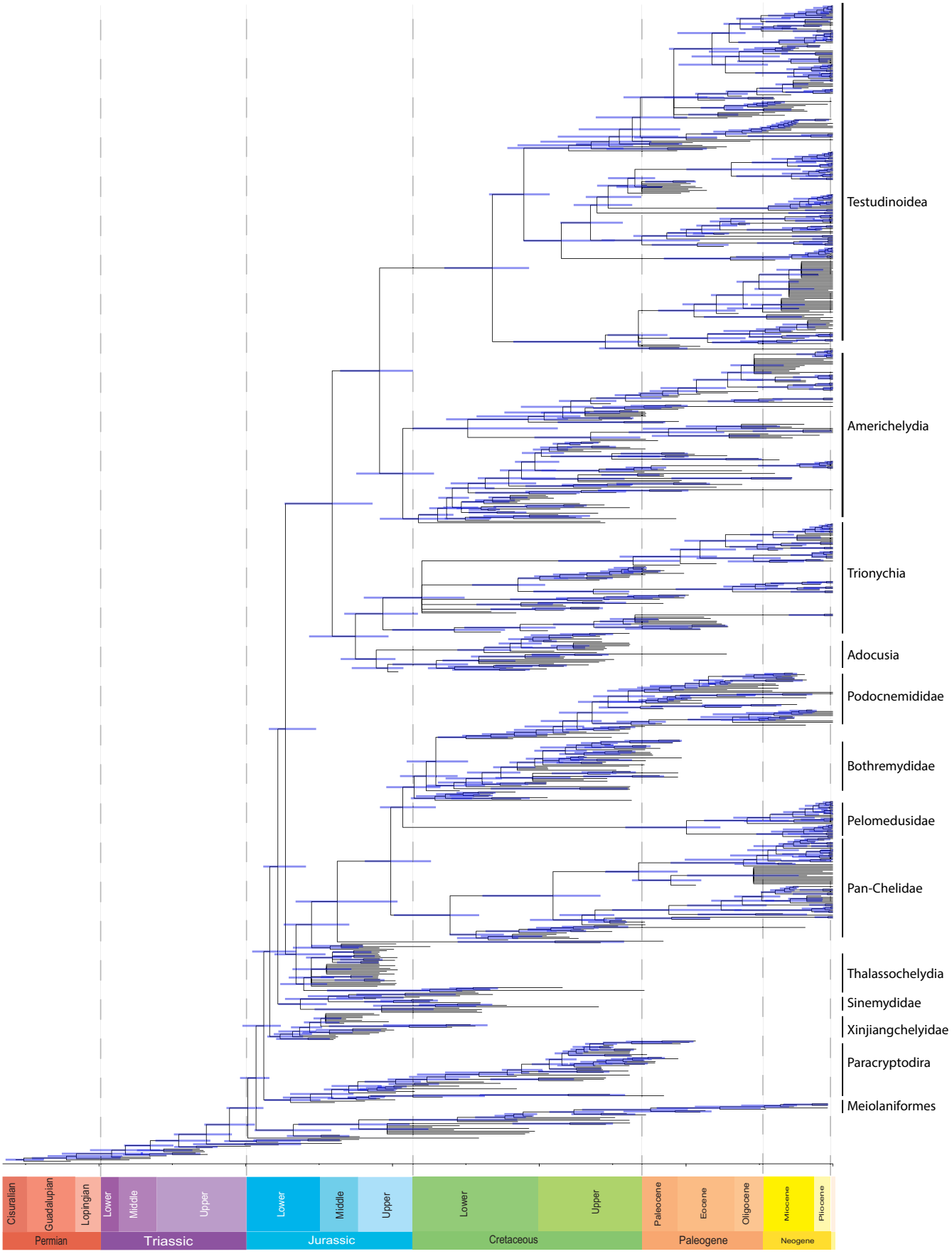

FIGURE A1 The "Ev19" time-calibrated supertree, represented by the 50% majority rule tree. Blue bars represent the 95% highest posterior density (HPD) age ranges for each node.

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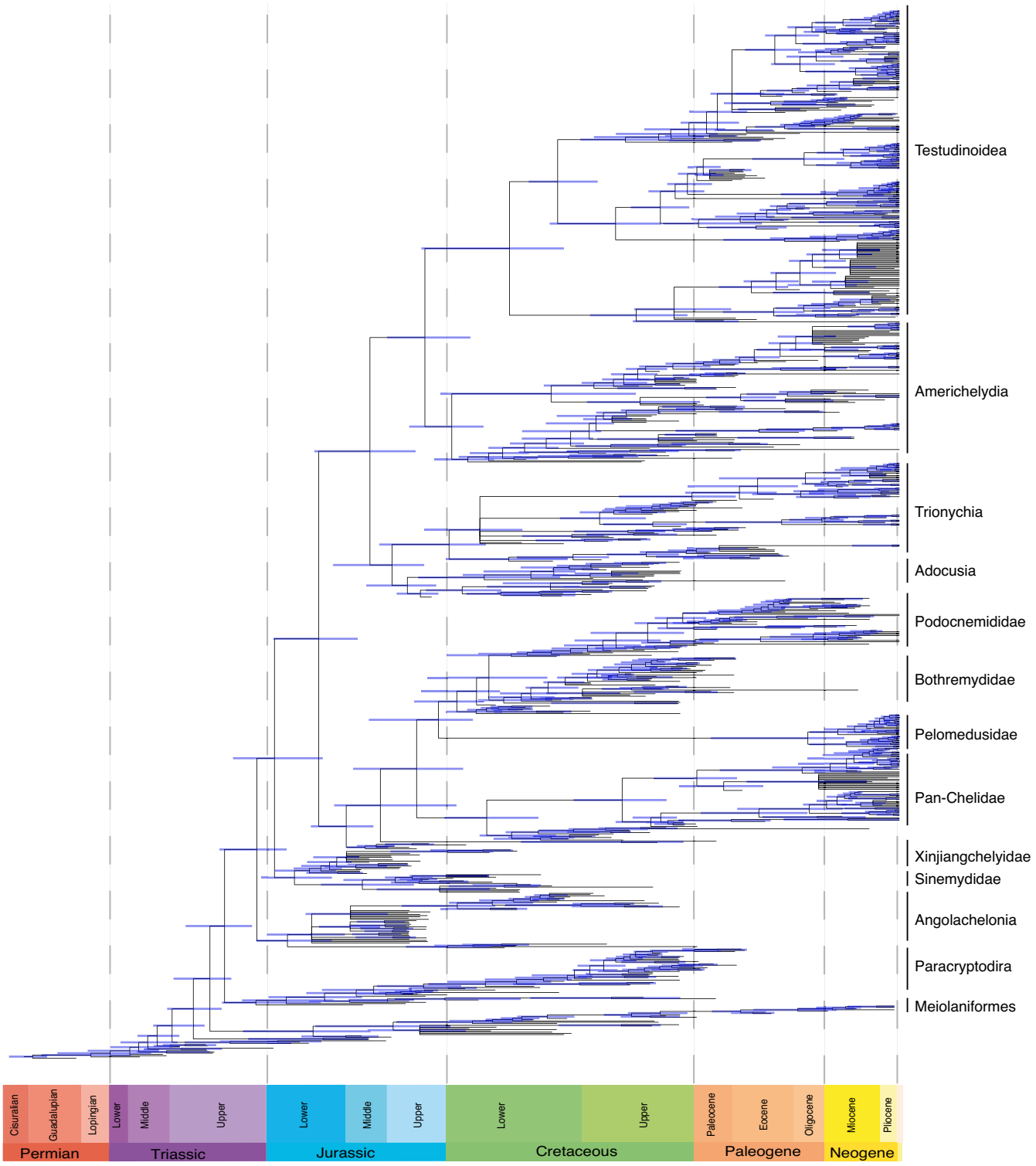

FIGURE A2 The "St18" time-calibrated supertree, represented by the 50% majority rule tree. Blue bars represent the 95% highest posterior density (HPD) age ranges for each node.

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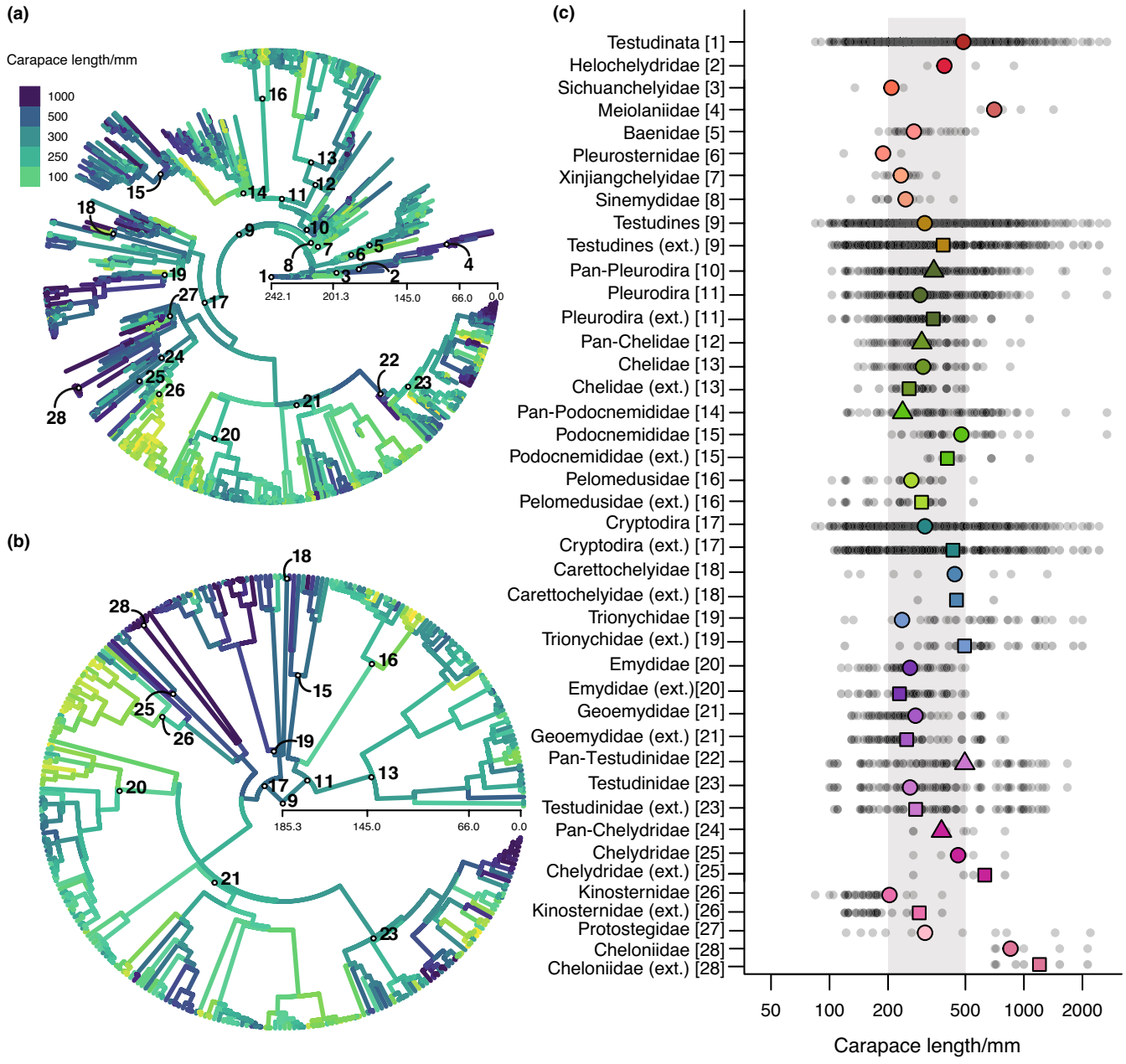

FIGURE A3 Ancestral body sizes ($\log_{10}$ maximum dorsal carapace length in millimeters) mapped onto Ev19 supertree, with (a) complete tree and (b) extant-only subtree. Ancestral body size for different taxonomic groups (c); small gray dots indicate all taxa within that lineage; colored triangles represent the ancestral estimates of stem-groups; circles represent ancestral estimates of the crown groups; and squares represent ancestral estimates of the crown groups without the fossil taxa. Gray area indicates sizes between 200 and 500 mm. The numbers indicate the same groups in a–c.

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TABLE A1 Sources of phylogenetic information for supertrees construction.

Group	References
Testudinata	Evers et al. (2019), Sterli et al. (2018) Obs 1: Joyce (2017): used to include taxa that were not sampled by the above topologies
Meiolaniformes	Sterli (2015), Sterli et al. (2018) Obs 1: In "Ev19": the position of *Chubutemys* and *Kallokibotion* was defined according to Evers et al. (2019)
Helochelydridae	Joyce (2017) Obs 1: *Aragochersis*: according to Pérez-Garcia, Espílez, et al. (2020)
Sichuanchelyidae	Joyce (2017)
Compsemydidae	Joyce and Anquetin (2019) Obs 1: *Peltochelys duchastelii*: according to Joyce and Rollot (2020)
Paracryptodira	Joyce and Rollot (2020) Obs 1: Position of *Dinochelys*, *Compsemydidae*, *Uluops* e Baenoidea
Baenidae	Joyce and Lyson (2015) Obs 1: Eubaeninae (Lyson et al., 2019) + "*Baena" escavada* (Joyce & Lyson, 2015)
Pleurosternidae	Joyce and Rollot (2020) *Siamochelys peninsularis*: according to Sterli et al. (2018). Obs 1: Sister group of Paracryptodira
Xinjiangchelyidae	Rabi et al. (2013) Obs 1: Xinjianchelys (less inclusive clade) according to Evers et al. (2019) Sampled made by Evers and Benson (2018) and Evers et al. (2019) include *Xinjianchelys radiplicatoides*, *Xinjianchelys wusu*, *Annemys* IVPP V18106, *Annemys levensis*, and *Annemys latiens*. *A. latiens* and *A. levensis* are included in Rabi et al. (2013) as *Xinjianchelys latiens* e *Xinjianchelys levensis*, but other Xinjianchelys in Evers et al. (2019) are not. Because Xinjianchelys is monophyletic in Rabi et al. (2013) (if *Larachelus* and *Brodiechelys* are included), we assume the Evers et al.'s (2019) topology includes only taxa from this clade (i.e., clade that includes *Xinjianchelys*, *Larachelus* e *Brodiechelys*, but not *Protoxinjiangchelys* or *Tienfuchelys*), thus the relationship between other xinjiangchelidis follows Rabi et al. (2013)
Sinemydidae	Evers et al. (2019), Shao et al. (2018) Obs 1: *Hoyasemys jimenezi*: according to Pérez-García, Fuent, et al. (2012) Obs 2: *Galvechelone lopezmartinezae*: according to Pérez-Garcia and Murelaga (2012)
Angolachelonia	Evers et al. (2019)
Thelassochelydia	Anquetin et al. (2017) Obs 1: In "St18," *Santanachelys* is included within Eurysternidae
Sandownidae	Evers et al. (2019)
Platychelyidae	López-Conde et al. (2017)
Dortokidae	Cadena and Joyce (2015)
Pan-Chelidae	Holley et al. (2020), Pereira et al. (2017) Obs 1: *Linderochelys* and *Salamanchelys*: according to Hermanson et al. (2020) Obs 2: *Yaminuechelys sulcipeculiaris*: according to Oriozabala et al. (2020)
Pelomedusidae	Pereira et al. (2017), Petzold et al. (2014)
Pan-Podocnemididae	Hermanson et al. (2020)
Adocidae	Syromyatnikova and Danilov (2013) Obs 1: *Adocus inexpectatus*: according to Danilov et al. (2013)
Nanhsiungchelyidae	Tong and Li (2019) Obs 1: *Basilemys gaffney*, *Basilemys morriensis*, and *Zangerlia testudinomorpha*: Mallon and Brinkman (2018)
Pan-Carettochelys	Havlik et al. (2014)
Trionychia	Pereira et al. (2017), Brinkman et al. (2017; implied weighting tree); other added according to Georgalis and Joyce (2017) and Vitek and Joyce (2015) Obs 1: Plastomenidae according to Joyce et al. (2018) Obs 2: *Axestemys* according to Vitek and Joyce (2015) Obs 3: *Apalone amorense*: according to Valdes et al. (2017) Obs 4: *Aspideretoides foveatus* and *Gobiapalone orlovi*: according to Brinkman et al. (2017)

(Continues)

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TABLE A1 (Continued)

Group	References
Pan-Testudinoidea	Pereira et al. (2017), Vlachos (2018) (general topology) Pan-Emydidae: Pereira et al. (2017), Vlachos (2018) Obs 1: Polytomy within *Pseudemys*, *Graptemys* and *Trachemys* Pan-Geoemydidae: Pereira et al. (2017), Vlachos (2018) Obs 2: *Banhxeochelys* and *Guangdongemys* according to Garbin et al. (2019) Obs 3: *Hardella siamensis*: according to Claude et al. (2007) Obs 4: *Pangshura tatrotia*: according to Joyce and Lyson (2010) Pan-Testudinidae: Pereira et al. (2017), Vlachos (2018), and Vlachos and Rabi (2018) Obs 5: Extant taxa were included following Pereira et al. (2017); extinct taxa were positioned according to Vlachos and Rabi (2018) and Vlachos (2018) Obs 6: *Gopherus*: Vlachos (2018) Obs 7: Polytomy within *Chelonoidis* Geochelona: Pereira et al. (2017), Pérez-García, Vlachos, et al. (2020), and Vlachos and Rabi (2018) Pan-Testudona: Vlachos and Tsoukala (2016) Obs 8: *Impregnochelys* and *Gigantochersina*: according to Pérez-García et al. (2020)
Pan-Chelydridae	Joyce (2016)
Pan-Kinosternoidea	Joyce and Bourque (2016) Obs 1: *Kinosternon*: polytomy (we added taxa from Pereira et al.'s, 2017 topology) Obs 2: *Yelmochelys rosarioae*: according to Brinkman et al. (2016) Obs 3: *Lutemys warren*: according to Lyson et al. (2019) Obs 4: Kinosterninae: Joyce and Bourque (2016)
Pan-Chelonioidea	Evers et al. (2019), Gentry et al. (2019) Obs 1: *Mexichelys*, *Argillochelys antiqua*, and *Procolpochelys*: according to Zvonok and Danilov (2017) Obs 2: *Prionochelys*, *Euclastes wielandi***, *Asmodochelys*: according to Gentry et al. (2019) Obs 3: *Osonachelus decorata*: according to Lapparent de Broin et al. (2014) Obs 4: *Allopleuron qazaqstanense* and *Allopleuron lipsiensis* according to Karl et al. (2012) Obs 5: *Rhinochelys amaberti* according to Scavezzoni and Fischer (2018) Obs 6: Ctenochelyidae: Evers et al. (2019) Obs 7: *Santanachelys*: Protostegidae, according to Gentry et al. (2019), Evers et al. (2019), and Scavezzoni and Fisher (2018), closely related to *Solnhofia* (Thalassochelyidae according to Anquetin et al., 2017; Evers et al., 2019), Protostegidae become more basal, within Thalassochelyidae Obs 8: The position of Cheloniidae and Ctenochelyidae according to Evers et al. (2019) Obs 9: *Carolinochelys* and *Trachyaspis* closely related to Cheloniidae is supported by Weems and Brown (2017) and Zvonok and Danilov (2017) Obs 10: *Pacifichelys*, *Erquelinnesia*, *Tasbacka* spp., "*Argillochelys*" *africana* and *Euclastes* is supported partially by Weems and Brown (2017) and based on Zvonok and Danilov (2017) Obs 11: Lophochelyinae as sister group of those groups, excluding *Toxochelys*, and *Mexichelys* is supported by Parham and Pyenson (2010), Weems and Brown (2017), and Zvonok and Danilov (2017)

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TABLE A2 Results of generalized least squares (tsGLS) and ordinary least squares (OLS) regressions using turtle mean, maximum, and minimum body size and paleotemperature data.

	tsGLS							OLS					
	Phi	*p*. R^2	AIC	Var.	Coef.	*t*-Value	*p*-Value	*p*. R^2	AIC	Var.	Coef.	*t*-Value	*p*-Value
Body size mean	0.761	−.004	−57.426	interc.	2.494	46.05	<.000	−.009	−40.37	interc.	2.47	69.942	<.000
~δ^{18}O (Prokoph)				δ^{18}O	−0.01	−1.140	.266			δ^{18}O	−0.025	−1.061	.300
Body size mean	0.121	−.0003	−36.809	interc.	2.558	132.713	<.000	−.0004	−38.663	interc.	2.558	144.934	<.000
~δ^{18}O (Zachos)				δ^{18}O	−0.004	−0.452	.663			δ^{18}O	0.01	−0.508	.626
Body size max.	0.859	−.038	−14.857	interc.	3.12	16.439	<.000	.185	13.608	interc.	3.132	28.813	<.000
~δ^{18}O (Prokoph)				δ^{18}O	0.046	1.130	.271			δ^{18}O	0.085	1.166	.256
Body size max.	0.469	−.043	−8.991	interc.	3.163	29.724	<.000	−.161	−8.652	interc.	3.130	39.545	<.000
~δ^{18}O (Zachos)				δ^{18}O	0.070	1.348	.214			δ^{18}O	0.085	1.923	.091
Body size min.	0.937	−.011	−45.143	interc.	2.155	12.262	<.000	−.237	−17.639	interc.	1.978	34.891	<.000
~δ^{18}O (Prokoph)				δ^{18}O	0.03	−1.417	.171			δ^{18}O		−2.661	.014
Body size min.	0.420	−.0003	−26.379	interc.	1.988	46.845	<.000	−.00001	−27.545	interc.	1.994	64.800	<.000
~δ^{18}O (Zachos)				δ^{18}O	0.007	0.33	.75			δ^{18}O	−0.001	−0.048	.963

Note: Body size ($\log_{10}$ maximum dorsal carapace length in millimeters) and paleotemperature (δ^{18}O data as a proxy for paleotemperature from two different sources: Prokoph et al., 2008; Zachos et al., 2008) data were divided into time bins (24 time-bins when the Prokoph et al., 2008 δ^{18}O data were used and 10 time-bins when the Zachos et al., 2008 data were used).

Abbreviations: Coef., coefficient; interc., intercept; p.R^2, Nagelkerke pseudo *R*-squared; SD, standard deviation; Var., variable.

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