The multi-peak adaptive landscape of crocodylomorph body size evolution

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Abstract

Background: Little is known about the long-term patterns of body size evolution in Crocodylomorpha, the > 200-million-year-old group that includes living crocodylians and their extinct relatives. Extant crocodylians include 24 species and span a narrow range of phenotypes, being mostly large-bodied (3–7 m) semi-aquatic predators. However, extinct crocodylomorphs exhibit a wider range of phenotypes, and many of the earliest taxa were much smaller (< 1.2 m). This suggests a pattern of size increase during the evolutionary history of Crocodylomorpha. Furthermore, the influence of abiotic and biotic factors on crocodylomorph body size evolution is currently poorly understood. In this study, we quantify patterns of body size disparity through the evolutionary history of crocodylomorphs. We use phylogenetic comparative methods to characterise the macroevolutionary patterns that gave rise to this disparity, and to quantitatively test hypotheses of abiotic (i.e., palaeotemperature and palaeolatitude) and intrinsic (habitat) factors as potential drivers.

Results: Crocodylomorphs reached an early peak in body size disparity during the Late Jurassic, and underwent essentially continual decline since then. A multi-peak Ornstein-Uhlenbeck model outperforms all other evolutionary models fitted to our data (either single- or multi-regime models), indicating that the macroevolutionary dynamics of crocodylomorph body size evolution are better described within the concept of adaptive landscape, with most body size variation emerging after shifts to new adaptive zones (macroevolutionary regimes). We did not find support for a consistent evolutionary trend towards larger sizes among lineages (i.e., Cope's rule), or strong correlations of body size with climate. Instead, the intermediate to large body sizes of some crocodylomorphs are better explained by group-specific adaptations. In particular, the

evolution of a more aquatic lifestyle (especially marine) correlates, in several clades, with increases in average body size, though not without exceptions.

Conclusions: On large phylogenetic scales, shifts between macroevolutionary regimes (representing lineage-specific innovations) are more important than isolated climatic factors. Shifts leading to larger body sizes are commonly associated with predominantly aquatic or semi-aquatic groups. This, combined with the extinction of smaller-sized regimes (particularly during the Late Cretaceous and Cenozoic), gave rise to the upward-shifted body size distribution of extant crocodylomorphs compared to their terrestrial ancestors.

Keywords: Crocodylomorpha, Crocodyliformes, body size evolution, adaptive landscape, phylogenetic comparative methods, Ornstein–Uhlenbeck models.

Background

Body size influences many aspects of ecology, physiology and evolutionary history [1, 2, 3, 4, 5, 6], and patterns of animal body size evolution are a long-standing subject of macroevolutionary investigation (e.g., [7, 8, 9, 10, 11]). As a major focus of natural selection, it is expected that significant variation should occur in the body size of animals, although confined within biological constraints, such as skeletal structure, thermoregulation and resource availability [4, 5, 12]. Furthermore, body size can often be easily measured or estimated from both fossil and modern specimens, and has

therefore been widely used in phenotypic macroevolutionary studies [5, 7, 8, 9, 11, 13, 14, 15, 16, 17].

With few exceptions (e.g., [18, 19]), previous studies of tetrapod body size evolution have focused on mammals (e.g., [14, 15, 16, 20, 21, 22, 23, 24]) and dinosaurs or birds (e.g., [25, 26, 27, 28, 29, 30, 31, 32, 33]). Little is known, however, about other diverse and morphologically disparate clades. Among those, Crocodylomorpha represents an excellent group for studying large-scale evolutionary patterns, with a rich and well-studied fossil record covering more than 200 million years, as well as living representatives [34, 35, 36]. Previous work has investigated multiple aspects of crocodylomorph macroevolution, including spatial and temporal patterns of diversity [35, 36, 37], as well as morphological variation, disparity, and evolution, with a particular focus on the skull [38, 39, 40, 41, 42, 43, 44].

Nevertheless, studies quantitatively investigating macroevolutionary patterns of body size in crocodylomorphs have been restricted to particular time periods (e.g., Triassic-Jurassic body size disparity [45]) or clades (e.g., metriorhynchids [46]), limiting broader interpretations. For instance, the influence of environmental temperature on the growth and adult body size of animals has long been acknowledged as an important phenomenon [4], and has been considered of significant influence on the physiology and distribution of crocodylians [47, 48]. There is also strong evidence for climate-driven biodiversity patterns in the group (e.g., [36, 37]). Nevertheless, it remains unclear whether extrinsic factors, such as temperature and geographic distribution, have impacted long-term patterns of crocodylomorph body size evolution [49].

Most of the earliest crocodylomorphs, such as *Litargosuchus* and *Hesperosuchus*, were small-bodied animals (with estimated total lengths of less than 1

metre [50, 51]), contrasting with some giant forms that appeared later, such as *Sarcosuchus* and *Deinosuchus* (possibly more than 10 metres long [52, 53]), as well as with the intermediate to large sizes of extant crocodylians (1.5–7 m [54, 55]). The absence of small-bodied forms among extant species indicates a long-term pattern of body size increase in crocodylomorphs. Directional trends of increasing body size through time (see [56]), differential extinction of small bodied taxa, or other factors, such as climate-driven evolutionary change could explain this observation. However, because patterns of body size evolution along phylogenetic lineages of crocodylomorphs have not been characterised, its causes are unaddressed.

Since the end of the last century, palaeontologists have more frequently used quantitative comparative methods to investigate the tempo and mode of evolution along phylogenetic lineages [57, 58, 59], including studies of body size evolution [5, 14, 27, 29, 15, 60]. More recently, numerous studies have employed a phylogeny-based model-fitting approach, using maximum likelihood or Bayesian framework to identify the best-fitting statistical macroevolutionary model for a given phylogenetic comparative dataset [31, 33, 61, 62, 63, 64, 65].

Many of those works have tested the fit of a uniform macroevolutionary model, with a single set of parameters applied across all branches of a phylogeny (e.g., [46, 64, 66, 67]). This approach can be problematic as the dynamics of evolutionary trends vary through time, space and among clades [68, 69, 70, 71, 72]. Therefore, uniform models are incompatible with the complexity of the natural world. We approach this in the context of the Simpsonian Adaptive Landscape [73, 74], which have proved to be a fruitful conceptual framework for characterizing macroevolutionary changes, encompassing ideas such as adaptive zone invasion and quantum evolution [71, 75, 76]. Macroevolutionary landscapes provide a conceptual bridge for dialogues between

studies of micro- and macroevolution, and have benefitted from the subsequent advancements of molecular biology and genetics [77]. Within this paradigm, uniform models primarily represent static macroevolutionary landscapes, with unchanged peaks (or maximum adaptive zones [11]) persisting through long time intervals and across the phylogeny [71, 74, 75].

Incorporating biological realism into statistical models of evolution is challenging [78]. Many existing models are based on a Brownian motion (BM) process resulting from random walks of trait values along phylogenetic lineages [57, 75, 79]. Uniform Brownian motion has many interpretations. For example, it can be used as a model of drift, or of adaptive evolution towards lineage-specific selective optima that undergo random walks through time, and seems reasonable for describing undirected stochastic change [57]. Elaborations of BM models were subsequently proposed. Among these, the BM model with a tendency for directional evolution was formulated by adding a parameter μ [80], similar to the slope of trait values through time. "Trend-shift" models have also been proposed, in which the trend parameter (μ) undergoes clade-specific or time-specific shifts (G. Hunt in [33]).

Several evolutionary models also describe trait evolution under an Ornstein–Uhlenbeck (OU) process [58, 61, 64, 81, 82], which describes the evolution of a trait towards or around a stationary peak or optimum value, at a given evolutionary rate. Thus, multi-regime OU models can account for the existence of multiple macroevolutionary regimes (or adaptive zones, in the Simpsonian Adaptive Landscape paradigm). Even though many OU-based models typically require *a priori* adaptive hypotheses for inferring the trait optima of regimes [61], more recent methods attempt to solve this problem by estimating location, values and magnitudes of regime shifts without *a priori* designation of selective regimes [71, 78, 83]. In particular, the

SURFACE method [83] aims to identify convergent adaptive zones by allowing regime shifts to occur and identifying convergent regimes using AICc (Akaike's information criterion for finite sample sizes [84]). Originally designated to identify convergent trait evolution across phylogenetic lineages, the SURFACE algorithm makes use of a multi-peak OU-model and can be a tool to determine heterogeneity of macroevolutionary landscapes [33, 85, 86]. In this work, we employ a model-fitting approach, using non-uniform macroevolutionary OU-based models (SURFACE), to characterize the adaptive landscape of body size evolution in Crocodylomorpha. This represents the first comprehensive investigation of major body size evolutionary patterns across the entire evolutionary history of crocodylomorphs.

Methods

Proxy for body size

Extinct Crocodylomorpha are morphologically diverse, and frequently known from incomplete remains. Therefore, precise estimation of their body sizes, and those of comparable fossil groups, can be challenging (see [87, 88] for related considerations). There are many methods and equations for estimating crocodylomorph body size (either body mass or length) available in the literature. The most frequently used equations are derived from linear regressions based on specimens of modern species, using both cranial [53, 89, 90, 91, 92, 93] and postcranial [94, 95] measurements as proxies. Although some of these approaches have been claimed to work well when applied to extinct taxa (e.g., [95]), they are expected to be less accurate for extinct species that have different body proportions to those of extant species [46, 88, 96, 97]. An alternative approach that has been suggested is to use clade-specific equations that are derived from regressions using fossil specimens with complete skeletons preserved,

such as the recently proposed equations for estimating body length in the highly specialised marine clade Thalattosuchia [46, 88]. Nevertheless, using this approach for the entire Crocodylomorpha would require numerous different equations and, consequently, complete specimens for all desired subclades.

Campione & Evans [98] demonstrated a universal scaling relationship between proximal (stylopodial) limb bone circumferences and the body masses of terrestrial tetrapods. For instance, their equations, using both femur and humerus circumference, have been applied to estimate body mass of fossil dinosaurs (e.g., [31, 32, 33, 98, 99]). However, due to a historical neglect of crocodylomorph postcranial anatomy, especially for Mesozoic taxa [97], relatively less information is available on this part of the skeleton. Based on data collected for the present study, total or partial skull lengths (i.e., complete skulls or lacking only the snouts) can be measured in fossil specimens of approximately 50% of crocodylomorph species, whereas femoral and humeral shaft circumferences or lengths can only be measured in 35% of species. This greatly reduces the number of taxa that can be sampled and limits the utility of using postcranial elements as a proxy for body size. Similar problems exist for other methods, such as the "Orthometric Linear Unit" proposed by Romer & Price [100] that uses dorsal centrum cross section [101], as well as volumetric reconstructions (e.g., [102, 103, 104, 105, 106]), since relatively complete postcranial specimens are required.

We sought an appropriate proxy for studying body size across all crocodylomorph evolutionary history that also maximised available sample size, to allow as comprehensive a study of evolutionary history as possible. Thus, we decided to use two cranial measurements as proxies for total body length: total dorsal cranial length (DCL) and dorsal orbito-cranial length (ODCL), which is measured from the anterior margin of the orbit to the posterior margin of the skull. By using cranial

measurements instead of estimated total body length, we are ultimately analysing patterns of cranial size evolution in crocodylomorphs. Nevertheless, by doing this we also avoid the addition of errors to our model-fitting analyses, since previous works have reported problems when estimating total body length from cranial measurements, particularly skull length (Fig. 1), as the equations were formulated using modern species and different crocodylomorph clades are likely to have body proportions distinct from those of living taxa (e.g., [46, 88, 97]). Furthermore, the range of body sizes among living and extinct crocodylomorphs is considerably greater than variation among size estimates for single species. Therefore, we expect to recover the most important macroevolutionary body size changes in our analyses even when using only cranial measurements. The use of ODCL, in addition to DCL, is justified as it allows us to examine the sensitivity of our results to changes in proportional snout length, as a major aspect of length change in crocodylomorph skulls results from proportional elongation or shortening of the snout [107, 108, 109]. Also, more taxa could be included in our analyses when doing so, because ODCL can be measured from some incomplete skulls.

The DCL dataset includes 219 specimens (representing 178 taxa), whereas the ODCL dataset includes 240 specimens (195 taxa). In total, measurements from 118 specimens (83 taxa) were collected via first-hand examination from specimens, using callipers and measuring tape. The remaining information was collected from the literature (98 specimens) or photographs (21 specimens) supplied by other researchers, and measurements were estimated using the software ImageJ (see Additional file 2 for the complete list of sampled specimens). We used mean values in those cases where we had cranial measurements for multiple specimens of the same taxon. For both the model-fitting and correlation analyses, we used log-transformed skull measurements in

millimetres. However, to help us further interpret and discuss our results, total body length was subsequently estimated using the equations presented by [91].

Phylogenetic framework

For the phylogenetic framework of Crocodylomorpha, the aim was to maximise taxon inclusion and to use a phylogenetic hypothesis that best represents the current consensus. We primarily used an informally modified version of the supertree presented by Bronzati et al. [35], which originally contained 245 taxa. Apart from modifications seeking to maximise congruence of the tree with the current understanding of the phylogeny of the group, we also added recently published species, and removed taxa that have not yet received a formal description and designation. Also, species not previously included in phylogenetic studies but for which we had body size data were included based on the phylogenetic position of closely related taxa (see Additional file 1 for more information on the supertree construction). Thus, our updated version of the supertree contains 296 crocodylomorph species, as well as nine closely related taxa used as outgroups for time-scaling the trees (see below).

To accommodate major uncertainties in the crocodylomorph phylogeny, we also constructed two other supertrees, with alternative topologies, varying the position of Thalattosuchia. Thalattosuchians are Jurassic–Early Cretaceous aquatic crocodylomorphs, some of which were probably fully marine [110]. They have classically been placed within Neosuchia, as the sister taxon of Tethysuchia [108]. Nevertheless, some authors have argued that this close relationship may result from the convergent acquisition of longirostrine snouts in both groups [107, 111], and some recent works have suggested alternative positions for Thalattosuchia, within or as the sister group of Crocodyliformes (i.e., only distantly related to Neosuchia [109, 112, 113,

114]). Accordingly, to test the influence of uncertainty over the phylogenetic position of Thalattosuchia, we performed our macroevolutionary analyses using three distinct topologies of Crocodylomorpha (Fig. 2). In the first topology, the more classic position of Thalattosuchia was maintained (Thalattosuchia as the sister taxon of Tethysuchia and within Neosuchia; as in the original supertrees of Bronzati et al. [34, 35]). In the two alternative topologies, Thalattosuchia was placed as the sister group of either Crocodyliformes (as non-crocodyliform crocodylomorphs), following the position proposed by Wilberg [109], or Mesoeucrocodylia (as the sister group of the clade formed by Neosuchia + Notosuchia in our topology), following Larsson & Sues [115] and Montefeltro et al. [113]. It is worth stressing that discrepancies among competing phylogenetic hypotheses do not concern only the “thalattosuchian problem” described above. However, our decision to further investigate only the impact of the different positions of Thalattosuchia is based on its high taxic diversity and the impact that its phylogenetic position has on branch lengths across multiple parts of the tree, factors that can substantially alter macroevolutionary patterns detected by our analyses.

For performing our macroevolutionary analyses, it was necessary to time-calibrate the phylogenies, assigning ages to both terminal taxa and nodes [116]. This is a crucial step in comparative analyses of trait evolution, as the use of different methods may impact upon the inference of evolutionary models and the interpretation of results [117, 118]. As such, we decided to use three different time-scaling methods, each one with benefits and drawbacks. For these methods, ages (first and last occurrence dates) were initially obtained from the Paleobiology Database, but were then checked using primary sources in the literature. To accommodate uncertainties related to the ages of terminal taxa (i.e., most taxon ages are based on single occurrences, known only within rather imprecise bounds), we treated these first and last occurrences dates as maximum

and minimum possible ages and drew terminal dates for time-calibration from a uniform distribution between these.

Firstly, we used the minimum branch length method (*mbl* [18]), in which a minimum branch duration is set *a priori*, to avoid the presence of undesirable and unrealistic zero-length branches [116, 118]. For our analyses, the minimum of 1 Myr was set. We also used two recently introduced probabilistic time-scaling methods. The *cal3* is a stochastic calibration method that requires estimates of sampling and diversification (branching and extinction) rates to draw likely divergence dates under a birth–death-sampling model [117, 119]. The fact that most crocodylomorph taxa are singletons (i.e., very few genera or species have multiple occurrences in different time intervals) prevented us from directly calculating speciation, extinction and sampling rates needed as inputs to the *cal3* method. Thus, when using this time-scaling method for our analyses, we adopted the same rates estimated for dinosaurs in Lloyd et al. [119] (i.e., extinction and speciation rates = 0.935; sampling rate = 0.018), which used the apparent range-frequency distribution of dinosaurs in the Paleobiology Database for these estimates. Although essentially different from that of dinosaurs, the crocodylomorph fossil record is arguably comparable enough to result in similar rates, and *a posteriori* comparison to other time-scaling methods demonstrated that results were reasonable. Finally, we also used the *extended Hedman* method, proposed by Lloyd et al. [119], which is an expansion of the Bayesian approach presented by Hedman [120], that uses the ages of successive outgroup taxa relative to the age of the node of interest to date this node by sampling from uniform distributions [119, 121].

Since the input phylogenies (i.e., the three alternatives topologies of the supertree, see above) were not completely resolved, we randomly resolved the polytomies, generating 20 completely resolved trees for each alternative phylogenetic

scenario (i.e., with different positions of Thalattosuchia). These trees were then time-scaled using the three time-calibration methods. Time-scaling with the *mbl* and *cal3* methods were performed using the package *paleotree* [122] in R version 3.5.1 [123], whilst the *Hedman* method was implemented also in R, using the protocol published by Lloyd et al. [119].

Macroevolutionary analyses

We applied a model-fitting approach to characterize patterns of body size evolution in Crocodylomorpha, with an emphasis on evolutionary models based on the Ornstein-Uhlenbeck (OU) process [33, 58, 61, 64, 83]. The first formulation of an OU-based model was proposed by Hansen (1997), to incorporate Felsenstein's [81] suggestion of using the Ornstein-Uhlenbeck (OU) process as a basis for comparative studies [61, 82]. OU-based models (also known as "Hansen" models) express the dynamics of a quantitative trait evolving along the branches of a phylogeny as the result of stochastic variation around a trait "optimum" (expressed as theta: θ), towards which trait values are deterministically attracted (the strength of attraction is given by alpha: α). The constant σ^2, describes the stochastic spread of the trait values over time (i.e., under a Brownian motion process). Accordingly, the OU model can be formulated as:

$$dX(t) = \alpha\,[\theta - X(t)]\,dt + \sigma dB(t)$$

This equation expresses the amount of change in trait X during the infinitesimal time interval from t to $t + dt$. As expressed above, the formulation includes a term describing trait attraction towards θ, which is the product of α and the difference between $X(t)$ and θ. The term $\sigma dB(t)$ describes stochastic evolution in the form of

Brownian motion (BM), with random variables of mean zero and variance of *d*t (thus, σ^2 is the rate of stochastic evolution). In this sense, if α is zero, the attraction term becomes zero, and the result is evolution by BM as a special case of OU [33, 61, 64]. The OU model can also simulate trait evolution patterns similar to that observed under other evolutionary models, such as BM with a trend incorporated, and "white noise" or stasis [33, 58, 64]. Thus, the parameters of the OU model are crucial for interpreting the mode of evolution [58, 61]. For example, the estimated ancestral trait value (i.e., the value of θ at the root of the tree) is given by the parameter Z_0. Also, by obtaining ln (2)/α, we are calculating the time taken for a new macroevolutionary regime to become more influential than the ancestral regime (i.e., how long it takes to θ to be more influential than Z_0). This parameter is often called the phylogenetic half-life (or $t_{0.5}$).

Among the methods that attempt to model adaptive evolution under the framework of an Ornstein-Uhlenbeck process (e.g., [78, 82, 124]), the SURFACE algorithm [83] estimates the fit of a non-uniform OU-based model by allowing shifts in trait optima (θ) among macroevolutionary regimes. SURFACE locates regime shifts using stepwise AICc (Akaike's information criterion for finite sample sizes [84, 125, 126]), with a forward phase (that searches for all regime shifts in the phylogeny) and a backward phase (in which improvements of AICc scores merge similar regimes, detecting convergent evolution). Although it allows θ to vary among regimes, SURFACE assumes fixed whole-tree values of σ^2 and α [83].

We compared the performance of two different OU-based models, one with a single trait optimum or a single macroevolutionary regime ("OU model") and another non-uniform model with multiple regimes ("SURFACE model"). To test if other macroevolutionary models could provide a better description of the observed patterns of crocodylomorph body size evolution, we also compared the OU-based models with

other BM-based models. First, the diffusion by Brownian motion (BM model), which assumes evolution via random walks, with a constant normally distributed deviation from the observed morphology, resulting in no directional trend in trait mean, but with increasing trait variance through time [57, 62, 63, 64]. Second, the "early burst" (EB model; also known as "ACDC model" [127]), in which the lineages experience an initial maximum in evolutionary rate of change, that decreases exponentially through time according to the parameter *r* [128]. This results in a rapid increase of trait variance in the early evolution of the lineages, followed by a deceleration [127, 128].

Finally, we also fitted a set of uniform and non-uniform trend-like models to our data. In the uniform "trend" model (i.e., with a single regime), the parameter μ is incorporated into the BM model to describe directional multi-lineage increase or decrease in trait values through time, in the entire clade [62, 63, 80]. Non-uniform "trend" models allow for shifts in the parameter μ, which can be explored in two different ways according to the formulations of non-uniform trend models formulated by G. Hunt and presented in Benson et al. [33]: temporal shifts in μ ("time-shift trend models") or shifts in μ at specific nodes of the tree ("node-shift trend models"). In time-shift trend models, evolutionary dynamics are uniform across all branches alive during each interval. Shifts to a new value of μ occurs at time-horizons and are applied to all lineages alive at that time. In node-shift trend models, values of μ can vary among lineages. In a similar approach to the forward phase of SURFACE, the shifts in these non-uniform trend-like models are detected via stepwise AICc. In both time-shift and node-shift models, the Brownian variance (σ^2) is constant across all regimes [33]. For our macroevolutionary analyses with the entire crocodylomorph phylogeny, we fitted trend-like models that allowed up to three time-shits and 10 node-shifts to occur.

We then performed a set of exploratory analyses to test which of these evolutionary models (SURFACE, OU, BM, EB and trend-like models) offered the best fit to our data, using the different time-scaling methods (*mbl*, *cal3* and *Hedman* methods) and both log-transformed cranial measurements (DCL and ODCL). To reduce the computational demands, we used only 20 randomly resolved trees of the original supertree topology (with Thalattosuchia positioned traditionally within Neosuchia). The aim was to compare the performance of the OU-based models, particularly the SURFACE model, against the other evolutionary models, but also to evaluate possible influences of the different time-scaling methods and body size proxies. Maximum-likelihood was employed to fit these models to our body size data and the phylogeny of Crocodylomorpha, and we compared the AICc scores of each model.

Previous works suggested caution when fitting OU models in comparative analyses. The issue of “large p small n” when using multi-regime OU models, demonstrated by Ho & Ané [129], can result in false positives and spurious support to more complex models [33, 72]. This issue may be reduced when using non-ultrametric trees (as done here), as this improves identifiability of the parameters of OU models [64, 129]. Another approach would be using the phylogenetic Bayesian information criterion (“pBIC”), proposed by Khabbazian et al. [72], as an alternative to using AICc for selecting the best fit. Ho & Ané [129] demonstrated that AICc is biased towards model overfit and suggested using pBIC, a modified Bayesian information criterion (mBIC [130]), which is more conservative and has low rates of false positive identification of OU model regime shifts [33, 72]. The pBIC criterion is still not implemented for all evolutionary models used in our analyses, which prevents its usage for comparative model-fitting analyses. However, we did use pBIC during the backward

phases of our SURFACE model searches to ensure that artefactually complex models were not returned.

Following these exploratory analyses, we focused our analyses on the SURFACE model, as the AICc scores showed this to be the preferred evolutionary model for our data (see the "Results" section). This second phase of analyses made use of all three alternative phylogenetic scenarios (varying the position of Thalattosuchia) to test the influence of phylogeny in interpretations of evolutionary regimes for body size in Crocodylomorpha. We fitted the SURFACE model to 20 randomly resolved trees from each of these alternative topologies, using again three different time-scaling methods (*mbl*, *cal3* and *Hedman* methods) and two log-transformed cranial measurements (DCL and ODCL). As before, we also implemented a conservative backward-phase that uses pBIC searches instead of AICc.

Two well-recognized crocodylomorph subclades, Notosuchia and Crocodylia, returned a high frequency of macroevolutionary regime shifts, representing an apparently complex evolutionary history under the SURFACE paradigm. However, SURFACE fits a single value of α to all regimes, and therefore could overestimate the strength of evolutionary constraint within regimes, and consequently miscalculate the number of distinct regimes within clades showing more relaxed patterns of trait evolution. We investigated this possibility by fitting the initial set of evolutionary models (SURFACE, OU, BM, EB and trend-like models) to the phylogenies of these two subclades (using 100 randomly resolved trees of each group, time-scaled with the *mbl* method) and their body size data (using only the ODCL dataset, since it includes more species). Differently from what was done for the entire crocodylomorph phylogeny, for Notosuchia we fitted trend-like models with up to 2 time-shifts and 5 node-shifts, whereas for Crocodylia we allowed up to 3 time-shifts and 7 node-shifts to

occur (given that these two clades include fewer species and fewer shifts are expected, and that models with an exceeding number of shifts usually receive weaker support). In addition, for these same clades, we also employed the OUwie model-fitting algorithm [82], fitting different BM and OU-based models which allow all key parameters to vary freely (since SURFACE allows only θ to vary, whereas it assumes fixed values of σ^2 and α for the entire tree). However, differently from SURFACE, OUwie needs *a priori* information on the location of regime shifts in order to be implemented. Thus, we incorporated the regime shifts identified by SURFACE into our data (phylogenetic and body size data) to fit four additional evolutionary models using the OUwie algorithm: BMS, which is a multi-regime BM model that allows the rate parameter σ^2 to vary; OUMV, a multi-regime OU-based model that allows σ^2 and the trait optimum θ to vary; OUMA, also a multi-regime OU model, in which θ and the constraint parameter α can vary; and OUMVA, in which all three parameters (θ, α and σ^2) can vary. Since computing all these parameters estimates can be an intensively demanding task [82], some of the model fits returned nonsensical values and were, therefore, discarded. Nonsensical values were identified by searching for extremely disparate parameter estimates, among all 100 model fits (e.g., some model fits found σ2 values higher than 100,000,000 and α lower than 0.00000001).

All macroevolutionary analyses were performed in R version 3.5.1 [123]. Macroevolutionary models BM, trend, EB, and OU with a single regime were fitted using the R package *geiger* [124]. The SURFACE model fits were performed with package *surface* [83]. Implementation of pBIC functions in the backward-phase of SURFACE model fits, as well as the functions for fitting non-uniform trend-like models, were possible with scripts presented by Benson et al. [33]. The additional

model-fitting analyses, using the OUwie algorithm, were implemented with the package *OUwie* [131].

Correlation with abiotic factors

To test whether abiotic environmental factors could be driving the evolution and distribution of body sizes in crocodylomorphs, we extracted environmental information from the literature. As a proxy for palaeotemperature, we used $\delta^{18}O$ data from two different sources. The dataset from Zachos et al. [132] assembles benthic foraminifera isotopic values from the Late Cretaceous (Maastrichtian) to the Recent. The work of Prokoph et al. [133] compiled sea surface isotopic values from a range of marine organisms. Their dataset is divided into subsets representing palaeolatitudinal bands. For our analyses, we used the temperate palaeolatitudinal subset, which extends from the Jurassic to the Recent, but also the tropical palaeolatitudinal subset, which extends back to the Cambrian. For the correlation analyses, we used 10 Myr time bins (see Additional file 1 for information on time bins), by taking the time-weighted mean $\delta^{18}O$ for data points that fall within each time bin. For the body size data used in the correlation tests, we calculated maximum and mean size values for each time bin, using both DCL and ODCL datasets. Correlations between our body size data and the proxies for palaeotemperature were first assessed using ordinary least squares (OLS) regressions. Then, to avoid potential inflation of correlation coefficients created by temporal autocorrelation (the correlation of a variable with itself through successive data points), we used generalised least squares (GLS) regressions with a first-order autoregressive model incorporated (see e.g., [36, 134, 135, 136]). Furthermore, to test the possible differential influence of temperature on marine versus continental

(terrestrial and freshwater) animals, we also created two additional subsets of our data, one with only marine and another with only non-marine crocodylomorphs.

Additionally, we collected palaeolatitudinal data for every specimen in our dataset from the Paleobiology Database (PBDB) and the literature, and tested the correlation between these and our body size data (DCL and ODCL datasets). To test whether our body size data is correlated with palaeolatitudinal data, we first applied OLS regressions to untransformed data. Then, to deal with possible biases generated by phylogenetic dependency, we used phylogenetic generalized least squares regressions (PGLS [137]). For this, branch length transformations were optimised between bounds using maximum likelihood using Pagel's λ [138] (i.e., argument λ= "ML" within in the function pgls () of the R package *caper* [139]). As for the correlation analyses between our body size data and palaeotemperature, we also analysed marine and only non-marine taxa separately.

To explore the effects of these two abiotic factors on the distribution of body sizes at more restricted levels (temporal and phylogenetic), we repeated our regression analyses using subsets of both ODCL and DCL datasets, including body size data only for species of Crocodylia, Notosuchia, Thalattosuchia, and Tethysuchia. For crocodylians, correlations with paleotemperature were restricted to the Maastrichtian until the Recent (i.e., data from [132]). All correlation analyses used log-transformed cranial measurements (DCL and ODCL) in millimetres and were performed in R version 3.5.1 [123]. GLS regressions with an autoregressive model were carried out using the package *nlme* [140], whereas PGLS regressions used the package *caper* [139].

Results

Comparative model-fitting analyses

Comparisons between the AICc scores for all the evolutionary models fitted to our crocodylomorph body size data (Fig. 3) show extremely strong support for the SURFACE model (note that lower AICc values indicate higher support). This is observed for all time-scaling methods (*mbl*, *cal3* and *Hedman* methods) and both body size proxies (DCL and ODCL). All uniform models exhibit relatively similar AICc scores, including the OU model with a single macroevolutionary regime, and all of these have poor support compared to the SURFACE model. Node-shift trend models received higher support than both uniform and time-shift trend models for most phylogenies, but have AICc values that are more similar to the set of uniform models than to the SURFACE models. Single-regime OU models only have better AICc scores than multi-trend models when trees are time-scaled with the *mbl* method. Even the best trend-like model (usually the models with six or seven node-shifts) have significantly weaker support than SURFACE, regardless of the time-calibration method (see Additional file 3 for a complete list of AICc scores, including for all trend-like models). Based on the extremely strong support found for the SURFACE model, as well as on the capability of the SURFACE algorithm to locate the regime shifts across the phylogeny [83], we decided to focus on the SURFACE model fits to characterize in more detail the patterns of crocodylomorph body size macroevolution.

Appraising the SURFACE model fits

Aiming to minimise the problem of biased AICc support for more complex models (see [72, 129]), we implemented two rounds of SURFACE model fits: one using the original algorithm [83], with stepwise AICc searches in the two phases of SURFACE; and another using a modified version of the SURFACE algorithm presented by Benson et al. [33], which uses pBIC searches in the backward-phase. This latter approach is more

conservative and potentially should be able to indicate when overly complex models are being inappropriately supported, as we used the same tree topologies used for SURFACE fits using only AICc searches. Comparisons between our SURFACE results using pBIC and only AICc show that, in almost all cases, identical model fits are found for the same trees, with the same parameter estimates (Table 1). For the very few trees in which this is not true, the models are still very similar, with only minimal differences in the parameters values, mainly in θ values. This pattern was maintained when using any time-scaling method, cranial measurement or tree topology, indicating that our SURFACE model fits are not erroneously complex.

Table 1. Parameter estimates from some of our SURFACE model fits, using both stepwise search algorithms.

Tree number	**Parameter estimates**							
	full-AICc searches				**pBIC in the backward-phase**			
	α	**σ^2**	**Z_0**	**Number of regimes**	**α**	**σ^2**	**Z_0**	**Number of regimes**
1	0.217	0.005	1.642	10	0.217	0.005	1.642	10
2	16.06	0.418	1.648	8	16.06	0.418	1.648	8
3	0.162	0.004	1.647	10	0.162	0.004	1.647	10
4	0.148	0.004	1.653	10	0.148	0.004	1.653	10
5	0.128	0.003	1.639	10	0.128	0.003	1.639	10
6	0.055	0.002	1.696	9	0.055	0.002	1.696	9
7	0.058	0.002	1.704	10	0.058	0.002	1.704	10
8	0.08	0.003	1.657	9	0.08	0.003	1.657	9
9	0.148	0.003	1.641	9	0.148	0.003	1.641	9
10	0.523	0.012	1.648	8	0.523	0.012	1.648	8

SURFACE search algorithms: full-AICc searches and backward-phase of SURFACE with pBIC searches. Model fits of the first ten trees (using the ODCL dataset, the *mbl* time-scaling method and with Thalattosuchia within Neosuchia). Z_0 values in $\log_{10}$ millimetres. "Number of regimes"

represents the number of main ("convergent") regimes for each model fit. See Additional file 4 for plots of all SURFACE model fits, containing information about parameter estimates.

SURFACE model fits exhibit a strong correlation between AICc/pBIC scores and the number of macroevolutionary regime shifts (Fig. 4; see Additional file 4 for plots of all SURFACE model fits). In general, model fits with lower (i.e., better) AICc/pBIC values tend to have more regime shifts. In other words, more complex models seem to be favoured by better AICc/pBIC values. Additionally, apart from higher (i.e., worse) AICc/pBIC values, simpler SURFACE model fits also tend to exhibit lower α values. Thus, simpler model fits are characterised by high-AICc/pBIC scores and low values of α. Because we used the same randomly resolved tree topologies for each of the time-scaling methods (*mbl*, *cal3* and *Hedman*), we were able to compare the SURFACE model fits of these same trees obtained across different branch-length calibration methods, by calculating pBIC scores (e.g., calculating the pBIC score the regime configuration obtained from analysis of the *cal3*-calibrated tree on the *mbl*-calibrated tree; see Additional file 5 for all cross plotting of SURFACE model fits on tress using different time-scaling methods). This shows that many of the simplest SURFACE model fits are suboptimal (i.e., received worse pBIC scores) compared to more complex regime configurations obtained during searches on trees with different branch-lengths (Table 2). The simple models returned by some of our searches therefore represent failure of the stepwise-AICc search to find the best regime configuration and are consequently not considered when we describe the macroevolutionary patterns of body size in crocodylomorphs. Suboptimal model fits were more frequent on topologies with Thalattosuchia placed as the sister group of Crocodyliformes, particularly when time-scaled using *mbl* and *cal3* methods. Although we cannot fully explain why the frequency of suboptimal model fits varied among

topologies with alternative positions of Thalattosuchia, it is expected that AIC procedures face difficulties when finding the best fits for complex datasets [141], even when using pBIC. However, the SURFACE model fits represent a useful simplification of major patterns of body size evolution in a group, and particularly the shifts of average body sizes among clades on the phylogeny. In this respect, they provide an overview of crocodylomorph body size evolution that is otherwise lacking from current literature.

Table 2. Examples of comparisons between simpler and more complex SURFACE model fits for the same trees.

Tree number and original time-scaling method	**pBIC scores**	
	Simple model	**Complex model**
Tree 3 (*mbl*-calibrated)	**mbl fit on mbl tree** -130.2	**Hedman fit on mbl tree** -158.9*
Tree 3 (*cal3*-calibrated)	**cal3 fit on cal3 tree** -139.1	**Hedman fit on cal3 tree** -157*
Tree 4 (*cal3*-calibrated)	**cal3 fit on cal3 tree** -132.6	**Hedman fit on cal3 tree** -133.8*
Tree 5 (*mbl*-calibrated)	**mbl fit on mbl tree** -105.7	**cal3 fit on mbl tree** -133.5*
Tree 6 (*mbl*-calibrated)	**mbl fit on mbl tree** -130.1	**Hedman fit on mbl tree** -160.4*
Tree 7 (*Hedman*-calibrated)	**Hedman fit on Hedman tree** −164.9*	**mbl fit on Hedman tree** -152.8

We obtained pBIC scores for regime configuration mapped onto trees with the same topology but using different time-calibration methods. By doing this, we were able to compare the pBIC scores between simpler and more complex SURFACE model fits. Model fits shown are for trees with Thalattosuchia as the sister group of Crocodyliformes and using body size data from the ODCL dataset only. See Additional file 5 for all cross plotting of regime configurations.

Our SURFACE analyses using different body size proxies (DCL and ODCL) and time-scaling methods (*mbl*, *cal3* and *Hedman* methods) enabled us to assess the influence of these factors on our SURFACE results. First, in general, alternative time-scaling methods did not cause substantial modifications to the SURFACE model fits in terms of numbers of regimes or parameter values. However, as these methods generate different divergence times, branch lengths and ages estimated for the origin of subclades are expected to be distinct. Comparatively, while the *Hedman* method tended to estimate arguably too old ages for the origins of some clades (estimating, for example, the origin of the crown-group to be as old as the Late Jurassic compared to the Late Cretaceous ages of the oldest known unequivocal crocodylians), trees that used the *cal3* method often included branches with lengths very close to zero. Furthermore, trees that were time-scaled using *cal3* recovered comparatively more suboptimal SURFACE model fits than those that used the other two methods. Thus, we favour the SURFACE model fits with trees calibrated using the *mbl* method when describing and discussing our SURFACE results (even though we did not completely discard those generated using the other two methods).

Second, comparable results are found across model fits using different cranial measurements (DCL and ODCL), but the same time-scaling methods and tree topologies. Although there are slightly more suboptimal model fits when using the DCL dataset, we do not have enough evidence to support the idea that the use of a different cranial measurement is causing this pattern, as due to taxon sampling the phylogenetic trees used for fitting models using DCL and ODCL are different. However, in order to minimise the number of model fits used to characterise crocodylomorph body size evolution, we focused the description of macroevolutionary patterns on the results obtained from the ODCL dataset, as it includes more species than the DCL dataset, and

we usually obtain more realistic estimated body size values (for θ and Z_0) when using the ODCL equation presented by [91].

The position of Thalattosuchia had an influence on range of the attraction parameter (α), which is a whole-tree, fixed parameter in the SURFACE model fits. When Thalattosuchia is placed as the sister taxon of Crocodyliformes, the lowest values of α were obtained (ranging from 0.0072 to 0.1399), perhaps reflecting the more frequent suboptimal model fits for this scenario, and consequently the highest phylogenetic half-lives ($t_{0.5}$ = 4.95 to 95.99 Myr). In the other two alternative scenarios (i.e., Thalattosuchia either within Neosuchia or as the sister group of Mesoeucrocodylia), comparable values of α were found, ranging from 0.0136 to 0.6595, with considerably shorter phylogenetic half-lives ($t_{0.5}$ = 1.05 to 50.89 Myr).

Describing the body size macroevolutionary patterns in Crocodylomorpha

We used our SURFACE model fits to describe patterns of crocodylomorph body size evolution, focusing on the best model fits from the analyses implemented with pBIC searches (i.e., the low-pBIC/high-α model class), using body size data from the ODCL dataset and trees time-calibrated mainly (but not only) with the *mbl* method (see Additional file 4 for plots of all SURFACE model fits). Most SURFACE model fits identified more than four main macroevolutionary regimes (with different θ values). Those are distributed along crocodylomorph phylogeny by means of numerous regime shifts, usually more than 15, independently of the position of Thalattosuchia. Trait optima values for these regimes varied significantly among different crocodylomorph subclades and are described in detail below. Overall, regime shifts are frequently detected at the bases of well-recognised clades, such as Thalattosuchia, Notosuchia and Crocodylia. Nevertheless, shifts to new regimes are not restricted to the origins of these

diverse clades, since many other regime shifts are observed across crocodylomorph phylogeny, including regimes containing only a single species.

Our SURFACE results indicate an ancestral regime of small body sizes for Crocodylomorpha, regardless of the topology or time-scaling method used (Figs. 5, 6, and 7). This is consistent with the small body sizes of most non-crocodyliform crocodylomorphs such as *Litargosuchus leptorhynchus* and *Hesperosuchus agilis* [50, 51]. Trait optima for this initial regime (Z_0) ranged from 66 to 100 cm (total body length was estimated only after the SURFACE model fits, based on the equation from [91]; see the "Methods" section). Very few or no regime shifts are observed among non-crocodyliform crocodylomorphs (Figs. 5, 6 and 7b), except for when Thalattosuchia is placed outside Crocodyliformes (Fig. 7a). But even in this latter case, shifts are seen only within or at the base of Thalattosuchia. For example, some trees time-scaled with *mbl* (tree number 11; Fig. 7b) and *cal3* (trees number 13 and 15) methods show a Late Triassic regime shift towards much larger body lengths (θ = 560–880 cm) at the base of Thalattosuchia, but many model fits that used these methods also exhibit much simpler models, with very few regime shifts. When using the *Hedman* method, however, a shift at the base of Thalattosuchia is more frequently observed, in many cases representing the oldest regime shift in the evolutionary history of Crocodylomorpha, and the only one to occur before the Triassic-Jurassic boundary (although the oldest thalattosuchian fossils only occur in the Early Jurassic). Regardless of the position of Thalattosuchia, the ancestral regime of all crocodylomorphs (Z_0) was inherited by protosuchids (such as *Protosuchus*, *Orthosuchus*, and *Edentosuchus*) and some other non-mesoeucrocodylian crocodyliforms (e.g., *Shantungosuchus*, *Fruitachampsa*, *Sichuanosuchus* and *Gobiosuchus*).

Patterns of body size evolution at the base of Mesoeucrocodylia are influenced by the position of Thalattosuchia. In nearly all model fits with Thalattosuchia within Neosuchia (Figs. 5 and 6), a regime of smaller body sizes (θ = 130–230 cm) is observed at the base of the branch leading to Mesoeucrocodylia, with the same regime frequently inherited by the branches leading to both Notosuchia and Neosuchia. When thalattosuchians are placed as the sister group of Crocodyliformes, a similar pattern is observed in most trees time-scaled with the *Hedman* method, but also in trees number 13 and 15 with the *cal3* method, and number 11 (Fig. 7a) with the *mbl* method. With Thalattosuchia as the sister group of all the other mesoeucrocodylians (i.e., Notosuchia + Neosuchia), most trees exhibit a change to a regime of larger sizes (θ = 210–490 cm) occurring at the branch leading to Mesoeucrocodylia (Fig. 7b), although some model fits (e.g., trees number 5, 8, 10, and 16 using all time-scaling methods) show no shift at the base Mesoeucrocodylia (i.e., inheriting the same regime as non-mesoeucrocodylian crocodyliforms). When a change at the base of Mesoeucrocodylia is observed, this same regime is usually inherited by Neosuchia, and shifts to regimes of smaller sizes (θ = 66–140 cm) are subsequently seen either at the base of or within Notosuchia.

The position of Thalattosuchia also has an impact on the configuration of regime shifts among non-eusuchian neosuchians. The regime of relatively smaller sizes at the base of Mesoeucrocodylia is maintained at the base of Neosuchia in most model fits of trees with Thalattosuchia within Neosuchia (Fig. 5 and 6). Subsequently, regime shifts towards larger sizes (θ = 210–500 cm) are seen among some taxa such as goniopholidids, *Agaresuchus* and *Allodaposuchus*, whereas shifts to regimes of smaller θ values (41–140 cm) are also detected in branches associated with small taxa (e.g., atoposaurids, susisuchids and *Pietraroiasuchus*). More complex models of trees with Thalattosuchia placed as the sister group of Crocodyliformes (e.g., tree 11, using the

mbl method; Fig. 7a) show the same pattern. Comparatively, when Thalattosuchia is placed as the sister taxon of Mesoeucrocodylia (Fig. 7b), the regime of larger sizes seen at the base of Neosuchia is frequently inherited by most non-eusuchian neosuchians (except for some of the smallest taxa, such as atoposaurids and susisuchids), resulting in fewer regime shifts amongst non-eusuchian neosuchians than in the other two alternative scenarios.

Within Notosuchia, most model fits show many taxa inheriting the same regime of smaller sizes present at the base of the clade (θ = 66–140 cm), regardless of the position of Thalattosuchia and the time-scaling method used. Nevertheless, the group is also characterised by many additional regimes, with considerably variable trait optima, usually ranging from 66 to 460 cm. Shifts to regimes of smaller sizes are often seen in uruguaysuchids, *Anatosuchus*, *Pakasuchus* and *Malawisuchus*, with θ values very similar to or the same as the ancestral crocodylomorph regime (Z_0). Furthermore, shifts towards larger sizes are seen among peirosaurids (θ = 210–250 cm), and, more dramatically, in sebecosuchids and in the armoured sphagesaurid *Armadillosuchus arrudai* (θ = 320–850 cm).

Tethysuchia and Thalattosuchia are characterised by a dominance of macroevolutionary regimes of large body sizes (θ = 320–980 cm), usually with lower body size disparity than Notosuchia. When Thalattosuchia is placed as sister taxa of either Tethysuchia, within Neosuchia (Fig. 5 and 6), or Mesoeucrocodylia (Fig. 7b), both Tethysuchia and Thalattosuchia share the same regime of large sizes (θ = 460–610 cm), which is subsequently inherited by many of their members. In the first scenario, the shift to this regime takes place during the Early Jurassic, in the neosuchian branch that leads to the dichotomy Thalattosuchia + Tethysuchia. In the second case, most model fits show the shift regime occurring earlier in time, during the Late Triassic, at

the base of Mesoeucrocodylia or among non-mesoeucrocodylian crocodyliforms. In the last alternative phylogenetic scenario, when Thalattosuchia is placed as the sister taxon of Crocodyliformes (Fig. 7a), even though Tethysuchia and Thalattosuchia do not share the same inherited regime, the model fits indicate that independent regime shifts to larger sizes occur at the bases of both clades, usually with very similar (or the same) trait optima values (also around 500 cm).

Within Tethysuchia, many trees exhibit a regime shift towards even larger sizes in a clade formed by the giant forms *Sarcosuchus imperator* and *Chalawan thailandicus* (θ = 840–980 cm). Among thalattosuchians, a shift to a regime with the same trait optimum (i.e., convergent) as that of the largest tethysuchians is usually observed in the teleosaurid clade formed by *Machimosaurus* and *Steneosaurus*. Despite the dominance of regimes of larger sizes, there are regimes of smaller sizes within Tethysuchia and Thalattosuchia, exemplified by some trees with isolated shifts in *Pelagosaurus typus*, *Teleosaurus cadomensis* and *Platysuchus multiscrobiculatus*, in Thalattosuchia, and *Vectisuchus leptognathus* and *Hyposaurus rogersii*, in Tethysuchia.

Crocodylia is also characterized by a dominance of macroevolutionary regimes of relatively large sizes, as in Thalattosuchia and Tethysuchia. Indeed, regimes towards larges sizes are frequently associated with clades of predominantly aquatic or semi-aquatic forms, although not strictly restricted to them. Regarding Crocodylia, a Cretaceous regime shift is usually detected at the base of the clade (Figs. 5, 6, and 7), changing from the macroevolutionary regime of smaller sizes (θ = 110–210 cm) found for non-crocodylian eusuchians (such as hylaeochampsids and some allodaposuchids) to a regime of larger trait optima (θ = 320–340 cm). This same ancestral regime for all crocodylians is inherited by many members of the clade, particularly within Crocodyloidea and Gavialoidea. Although some model fits show Crocodylia inheriting

the same regime as closely related non-crocodylian eusuchians, these trees are less common in general. In these trees, shifts towards larger body sizes are seen in members of Crocodyloidea and Gavialoidea, but they only occur later in time and arise independently. In comparison to the other two main lineages of Crocodylia, Alligatoroidea is characterized by a regime of lower trait optima values (θ = 210–230 cm), which frequently occurs as a Late Cretaceous shift at the base of the clade. But Alligatoroidea is also distinct from the other two clades by exhibiting more regime shifts, reflecting its great ecological diversity and body size disparity (ranging from very small taxa, such as the caimanine *Tsoabichi greenriverensis*, to the huge *Purussaurus* and *Mourasuchus*).

Investigating the modes of body size evolution within Notosuchia and Crocodylia

The significant number of regime shifts that occur within both Notosuchia and Crocodylia led us to more deeply scrutinise the modes of body size evolution in these two clades. We conducted another round of model-fitting analyses, initially fitting the same evolutionary models (SURFACE, OU, BM, EB and trend-like models) to subtrees representing both groups. In addition, we used the same regime shifts identified by the SURFACE algorithm to fit four additional models using the OUwie algorithm (BMS, OUMV, OUMA and OUMVA), which allow more parameters to vary, but need regime shifts to be set *a priori*.

The results of these analyses indicate different modes of body size evolution during the evolutionary histories of these two groups. In Crocodylia (Fig. 8a; see Additional file 3 for a complete list of AICc scores), AICc scores indicate a clear preference for OU-based models, with highest support found for the SURFACE model, but also strong support for the uniform OU model, as well as OUMA and OUMVA

models. The SURFACE algorithm frequently identified three main macroevolutionary regimes for crocodylians (with θ values around 200, 350 and 750 cm, respectively), with α ranging from 0.053 to 0.247 and σ^2 between 0.0014 and 0.0054. When allowed to vary among regimes (i.e., in models OUMA and OUMVA), ranges of both parameters increase significantly, with some model fits displaying extremely unrealistic parameter values, which might explain the stronger support found for SURFACE compared to these latter models. Among the BM-based models, even the best trend-like model (usually the one with the best AICc scores among BM-based models) received consistently worse support than any of these four OU-based models.

Our results show a different scenario for Notosuchia, for which we found comparable support for all evolutionary models analysed (Fig. 8b). Among OU-based models, slightly better AICc scores were found for the SURFACE model. However, this model received virtually the same support as the BMS model, the best of the BM-based models. BMS is a multi-regime BM model that allows the rate parameter (σ^2) to vary, and, as α is effectively set to zero, represents diffusive model of evolution. The support found for this model might suggest a more relaxed mode of body size evolution in notosuchians, which is consistent with the wide range of body sizes observed in the group, even among closely-related taxa. Indeed, even though we sampled twice as many crocodylians (N = 70) as notosuchians (N = 34), many SURFACE model fits found three main macroevolutionary regimes for notosuchians, similar to what was found for Crocodylia (although model fits with less regimes were more frequent for Notosuchia than in Crocodylia). For these, θ values were usually around 80, 150 and 280 cm, with α usually ranging from 0.0124 to 0.6213 and σ^2 between 0.0011 and 0.0201. When the same regimes detected by the SURFACE algorithm were used by the OUwie algorithm to fit the BMS model, values of σ^2 rarely varied significantly from the range of whole-

tree σ^2 estimated for the SURFACE model fits. The few exceptions were usually related to regimes with unrealised θ values, as in the case of the armoured sphagesaurid *Armadillosuchus arrudai* (probably with more than 2 metres in total length, whereas other sampled sphagesaurids reach no more than 1.2 m [142]), and sebecosuchians (top predators of usually more than 2.5 metres [97]), even though these values might still be realistic when simulating trend-like dynamics (i.e., in a single lineage with extremely disparate trait values [19, 57]).

The influence of palaeolatitude and palaeotemperature

Most of the correlation analyses between our body size data and the different datasets of the abiotic factors palaeotemperature and palaeolatitude yielded very weak or non-significant correlations (see Additional file 1 for all regression results). Our phylogenetic regressions of body size and palaeolatitudinal data found some significant correlations. However, in all cases the coefficient of determination (R^2) was very low (always smaller than 0.1), indicating that the correlation is very weak and only a small proportion (less than 10%) of the body size variation observed can be explained by the palaeolatitudinal data (Fig. 9).

The situation was similar regarding temporal patterns of body size compared to global palaeotemperature, with most analyses revealing very weak or non-significant correlations. In some cases, we did find significant correlations, but they were frequently inconsistent (i.e., correlations did not persist in both ODCL and DCL datasets or were absent when accounting for serial autocorrelation using GLS). The lack of strong correlations between environmental variables and body size is consistent with the results from our macroevolutionary analyses, which found strong support for a multi-regime OU model (SURFACE). This suggests that shifts between adaptive zones

are more important in determining large-scale macroevolutionary patterns of crocodylomorph body size evolution than abiotic factors, at least when analysed separately.

However, one important exception was found between mean body size values and palaeotemperatures from the Late Cretaceous (Maastrichtian) to the Recent (data from [132]). Using either all taxa in the datasets or only non-marine species, we found moderate to strong correlations (R^2 ranging from 0.376 to 0.635), with higher mean body size values found in time intervals with lower temperatures (i.e., positive slopes, given that the $\delta^{18}O$ proxy is inversely proportional to temperature). The correlation was present even when we applied GLS regressions with an autoregressive model (Table 3), which returned very low to low autocorrelation coefficients (Phi = 0.01–0.15). This suggests that temperature might have had an influence in determining the body size distribution of crocodylomorphs at smaller temporal and phylogenetic scales (Fig. 10a). For this reason, we decided to further scrutinise the relationships between the distribution of body sizes and these abiotic factors at these smaller scales, repeating our regression analyses using only data for Crocodylia, Notosuchia, Thalattosuchia, and Tethysuchia (see the “Methods” section).

These additional regressions corroborate the hypothesis that at least some crocodylomorph subclades show a correspondence between body size and global palaeotemperature. Although most of the regressions provided non-significant or weak/very weak correlations (see Additional file 1 for all regression results), including all regressions of body size on palaeolatitudinal data, both maximum and mean body size values of Crocodylia are strongly correlated to palaeotemperature through time (Table 4). The positive slopes and coefficients of determination (R^2 = 0.632 and 0.647) indicate that the lowest temperatures are associated with the highest body size values in

the crown-group. However, correlations with data from other subclades (Notosuchia, Thalattosuchia and Tethysuchia) were mostly non-significant, suggesting that this relationship between body size and temperature was not a widespread pattern among all groups.

Table 3. Regression results of mean values of body size values on palaeotemperature.

Dataset	GLS				OLS (untransformed)			
ODCL with all taxa	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.046	2.022	0.055 (0.002)	-31.576	0.635	2.023	0.054 (0.003)	-33.557
DCL with all taxa	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	0.014	2.433	0.081 (0.011)	-19.577	0.527	2.433	0.081 (0.01)	-21.575
ODCL non-marine	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.157	1.964	0.06 (0.007)	-24.96	0.502	1.965	0.06 (0.013)	-26.706
DCL non-marine	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.089	2.345	0.07 (0.027)	-16.045	0.376	2.346	0.07 (0.034)	-18.272

Results of GLS (with an autoregressive model) and OLS (untransformed data) regressions. Mean body size represented by mean values of log-transformed cranial measurements (DCL and ODCL), in millimetres. Data from both ODCL and DCL datasets was divided into subsets with all crocodylomorphs or only non-marine species. N = 10 in all four subsets (number of time bins analysed). Palaeotemperature data from [132], represented by $\delta^{18}O$ data from the Late Cretaceous to Recent. Only significant correlations ($p < 0.05$) are shown.

Table 4. Regression results of maximum and mean body size values on palaeotemperature

Dataset	GLS				OLS (untransformed)			
ODCL maximum size	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	0.19	2.133	0.121 (0.017)	-11.989	0.554	2.124	0.127 (0.008)	-13.662
ODCL mean size	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.297	1.98	0.075 (0.0003)	-29.953	0.698	1.987	0.07 (0.001)	-31.137
DCL maximum size	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.215	2.618	0.165 (0.001)	-10.724	0.632	2.627	0.157 (0.003)	-12.355
DCL mean size	**Phi**	**Intercept**	**Slope**	**AIC**	**R^2**	**Intercept**	**Slope**	**AIC**
	-0.235	2.386	0.105 (0.0007)	-20.748	0.647	2.395	0.098 (0.003)	-22.325

Results of GLS (with an autoregressive model) and OLS (untransformed data) regressions. Mean and maximum body size represented by mean and maximum values of log-transformed cranial measurements (DCL and ODCL), in millimetres. N = 10 in all four datasets (number of time bins analysed). Palaeotemperature data from [132], represented by $\delta^{18}O$ data from the Late Cretaceous to Recent. Only significant correlations ($p < 0.05$) are shown.

Discussion

The adaptive landscape of crocodylomorph body size evolution

Crocodylomorph body size disparity increased rapidly during the early evolution of the group, from the Late Triassic to the Early Jurassic (Hettangian–Sinemurian), which is mostly a result of the appearance of the large-bodied thalattosuchians (Fig. 10c). After a decline in the Middle Jurassic, body size disparity reaches its maximum peak in the Late Jurassic, with the appearance of atoposaurids, some of the smallest crocodylomorphs, as well as large teleosaurids (such as *Machimosaurus*). This increase in disparity may have occurred earlier than our results suggest, given that Middle Jurassic records of atoposaurids [143] could not be included in our analyses due to their highly incomplete preservation.

Since this peak in the Middle/Late Jurassic, crocodylomorphs underwent an essentially continuous decline in body size disparity, with some short-term fluctuations related to the extinction or diversification of particular lineages. The Early Cretaceous witnessed the extinction of thalattosuchians, and a sharp decrease in disparity is seen from the Berriasian to the Barremian (although this time interval is also relatively poorly sampled in our dataset). A subsequent increase in disparity is seen in the Aptian, probably reflecting the appearance of small-bodied crocodylomorphs (such as susisuchid eusuchians). Nevertheless, this is followed by a continuing decline for the remainder of the Cretaceous (in spite of the occurrence of highly disparate notosuchians). The Cenozoic is also characterised by an overall decrease in disparity, even though some short-term increases in disparity do occur, mostly related to the presence of smaller-bodied crocodylians in the Palaeogene (such as *Tsoabichi*).

We characterised the macroevolutionary patterns that gave rise to these patterns of body size disparity through time, by performing comparative model-fitting analyses. Our results indicate a strong support found for a multi-peak OU model (i.e., the SURFACE model; Fig. 3). Within the concept of adaptive landscape [73, 74, 75], we can interpret the SURFACE regimes, with different trait optima, as shifts to new macroevolutionary adaptive zones [11, 144]. Thus, the support found for the SURFACE model indicates that lineage-specific innovations and/or adaptations in body size play an important role in determining the patterns of crocodylomorph body size evolution. Our comparative model-fitting analyses also indicate that uniform or BM-based models provide poor explanations for the overall patterns of crocodylomorph body size evolution. Thus, we reject the hypothesis of long-term, multi-lineage trends during the evolution of crocodylomorph body size. This is true even for Crocodylia, which shows increases in maximum, minimum and mean body sizes during the past 70 million years

(Fig. 10b), a pattern that is classically taken as evidence for trend-like dynamics [56]. In fact, explicitly phylogenetic models of the dynamics along evolving lineages reject this.

We can also reject diffusive, unconstrained Brownian-motion like dynamics for most of Crocodylomorpha, although Notosuchia might be characterised by relatively unconstrained dynamics (Fig. 8). Single-regime (=uniform) models received poor support in general, which might be expected for long-lived and disparate clades such as Crocodylomorpha, that show complex and non-uniform patterns of body size evolution (see [5, 11, 58, 61]). Although multi-regime trend-like models received stronger support than uniform models for most phylogenies (Fig. 3), multi-peak OU models (SURFACE) received overwhelmingly still greater support. This suggests that the macroevolutionary landscape of crocodylomorph body size evolution is best described by shifts between phylogenetically defined regimes that experience constrained evolution around distinct trait optima [61, 71, 75, 83].

The success of a multi-peak OU model indicates that, in general, a significant amount of crocodylomorph body size variance emerged through pulses of body size variation, and not from a gradual, BM-based dispersal of lineages through trait (body size) space. These pulses, represented by regime shifts, indicate that lineage-specific innovations (such as ecological diversification; see below) and adaptations are important for the large-scale patterns of crocodylomorph body size evolution.

This can also explain the weak support found for the early burst ("EB") model in our analyses. The early burst model attempts to simulate Simpson's [73] idea of diversification through "invasion" of new adaptive zones (niche-filling). It focuses on a particular pattern of adaptive radiation, with evolutionary rates higher in the early evolution of a clade and decelerating through time [128]. Our results show that, overall, the EB model offers a poor explanation for the evolution of body size in

crocodylomorphs, in agreement with previous works that suggested that early bursts of animal body size receive little support from phylogenetic comparative methods [128]. However, this does not reject Simpson's hypothesis that abrupt phenotypic shifts along evolving lineages ("quantum evolution") results from the distribution of opportunities (unfilled niches). Pattern of crocodylomorph body size evolution could still be explained by niche-filling if niche availability was distributed through time rather than being concentrated early on the evolution of the clade. This is one possible explanation of the pattern of regime shifts returned by our analyses, and might be particularly relevant for clades with long evolutionary histories spanning many geological intervals and many episodes of possible radiation.

Bronzati et al. [35] examined variation in rates of species diversification among clades using methods based on tree asymmetry. They found that most of crocodyliform diversity was achieved by a small number of significant diversification events that were mostly linked to the origin of some subclades, rather than via a continuous process through time. Some of the diversification shifts from Bronzati et al. [35] coincide with body size regime shifts found in many of our SURFACE model fits (as at the base of Notosuchia, Eusuchia and Alligatoroidea; Fig. 11). However, many of the shifts in body size regimes detected by our analyses are found in less-inclusive groups (as in the case of "singleton" regimes, that contain only a single taxon).

Ecological diversification and its implications for crocodylomorph body size distribution

Ecological factors seem to be important for the large-scale patterns of body size in crocodylomorphs. Many of the regime shifts to larger sizes detected by our SURFACE analyses occur at the base of predominantly aquatic or semi-aquatic clades, such as

Thalattosuchia, Tethysuchia and Crocodylia (Fig. 5–7), although there are also small-bodied aquatic/semi-aquatic clades, such as Atoposauridae. Some terrestrial clades also display relatively large sizes (such as sebecosuchians and peirosaurids, within Notosuchia). However, most terrestrial species are small-bodied (Fig. 12), including many of the earliest crocodylomorphs (such as *Litargosuchus leptorhynchus* and *Hesperosuchus agilis* [50, 51]; Fig. 12a), and are within body size regimes of lower values of θ (< 150 cm; Fig. 5–7). In contrast, the regimes with the highest values of θ (> 800 cm) are almost always associated with aquatic or semi-aquatic crocodylomorphs (e.g., the tethysuchians *Sarcosuchus imperator* and *Chalawan thailandicus*, the thalattosuchians *Machimosaurus* and *Steneosaurus*, and the crocodylians *Purussaurus* and *Mourasuchus*).

To further investigate this, we subdivided our body size data into three discrete categories to represent different generalised lifestyles: terrestrial, semi-aquatic/freshwater, and aquatic/marine. We initially found a relationship between the lifestyle and body size using analysis of variance (ANOVA), showing that terrestrial, freshwater and marine species had significantly different body sizes (Fig. 12b; Table 5). Next, we accounted for phylogenetic dependency, by applying a phylogenetic ANOVA [145, 146]. This asks specifically whether evolutionary habitat transitions are consistently associated with particular body size shifts as optimised on the phylogeny and returned non-significant results. This indicates that, although crocodylomorphs with more aquatic lifestyles (particularly marine species) tend to be large-bodied, the evolutionary transitions between these lifestyle categories were probably not accompanied by immediate non-random size changes. Furthermore, the smaller bodies of some lineages (e.g., atoposaurids, *Tsoabichi* and *Pelagosaurus*) show that adaptive peaks of smaller sizes are also viable among aquatic/semi-aquatic species. This suggests

that, even though there seem to be an ecological advantage for larger-sized freshwater/marine crocodylomorphs, the body size lower limit (i.e., minimum body sizes achieved) of these aquatic species might have been comparable to that of terrestrial ones.

Table 5. Pairwise comparison between body size of crocodylomorphs subdivided into three lifestyle categories.

Category	Mean	Std. Deviation	Std. Error	Pairwise comparisons	t-value	ANOVA q-value	Phylo ANOVA q-value
Terrestrial	1.854	0.223	0.0333	**Terrestrial – Freshwater**	4.196	< 0.001*	1
Semi-aquatic/ freshwater	2.026	0.249	0.0249	**Terrestrial – Marine**	8.721	< 0.001*	0.138
Aquatic/ marine	2.263	0.185	0.0261	**Freshwater – Marine**	5.997	< 0.001*	0.537

Body size data from the ODCL dataset (log-transformed cranial measurement, in millimetres). Number of species in each category: 45 (terrestrial), 100 (semi-aquatic/freshwater), and 50 (aquatic/marine). Results of one-way analysis of variance (ANOVA), without accounting for phylogenetic dependency, and phylogenetic ANOVA [145, 146]. *Bonferroni-corrected p-values (q-values) significant at alpha = 0.05

Previous studies have investigated a possible link between an aquatic/marine lifestyle and larger body sizes in other animals, particularly in mammals (e.g., [17, 21, 24]). For instance, it has been previously shown that aquatic life in mammals imposes a limit to minimum body size [24, 147] and relaxes constraints on maximum size [148]. Therefore, aquatic mammals (especially marine ones) have larger body sizes than their terrestrial relatives [21, 149]. We document a similar pattern in crocodylomorphs, although the phylogenetic ANOVA results (Table 5) revealed that changes in size are not abrupt after environmental invasions (as also suggested by the diminutive size of

some semiaquatic lineages, such as atoposaurids and some crocodylians). As animals lose heat faster in water than in air (given the different rates of convective heat loss in these two environments), it has demonstrated that thermoregulation plays an important role in determining the larger sizes of aquatic mammals [24, 147, 150]. Although mammals have distinct thermal physiology to crocodylomorphs (which are ectothermic poikilotherms), it has been reported that American alligators (*Alligator mississippiensis*) heat up more rapidly than cool down, and that larger individuals are able to maintain their inner temperature for longer than smaller ones [151]. Thus, given that both heating and cooling rates are higher in water than in air [151], larger aquatic/semi-aquatic animals could have advantages in terms of physiological thermoregulation. If extinct crocodylomorphs had similar physiologies, this could provide a plausible explanation for the larger sizes of non-terrestrial species.

Cope's rule cannot explain the evolution of larger sizes in Crocodylomorpha

Previous interpretations of the fossil record suggest a dominance of small sizes during the early evolution of crocodylomorphs [45, 152], inferred from the small body sizes of most early crocodylomorphs. Consistent with this, our SURFACE results revealed a small-bodied ancestral regime for Crocodylomorpha (Z_0 between 66 and 100 cm), which was inherited virtually by all non-crocodyliform crocodylomorphs. Larger non-crocodyliform crocodylomorphs have also been reported for the Late Triassic (e.g., *Carnufex carolinensis* and *Redondavenator quayensis*, with estimated body lengths of approximately 3 metres [153]), but the fragmentary nature of their specimens prevented us from including them in our macroevolutionary analysis. Nevertheless, given the larger numbers of small-bodied early crocodylomorphs, taxa like *Carnufex* and

Redondavenator probably represent derived origins of large body size and their inclusion would likely result in similar values of ancestral trait optima (=Z_0).

The small ancestral body size inferred for crocodylomorphs, combined with the much larger sizes seen in most extant crocodylians and in some other crocodylomorph subclades (such as thalattosuchians and tethysuchians), suggests a pattern of increasing average body size during crocodylomorph evolutionary history. The idea is reinforced by the overall increase in crocodylomorph mean body size through time, particularly after the Early Cretaceous (Fig. 10b). The same pattern also occurs within Crocodylia during the past 70 million years (Fig. 10b), as some of the earliest taxa (such as *Tsoabichi*, *Wannaganosuchus* and *Diplocynodon deponiae*) were smaller-bodied (< 2m) than more recent species, such as most extant crocodylians (usually > 3m). Cope's rule is most frequently conceived as the occurrence of multi-lineage trends of directional evolution towards larger body sizes [7, 8, 11], and this can be evaluated using BM-based models that incorporate a directional trend (parameter μ[80]; see e.g., [33, 62]).

We find little support for trend-like models as a description of crocodylomorph or crocodylian body size evolution. Therefore, we reject the applicability of Cope's rule to crocodylomorph evolution. This reinforces previous works suggesting that multi-lineage trends of directional body-size evolution are rare over macroevolutionary time scales [33, 67, 154, 155] (but see [19]). Furthermore, our SURFACE model fits indicate that regime shifts towards smaller-bodied descendent regimes occurred approximately as frequently (9–13 times) as shifts to regimes of larger body sizes (13–16 times; Fig. 13). Together, these results indicate that long-term increases in the average body size of crocodylomorphs also cannot be explained either by multi-lineage trends of directional evolution towards larger size, or by a biased frequency of transitions to large-bodied descendent regimes.

Instead, the apparent trend towards larger body sizes can be explained by extinctions among small-bodied regimes. Crocodylomorph body size disparity decreased gradually through the Cretaceous (Fig. 10b). This occurred due to the decreasing abundance of small-bodied species. Despite this, our SURFACE model fits mostly indicate the survival of clades exhibiting small-bodied regimes ($\theta < 200$ cm) until approximately the end of the Mesozoic, (e.g., gobiosuchids, uruguaysuchids, sphagesaurids, hylaeochampsids and some allodaposuchids, Figs. 5, 6, and 7). Many of these small-bodied clades became extinct at least by the Cretaceous/Palaeogene (K/Pg) boundary, resulting in a substantial reduction of small-bodied species. Further reductions among the crown-group (Crocodylia) occurred by the Neogene, from which small-bodied species are absent altogether (Figs. 5, 6, and 7).

This predominance of regimes of large sizes today is also linked to the occurrence of large body sizes in Crocodylia. Our SURFACE analyses focusing on Crocodylia, indicate ancestral body size regimes with relatively high values of θ (Z_0 between 220 and 350 cm). The shift to a larger-sized regime (when compared to smaller-bodied eusuchian regimes) probably occurred at the Late Cretaceous (Figs. 5, 6, and 7), and this same regime was inherited by many members of the clade (predominantly semi-aquatic species). During the Palaeogene, however, shifts to regimes of smaller sizes also happen (such as in *Tsoabichi greenriverensis*, *Diplocynodon deponiae* and planocraniids), increasing body size disparity (Fig. 10c). The crocodylian body size distribution shifts upwards mainly during the latter part of the Cenozoic (from the Miocene; Fig. 10b), when even larger-bodied animals occur (e.g., *Purussaurus* and *Mourasuchus*), combined with the disappearance of lineages of smallest species.

Correlation of crocodylian body size with global cooling

Our time series regressions demonstrate a moderate to strong correlation between crocodylian size and palaeotemperature (Table 4). This results from the upward-shift of the crocodylian body size distribution, coinciding with cooling global climates in the second half of the Cenozoic [132, 156]. Even though this is an apparently counter-intuitive relationship, we do not interpret it as a result of direct causation. Previous studies have shown that crocodylian species richness decreased with declining global temperatures of the Cenozoic [36, 37]. Furthermore, the palaeolatitudinal ranges of both marine and continental crocodylomorphs have contracted as temperatures decreased (Fig. 9; see also [36, 37]). Therefore, the temperatures experienced by evolving lineages of crocodylians are not equivalent to global average temperatures. We propose that the association between global cooling and increasing crocodylian body size results from a systematic reduction of available habits/niches (due to a more restricted geographical distribution), with differential extinction of smaller-bodied species. The hypothesis of selective extinction is also consistent with the decreasing disparity of body size disparity of crocodylians during the Cenozoic (Fig. 10b).

Body size selectivity and diversification across Mesozoic boundaries

Numerous comparative studies have investigated a possible link between extinction risk and animal body size (e.g., [157, 158, 159, 160, 161]). For example, larger body sizes, in association with dietary specializations, might increase susceptibility to extinction in some animal groups, such as hypercarnivorous canids [162, 163]. On the other hand, the recovery of some animal clades after extinction events can also be associated with a subsequent increase in diversity and morphological disparity (e.g., Palaeogene mammals [14]), potentially leading to the exploration of new regions of body size space (i.e., invasions of new body size adaptive zones). Thus, although for some groups (and

for some extinctions) body size might play an important role, this is evidently not a generalised pattern across all animals.

For crocodylomorphs, little is known about possible influence of body size on differential extinction. In one of the few studies to quantitatively investigate this, Turner & Nesbitt [45], using femoral length as a proxy for total body size, recognized a drop in mean body size of crocodylomorphs across the Triassic-Jurassic (T–J) boundary. Our SURFACE results, however, indicate otherwise, as all Triassic crocodylomorphs are within a macroevolutionary regime of smaller sizes ($\theta < 100$ cm) when Thalattosuchia is placed within Neosuchia (Fig. 5 and 6). In the other two phylogenetic scenarios, the origin of thalattosuchians (which are predominantly large-bodied animals) is placed either at the middle of the Late Triassic or closer to the T–J boundary (Fig. 7). However, as the first records of thalattosuchians only occur in the Early Jurassic, mean body size increases immediately after the boundary (Fig. 10a). The differences between our results and those found by Turner & Nesbitt [45] might be related to the distinct body size proxies used, or to sampling, as those authors also included non-crocodylomorph taxa in the pseudosuchian lineage. In this context, we acknowledge that the inclusion in our analyses of larger non-crocodyliform crocodylomorphs, such as *Carnufex carolinensis* (~ 3 metres [153]), might change our results. Thus, at the moment we do not have empirical or statistical evidence to demonstrate selectivity of body sizes in crocodylomorphs during the end-Triassic extinction.

The Early Jurassic was characterized by key events of crocodylomorph diversification [35] and an increase in morphological disparity [42], following the end-Triassic extinction. Similarly, our body size data suggests an increase in body size disparity after the T–J boundary (Fig. 10b). Although a decrease in disparity is observed subsequently, this is probably due to the relatively few crocodylomorphs known for the

latest Early Jurassic and the Middle Jurassic (Sinemurian–Aalenian [36]). Subsequently, the diversification of thalattosuchians during the Late Jurassic, together with the occurrence of smaller- to intermediate-bodied neosuchians (such as atoposaurids and goniopholidids), created the greatest observed disparity of crocodylomorph body sizes during their evolutionary history (Fig. 10).

Recent studies [164, 165, 166] suggested that a combination of environmental perturbations occurred during the Jurassic-Cretaceous (J/K) transition, which might have led to the extinction of some tetrapod lineages. For crocodylomorphs the boundary is characterised by a decrease in marine diversity [36, 164, 165], highlighted by declines in thalattosuchian diversity, especially among teleosaurids, which suffered widespread extinction (except, apparently, at lower palaeolatitudes [167]). Nevertheless, Wilberg [43] did not find evidence for a substantial decrease in crocodylomorph cranial disparity across the J/K boundary. Similarly, our SURFACE results do not suggest dramatic changes in body size space exploration immediately before or after the J/K boundary (Fig. 5–7), and there seems to be no defined body size selectivity across this boundary, as the multiple survivor crocodylomorph lineages were within regimes of very disparate optima values. Furthermore, the decrease in disparity observed in the middle of the Early Cretaceous (i.e., Valanginian–Barremian) is likely due to poor sampling [168], resulting in the scarcity of more completely preserved crocodylomorphs during these stages.

The Late Cretaceous is marked by a remarkable fossil richness of notosuchians, in Gondwana [169, 170], and the diversification of eusuchian crocodylians [171]. Notosuchia exhibits a wide range of body sizes (Fig. 12a), to some extent reflecting its remarkable diversity [36, 170] and morphological disparity [43, 44]. Our model-fitting analyses using only notosuchian data suggest more relaxed modes of body size

evolution (Fig. 9), which is consistent with their species richness and morphological disparity. This could be explained by a combination of intrinsic (i.e., innovations and/or adaptations, such as a highly modified feeding apparatus [172, 173]) and extrinsic factors (i.e., specific environmental conditions, such as the predominantly hot and arid climate of the Gondwanan landmasses occupied by notosuchians [36, 169]).

Even though our body size data show no specific pattern at the K/Pg boundary, a decline in body size disparity is present through the Late Cretaceous, combined with an increase in mean body size (Fig. 10), a pattern that generally continued through the Cenozoic (although with some short-term fluctuations). This supports the hypothesis that the K/Pg extinction had only minor impacts on crocodylomorphs [35, 36, 37, 43, 174]. Although subsampled data suggests a decline in terrestrial diversity during the Late Cretaceous, it occurred prior to the boundary, from the Campanian into the Maastrichtian, in both Europe and North America [36]. Indeed, different crocodylomorph subclades lost several species prior to the end of the Cretaceous (in particular notosuchians and non-crocodylian eusuchians [35, 36]; Figs. 5, 6, and 7), and multiple lineages within other groups, such as dyrosaurid tethysuchians and crocodylians, crossed the boundary with little change [37, 174, 175] (Figs. 5, 6, and 7). Our data suggest a long-term pattern of extinctions among small-bodied taxa, starting from the Late Cretaceous and continuing to the Recent. This may have resulted from a longstanding trend of global cooling [132, 156], resulting in more restricted geographical distributions, and reducing niche availability for crocodylomorphs. This is consistent with our SURFACE results (Figs. 5, 6, and 7), that show very few smaller-bodied regimes ($\theta < 150$ cm) during the Palaeogene and a complete absence after the Neogene. This pattern strikingly contrasts with that proposed for mammals, which may have experienced selectivity against larger bodied taxa across the boundary [176],

although an increase in body size is observed subsequently during the Palaeogene [14, 15]. It also differs from that suggested for squamates (lizards and snakes), for which survival was possibly associated with small body sizes [177].

Conclusions

After an early increase (with the highest peak in the Late Jurassic), crocodylomorph body size disparity experienced sustained decline during virtually its entire evolutionary history. This disparity decrease is combined with an increase of average body size through time, with highest peaks in the Middle Jurassic and today. In particular, the increase in mean body size seen during the Cenozoic (mostly related to crocodylians) is linked to an overall decrease in global temperatures.

To further characterise these patterns, we used comparative model-fitting analyses for assessing crocodylomorph body size evolution. Our results show extremely strong support for a multi-peak Ornstein-Uhlenbeck model (SURFACE), rejecting the hypothesis of evolution based on Brownian motion dynamics (including those representing the concept of Cope's rule). This suggests that crocodylomorph body size evolution can be described within the concept of a macroevolutionary adaptive landscape, with a significant amount of crocodylomorph body size variance evolving from pulses of body size changes, represented by shifts between macroevolutionary regimes (or adaptive zones). This is reflected in the regime shifts frequently detected at the base of well-recognised and diverse crocodylomorph subclades, such as Notosuchia, Thalattosuchia, and Crocodylia.

We did not find strong correlations between our body size data and abiotic factors, indicating that shifts between macroevolutionary regimes are more important for determining large-scale patterns of crocodylomorph body size than isolated climatic

factors. However, at more refined temporal and phylogenetic scales, body size variation may track changes in climate. In the case of Crocodylia, a global cooling event might explain the long-term increases in body size, as a result of systematic reduction of available habits/niches (due to a more latitudinally-restricted geographical distribution during cooler global climates), with differential extinction of smaller-bodied species.

Shifts towards larger sizes are often associated with aquatic/marine or semi-aquatic subclades, indicating that ecological diversification may also be relevant, and suggesting a possible link between aquatic adaptations and larger body sizes in crocodylomorphs. These shifts to larger sizes, occurred throughout crocodylomorph evolutionary history, combined with the extinction of smaller-sized regimes, particularly during the Late Cretaceous and Cenozoic, explain the overall increase in mean body size, as well as the large-bodied distribution of extant crocodylians compared to earlier taxa.

Abbreviations

<u>Cranial measurements</u>:

DCL: dorsal cranial length

ODCL: orbito-cranial length

<u>Evolutionary models</u>:

BM: Brownian motion

EB: Early burst

OU: Ornstein-Uhlenbeck

BMS: multi-regime BM model that allows parameter $\sigma 2$ to vary

OUMV: multi-regime OU model that allows θ and $\sigma 2$ to vary

OUMA: multi-regime OU model in which θ and α can vary

OUMVA: OU model in which all three parameters (θ, α and σ2) can vary

Model parameters:

θ: trait optimum of OU-based models

α: attraction parameter of OU-based models;

σ2: Brownian variance or rate parameter of BM or OU-based models

μ: evolutionary trend parameter of BM-based models

Z_0: estimated trait value at the root of the tree of OU-based models

Optimality criteria:

AIC: Akaike's information criterion

AICc: Akaike's information criterion for finite sample sizes

BIC: Bayesian information criterion

pBIC: phylogenetic Bayesian information criterion

Declarations

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Availability of data and material

The data generated and/or analysed during the current study, as well as R codes used for macroevolutionary analyses and supplementary results, are available in the data repository Zenodo, and can be accessed at https://zenodo.org/record/1344593.

Authors' contributions

PLG, RBJB and RJB designed the study. PLG collected and analysed the data. All authors participated in drafting the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

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Figure legends

Fig. 1

Real total body length, measured from some complete fossil crocodylomorph specimens, is plotted against total length estimated from the cranial measurements DCL (**a**) and ODCL (**b**) (equations from [91]), exemplifying the amount of error expected when using cranial measurements to estimate total body length of crocodylomorphs. R^2 value illustrates the strength of the correlation between real and estimated total lengths. Colours represent different mono- or paraphyletic crocodylomorph groups. See Additional file 1: Table S1 for information on the specimens used for the construction of these plots.

Fig. 2

Simplified cladogram showing the phylogenetic relationships among crocodylomorphs and the alternative positions of Thalattosuchia (dashed red lines), following hypotheses proposed by [34, 35, 109, 113, 115]. Silhouettes are from phylopic.org.

Fig. 3

AICc scores of the evolutionary models fitted to crocodylomorph phylogeny and body size data. Results shown for two cranial measurements datasets (ODCL in the left column and DCL in the right one), as well as using three different methods to time-calibrate 20 randomly resolved phylogenies of Crocodylomorpha: (**a**) *mbl*, (**b**) *Hedman*, and (**c**) *cal3* methods. For the trend-like models, only the AICc of the best model ("best trend") is shown.

Fig. 4.

AICc (left) and pBIC (right) plotted against the number of regime shifts of SURFACE model fits, using crocodylomorph topologies with alternative positions of Thalattosuchia: **a, b** Thalattosuchia within Neosuchia; **c, d** Thalattosuchia as the sister group of Crocodyliformes; **e, f** Thalattosuchia as the sister group of Mesoeucrocodylia. Numbers represent the 20 randomly resolved trees (time-calibrated using the *mbl* method) used for each model fit. Body size data from the ODCL dataset only.

Fig. 5

SURFACE model fit (using pBIC searches in the backward-phase) of tree number 10 among crocodylomorph topologies with Thalattosuchia placed within Neosuchia, using the ODCL dataset and time-calibrated with the *mbl* method. Attraction to unrealized low or high trait optima are highlighted in blue and red, respectively. Model fits of trees sharing the same position of Thalattosuchia show very similar regime configurations, regardless of the dataset used (ODCL or DCL) and the time-calibration method (see Additional file 4 for all SURFACE plots).

Fig. 6

a SURFACE model fit (using pBIC searches in the backward-phase) of tree number 16 among crocodylomorph topologies with Thalattosuchia placed within Neosuchia, using the ODCL dataset and time-calibrated with the *mbl* method. Attraction to unrealized low or high trait optima are highlighted in blue and red, respectively. **b** Simplified version of **a**, with independent multi-taxon regimes collapsed to single branches.

Fig. 7

SURFACE model fits of trees time-calibrated with the mbl method, using the ODCL dataset. **a** Model fit of tree number 14 with Thalattosuchia as the sister group of Crocodyliformes. However, many model fits of trees sharing this same position of Thalattosuchia show simpler model configurations, with significantly fewer regimes (see text for details). **b** Model fit of tree number 11 with Thalattosuchia as the sister group of Mesoeucrocodylia. A few model fits of other trees with Thalattosuchia in the same position are simpler, particularly when using the cal3 time-scaling method (see Additional file 4 for all SURFACE plots). **c, d** Simplified versions of **a** and **b**, respectively, with independent multi-taxon regimes collapsed to single branches.

Fig. 8

AICc scores of all evolutionary models fitted to the phylogenies and body size data of Crocodylia and Notosuchia. For the trend-like models, only the AICc of the best model ("best trend") is shown.

Fig. 9

Palaeolatitudinal distribution of extinct crocodylomorphs through time, incorporating body size information (circle sizes), with colours representing different mono- or paraphyletic (i.e., Crocodylomorph = non-mesoeucrocodylian crocodylomorphs, excluding Thalattosuchia; Neosuchia = non-crocodylian neosuchians) crocodylomorph groups. Body sizes are $\log_{10}$ values of orbito-cranial dorsal length (ODCL), in millimetres.

Fig. 10

a Phenogram with body size incorporated into crocodylomorph phylogeny, with colours representing different mono- or paraphyletic (i.e., Crocodylomorph = non-mesoeucrocodylian crocodylomorphs, excluding Thalattosuchia; Neosuchia = non-crocodylian neosuchians) crocodylomorph groups. Body size represented by $\log_{10}$ ODCL (orbito-cranial dorsal length) in millimetres. **b** Crocodylomorph body size and palaeotemperature through time. Mean $\log_{10}$ ODCL represented by dashed black line, shaded polygon shows maximum and minimum values for each time bin. Continuous light green displays mean $\log_{10}$ ODCL values only for Crocodylia. Palaeotemperature

($\delta^{18}O$) illustrated by red line (data from [132]). **c** Body size disparity through time. Disparity is represented by the standard deviation of $\log_{10}$ ODCL values for each time bin (only time bins with more than 3 taxa were used for calculating disparity). Error bars are accelerated bias-corrected percentile limits (BCa) of disparity from 1,000 bootstrapping replicates. Asterisks mark the events of largest interval-to-interval changes in disparity.

Fig. 11

Summary of our SURFACE results combined with the crocodylomorph diversification shifts found by Bronzati et al. [35]. Nodes with diversification shifts are indicated by arrows, the colours of which represent distinct trait optima values (total body length in centimetres, after applying formula from [91]), of different body size regimes. Black arrows indicate nodes for which diversification shifts were identified, but no body size regime shift was found by our model fits.

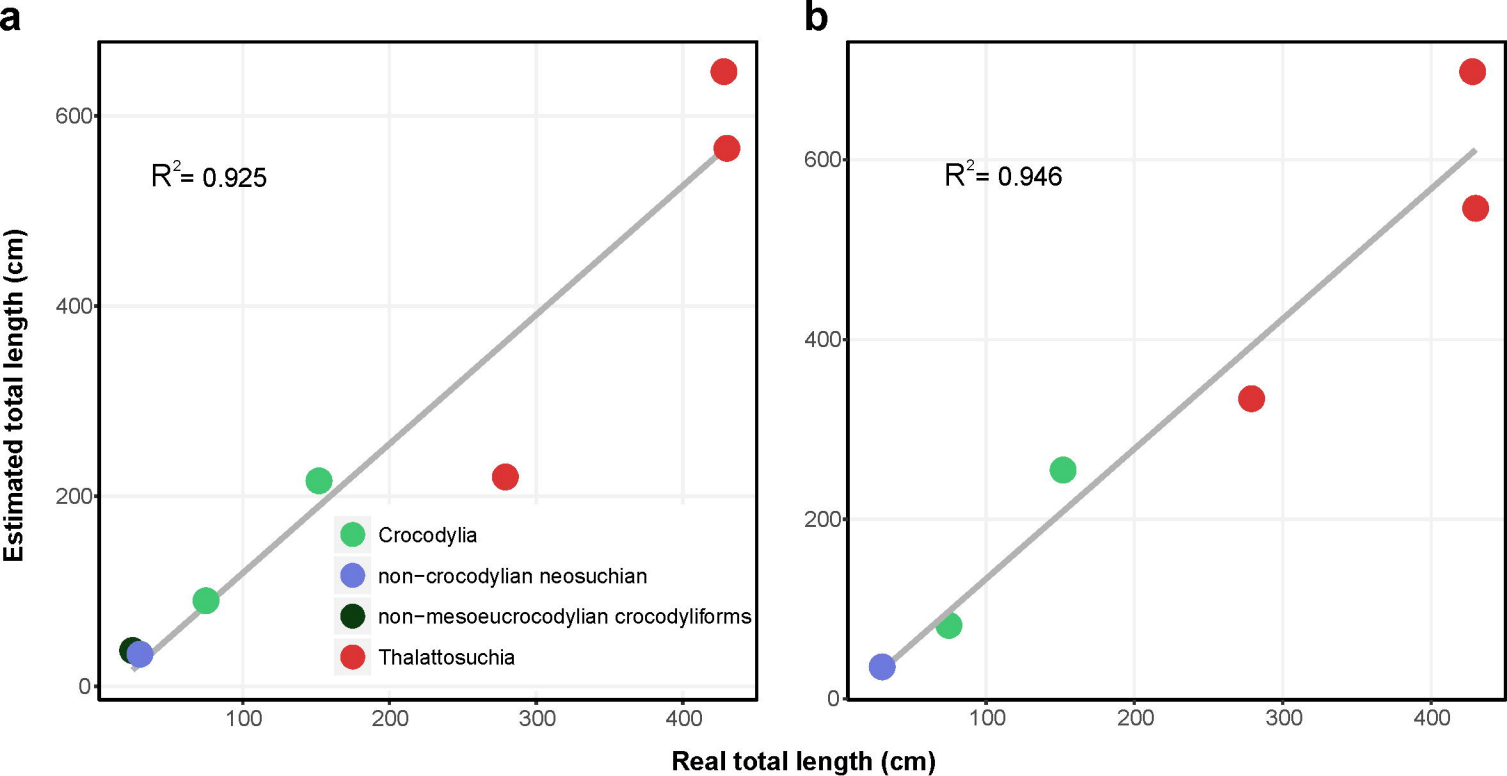
Fig. 12

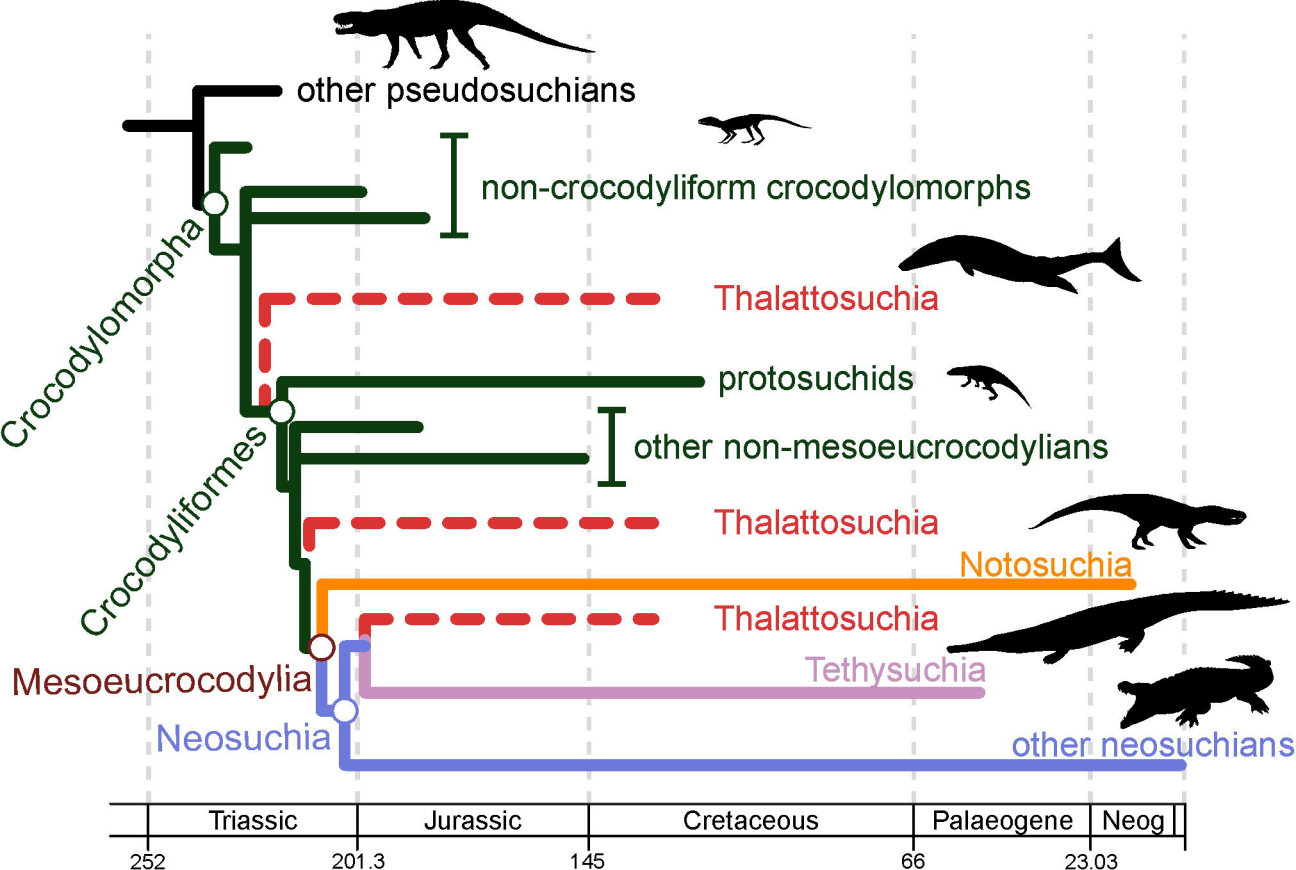
a Body size frequency distributions of different crocodylomorph groups (mono- or paraphyletic), constructed using the full set of 240 specimens in the ODCL dataset. Underlying unfilled bars represent values for all crocodylomorphs. Filled bars represent values for Crocodylia, Notosuchia, Thalattosuchia, non-mesoeucrocodylian crocodylomorphs (excluding thalattosuchians), Tethysuchia and non-crocodylian neosuchians (excluding tethysuchians and thalattosuchians). **b** Body size distributions of different crocodylomorph lifestyles, shown with box-and-whisker plots (on the left) and a mosaic plot (on the right). The 195 species from the ODCL dataset were

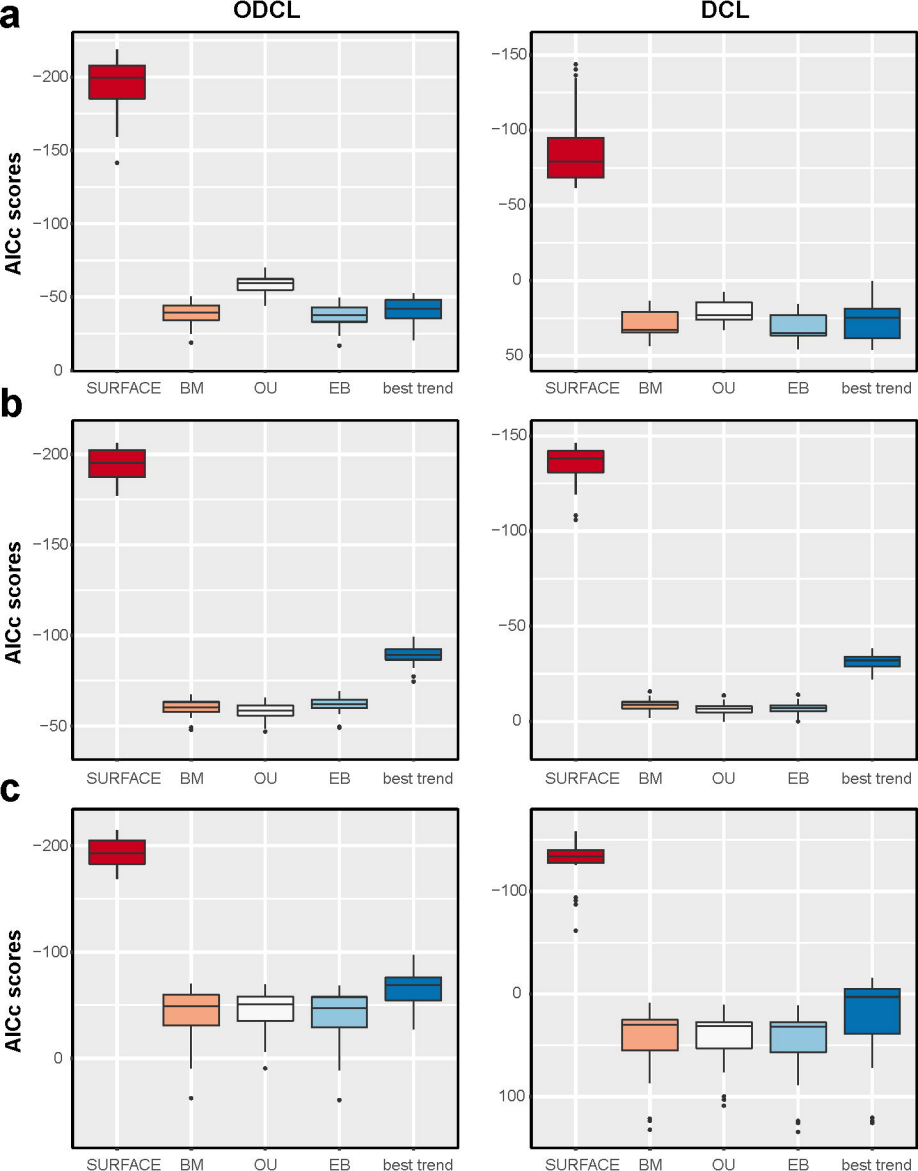
subdivided into terrestrial, semi-aquatic/freshwater and aquatic/marine categories (N = 45, 100 and 50, respectively) based on the literature. Body size is represented by $\log_{10}$ cranial length (ODCL, orbito-cranial length, in millimetres).

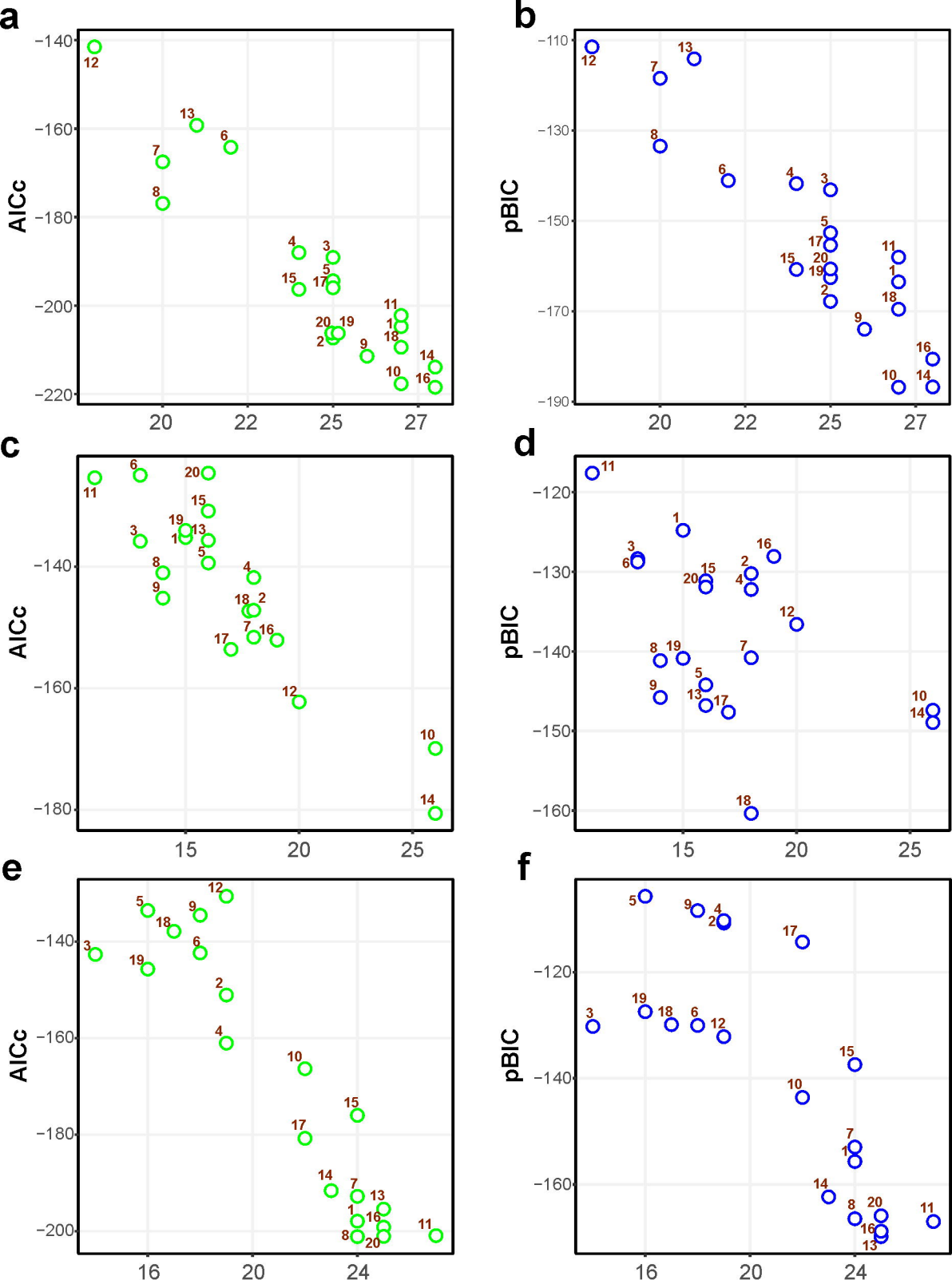
Fig. 13

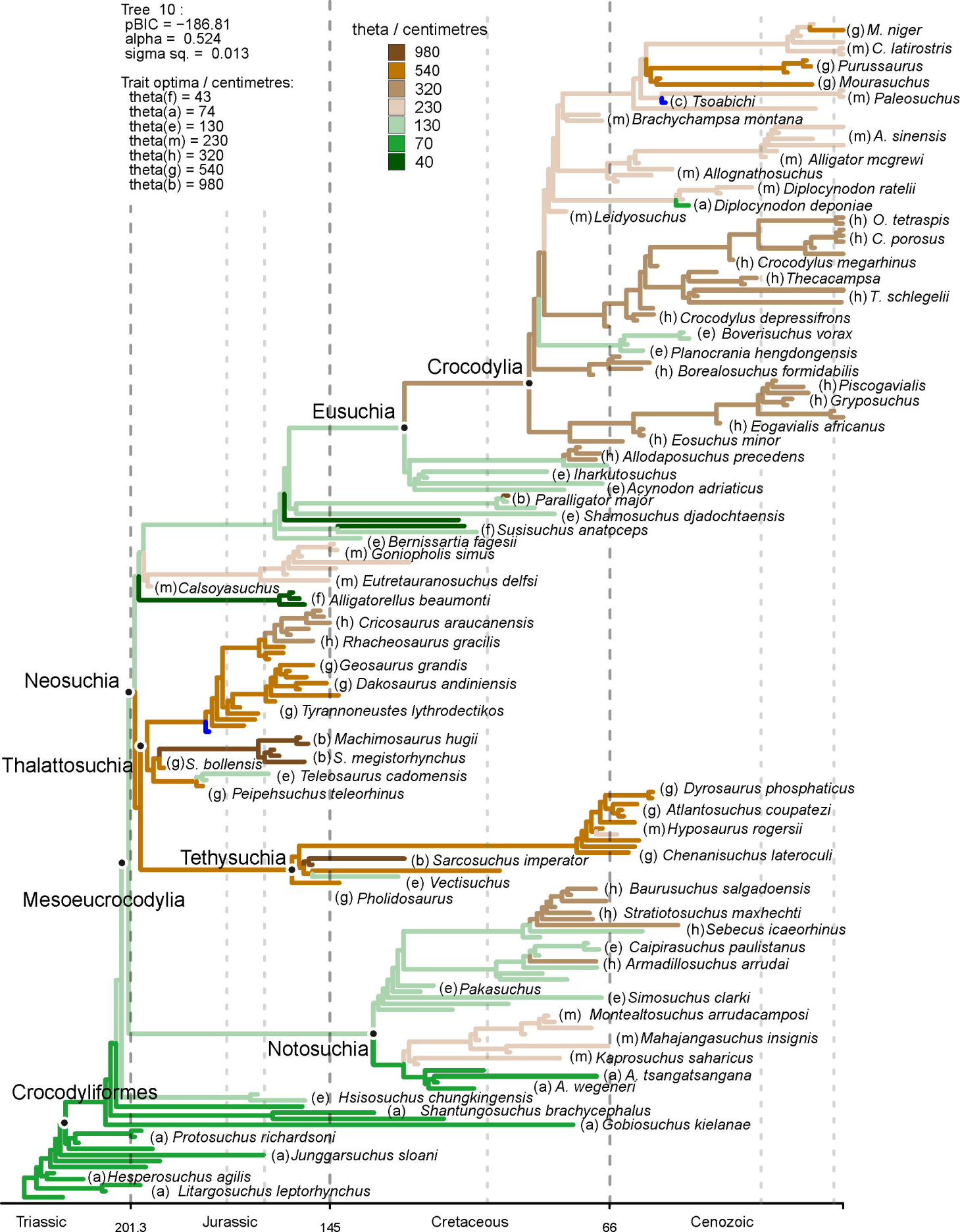
Distribution of regime shifts represented by the difference between descendant and ancestral regimes trait optima values (θ) plotted against the θ of the ancestral regime. Large red circles represent shifts that led to clades containing multiple taxa, while smaller pink circles represent "singleton" regimes, containing only single taxa. Vertical dashed line indicates the ancestral regime for all crocodylomorphs (Z_0), while horizontal dashed line can be used as a reference to identify regime shifts giving rise to larger (circles above the line) or smaller-bodied (circles below the line) descendants. Circles at the exact same position (i.e., shifts with the same θ values for both ancestral and descendant regimes) were slightly displaced in relation to one another to enable visualization. This plot was constructed using the θ values from trees with different positions of Thalattosuchia: **a** Tree number 10, with Thalattosuchia within Neosuchia; **b** Tree number 14, with Thalattosuchia as the sister group of Crocodyliformes; **c** Tree number 11, with Thalattosuchia as the sister group of Mesoeucrocodylia. θ values in $\log_{10}$ mm, relative to the cranial measurement ODCL (orbito-cranial dorsal length).

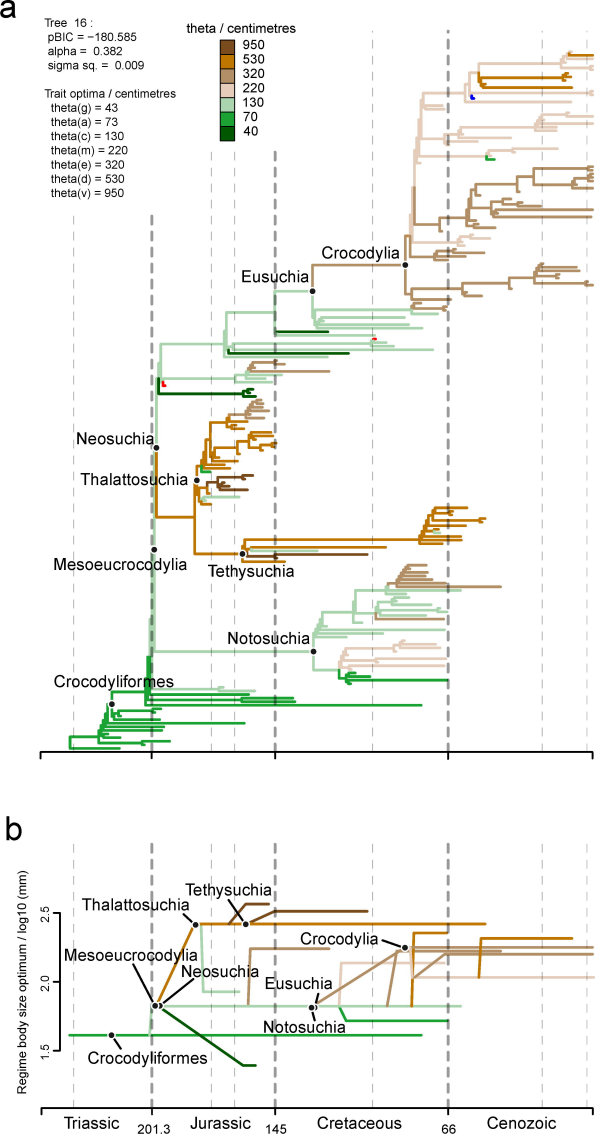

a
b
R^2= 0.925
R^2= 0.946
Estimated total length (cm)
Real total length (cm)
0
200
400
600
100
200
300
400
Crocodylia
non−crocodylian neosuchian
non−mesoeucrocodylian crocodyliforms
Thalattosuchia

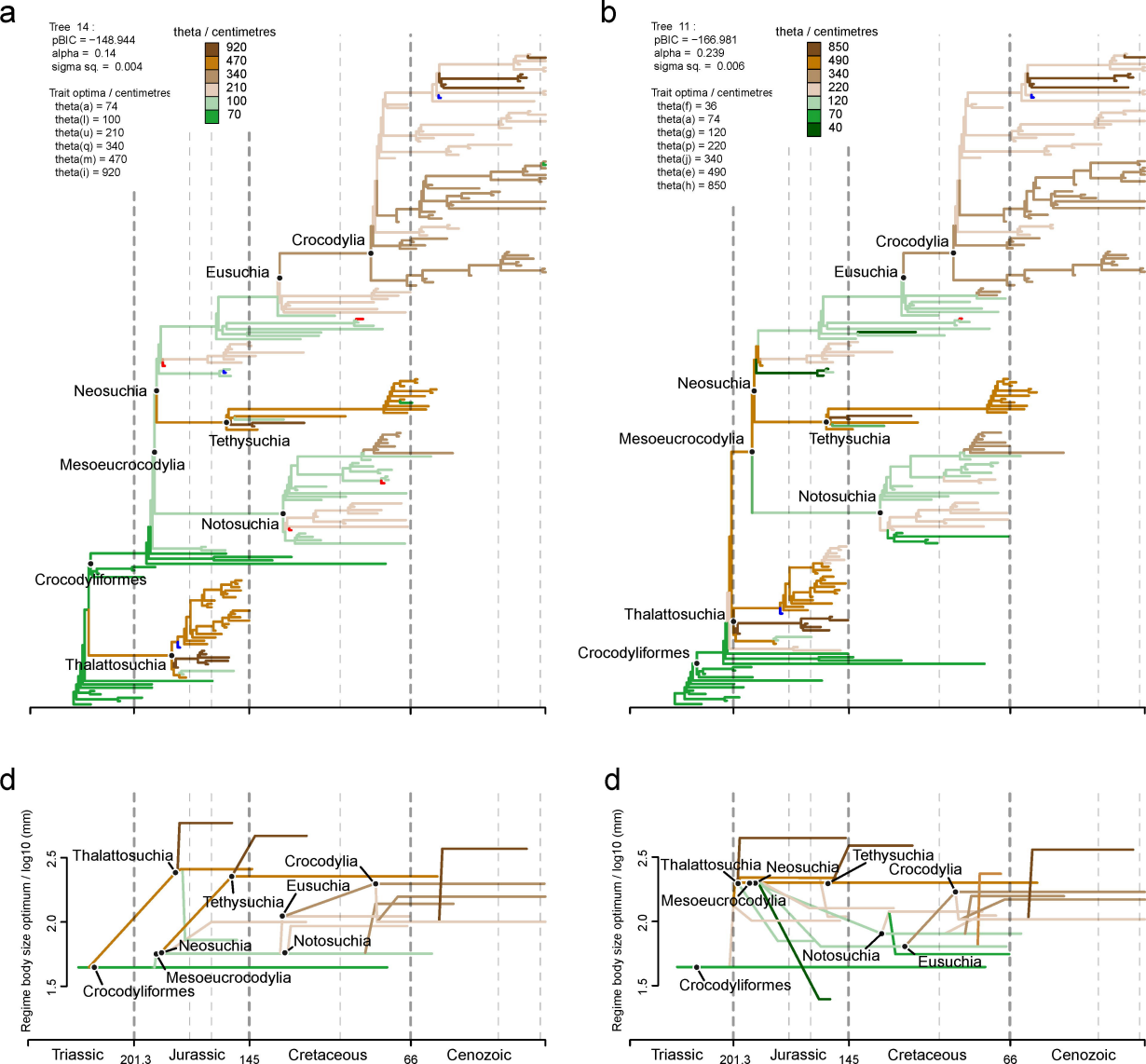

other pseudosuchians
non-crocodyliform crocodylomorphs
Crocodylomorpha
Thalattosuchia
protosuchids
other non-mesoeucrocodylians
Crocodyliformes
Thalattosuchia
Notosuchia
Thalattosuchia
Tethysuchia
Mesoeucrocodylia
Neosuchia
other neosuchians
Triassic
Jurassic
Cretaceous
Palaeogene
Neog
252
201.3
145
66
23.03

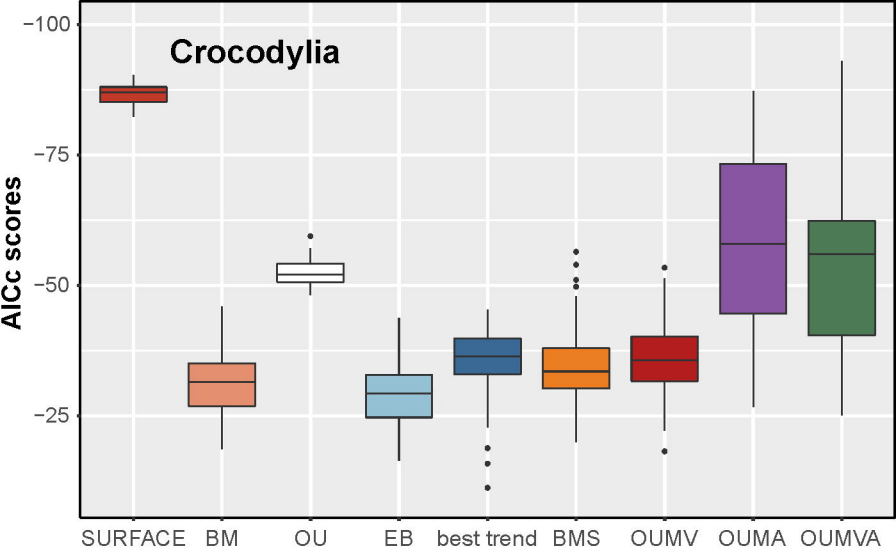

a
ODCL
DCL
AICc scores
−200
−150
−100
−50
0
−150
−100
−50
0
50
SURFACE
BM
OU
EB
best trend
b
AICc scores
−200
−150
−100
−50
−150
−100
−50
0
SURFACE
BM
OU
EB
best trend
c
AICc scores
−200
−100
0
−100
0
100
SURFACE
BM
OU
EB
best trend

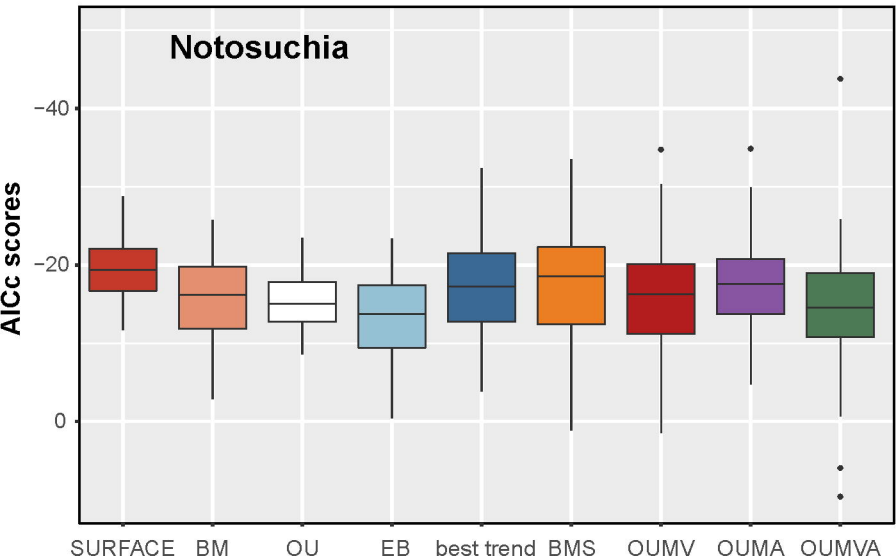

a
AICc
b
pBIC
c
AICc
d
pBIC
e
AICc
f
pBIC

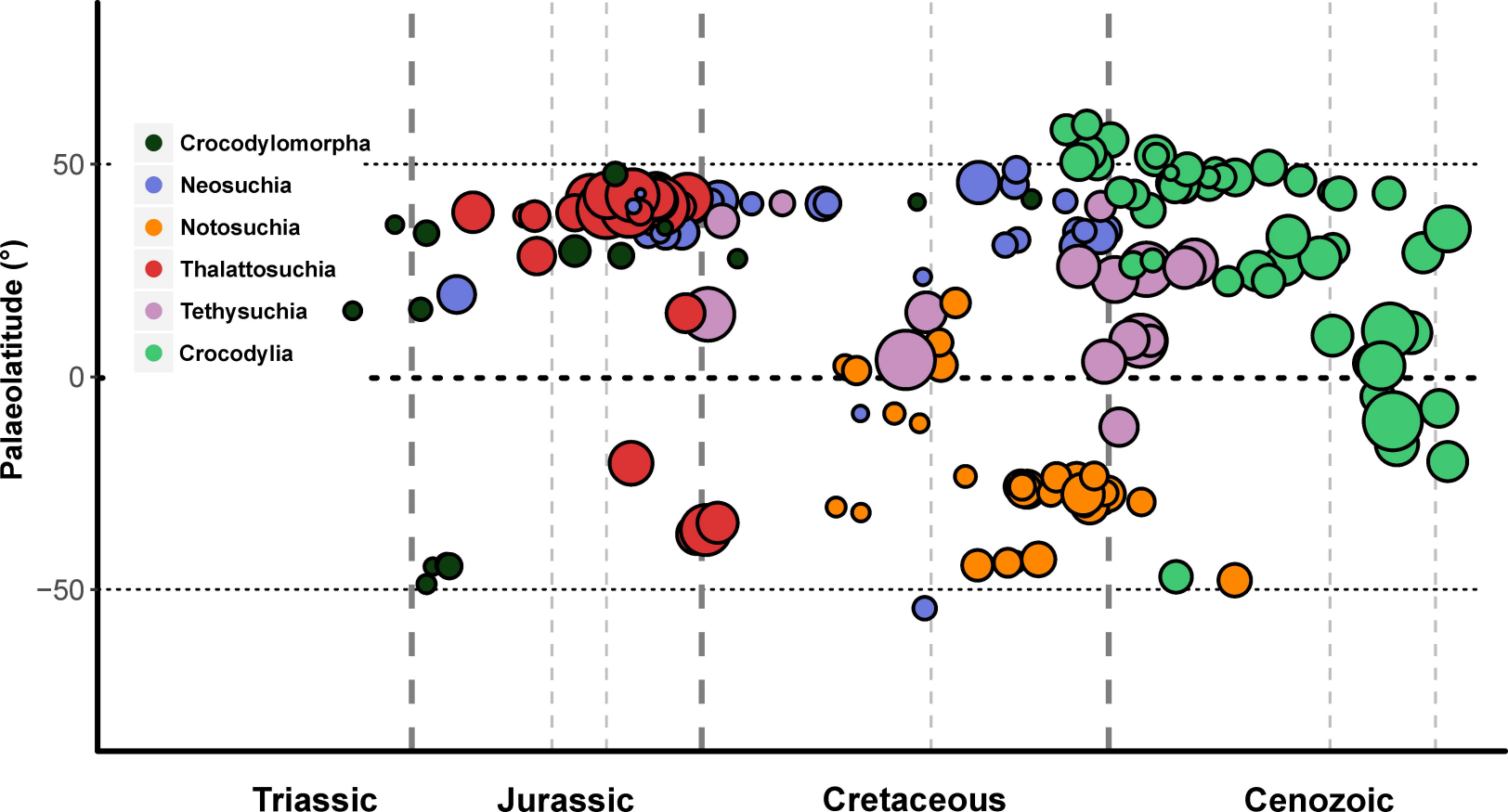

Tree 10 :
pBIC = −186.81
alpha = 0.524
sigma sq. = 0.013
Trait optima / centimetres:
theta(f) = 43
theta(a) = 74
theta(e) = 130
theta(m) = 230
theta(h) = 320
theta(g) = 540
theta(b) = 980
theta / centimetres
980
540
320
230
130
70
40
(g) M. niger
(m) C. latirostris
(g) Purussaurus
(g) Mourasuchus
(m) Paleosuchus
(c) Tsoabichi
(m) Brachychampsa montana
(m) A. sinensis
(m) Alligator mcgrewi
(m) Allognathosuchus
(m) Diplocynodon ratelii
(a) Diplocynodon deponiae
(m) Leidyosuchus
(h) O. tetraspis
(h) C. porosus
(h) Crocodylus megarhinus
(h) Thecacampsa
(h) T. schlegelii
(h) Crocodylus depressifrons
(e) Boverisuchus vorax
(e) Planocrania hengdongensis
(h) Borealosuchus formidabilis
Crocodylia
(h) Piscogavialis
(h) Gryposuchus
(h) Eogavialis africanus
Eusuchia
(h) Eosuchus minor
(h) Allodaposuchus precedens
(e) Iharkutosuchus
(e) Acynodon adriaticus
(b) Paralligator major
(e) Shamosuchus djadochtaensis
(f) Susisuchus anatoceps
(e) Bernissartia fagesii
(m) Goniopholis simus
(m) Eutretauranosuchus delfsi
(m) Calsoyasuchus
(f) Alligatorellus beaumonti
(h) Cricosaurus araucanensis
(h) Rhacheosaurus gracilis
(g) Geosaurus grandis
Neosuchia
(g) Dakosaurus andiniensis
(g) Tyrannoneustes lythrodectikos
(b) Machimosaurus hugii
Thalattosuchia
(g) S. bollensis
(b) S. megistorhynchus
(e) Teleosaurus cadomensis
(g) Peipehsuchus teleorhinus
(g) Dyrosaurus phosphaticus
(g) Atlantosuchus coupatezi
(m) Hyposaurus rogersii
(g) Chenanisuchus lateroculi
Tethysuchia
(b) Sarcosuchus imperator
(e) Vectisuchus
(g) Pholidosaurus
Mesoeucrocodylia
(h) Baurusuchus salgadoensis
(h) Stratiotosuchus maxhechti
(h) Sebecus icaeorhinus
(e) Caipirasuchus paulistanus
(h) Armadillosuchus arrudai
(e) Pakasuchus
(e) Simosuchus clarki
(m) Montealtosuchus arrudacamposi
(m) Mahajangasuchus insignis
Notosuchia
(m) Kaprosuchus saharicus
(a) A. tsangatsangana
(a) A. wegeneri
Crocodyliformes
(e) Hsisosuchus chungkingensis
(a) Shantungosuchus brachycephalus
(a) Gobiosuchus kielanae
(a) Protosuchus richardsoni
(a) Junggarsuchus sloani
(a) Hesperosuchus agilis
(a) Litargosuchus leptorhynchus
Triassic
201.3
Jurassic
145
Cretaceous
66
Cenozoic

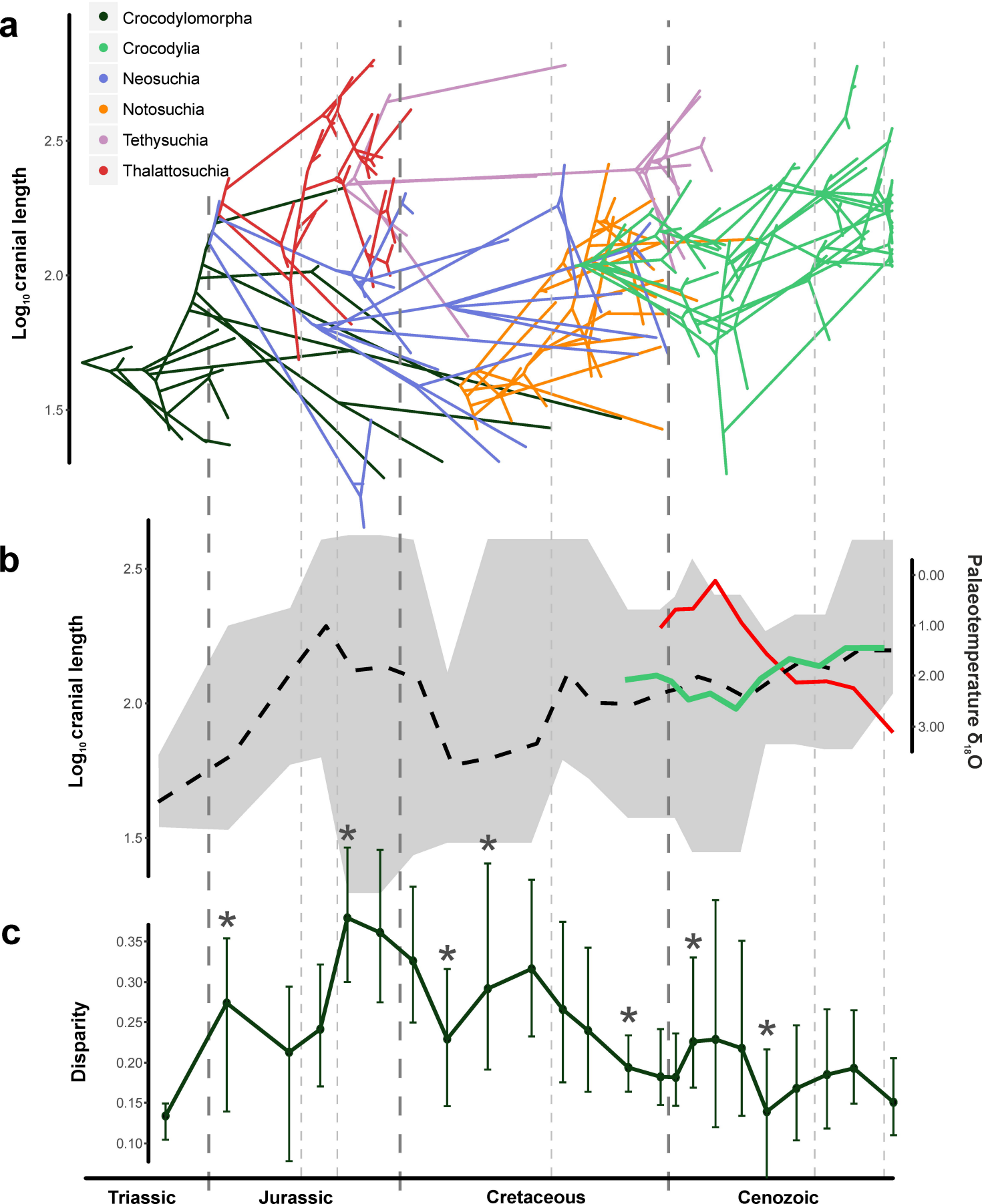

a
Tree 16 :
pBIC = −180.585
alpha = 0.382
sigma sq. = 0.009
Trait optima / centimetres
theta(g) = 43
theta(a) = 73
theta(c) = 130
theta(m) = 220
theta(e) = 320
theta(d) = 530
theta(v) = 950
theta / centimetres
950
530
320
220
130
70
40
Crocodylia
Eusuchia
Neosuchia
Thalattosuchia
Mesoeucrocodylia
Tethysuchia
Notosuchia
Crocodyliformes
b
Regime body size optimum / log10 (mm)
2.5
2.0
1.5
Tethysuchia
Thalattosuchia
Crocodylia
Mesoeucrocodylia
Neosuchia
Eusuchia
Notosuchia
Crocodyliformes
Triassic
201.3
Jurassic
145
Cretaceous
66
Cenozoic

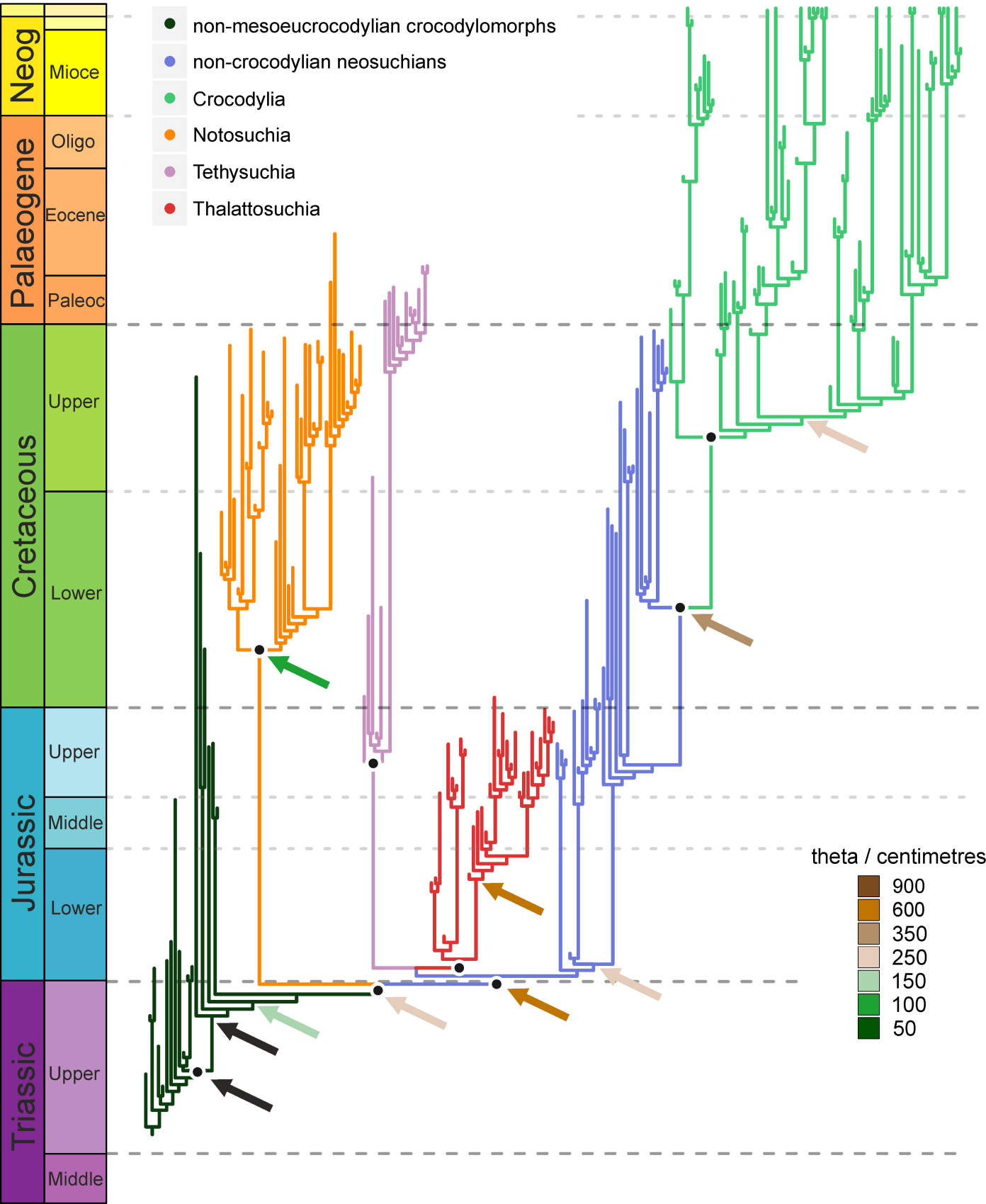

a
Tree 14 :
pBIC = −148.944
alpha = 0.14
sigma sq. = 0.004
Trait optima / centimetres
theta(a) = 74
theta(l) = 100
theta(u) = 210
theta(q) = 340
theta(m) = 470
theta(i) = 920
theta / centimetres
920
470
340
210
100
70
Crocodylia
Eusuchia
Neosuchia
Tethysuchia
Mesoeucrocodylia
Notosuchia
Crocodyliformes
Thalattosuchia
b
Tree 11 :
pBIC = −166.981
alpha = 0.239
sigma sq. = 0.006
Trait optima / centimetres
theta(f) = 36
theta(a) = 74
theta(g) = 120
theta(p) = 220
theta(j) = 340
theta(e) = 490
theta(h) = 850
theta / centimetres
850
490
340
220
120
70
40
Crocodylia
Eusuchia
Neosuchia
Mesoeucrocodylia
Tethysuchia
Notosuchia
Thalattosuchia
Crocodyliformes
d
Regime body size optimum / log10 (mm)
2.5
2.0
1.5
Thalattosuchia
Crocodylia
Eusuchia
Tethysuchia
Neosuchia
Notosuchia
Mesoeucrocodylia
Crocodyliformes
Triassic
201.3
Jurassic
145
Cretaceous
66
Cenozoic
d
Regime body size optimum / log10 (mm)
2.5
2.0
1.5
Thalattosuchia
Neosuchia
Tethysuchia
Crocodylia
Mesoeucrocodylia
Notosuchia
Eusuchia
Crocodyliformes
Triassic
201.3
Jurassic
145
Cretaceous
66
Cenozoic

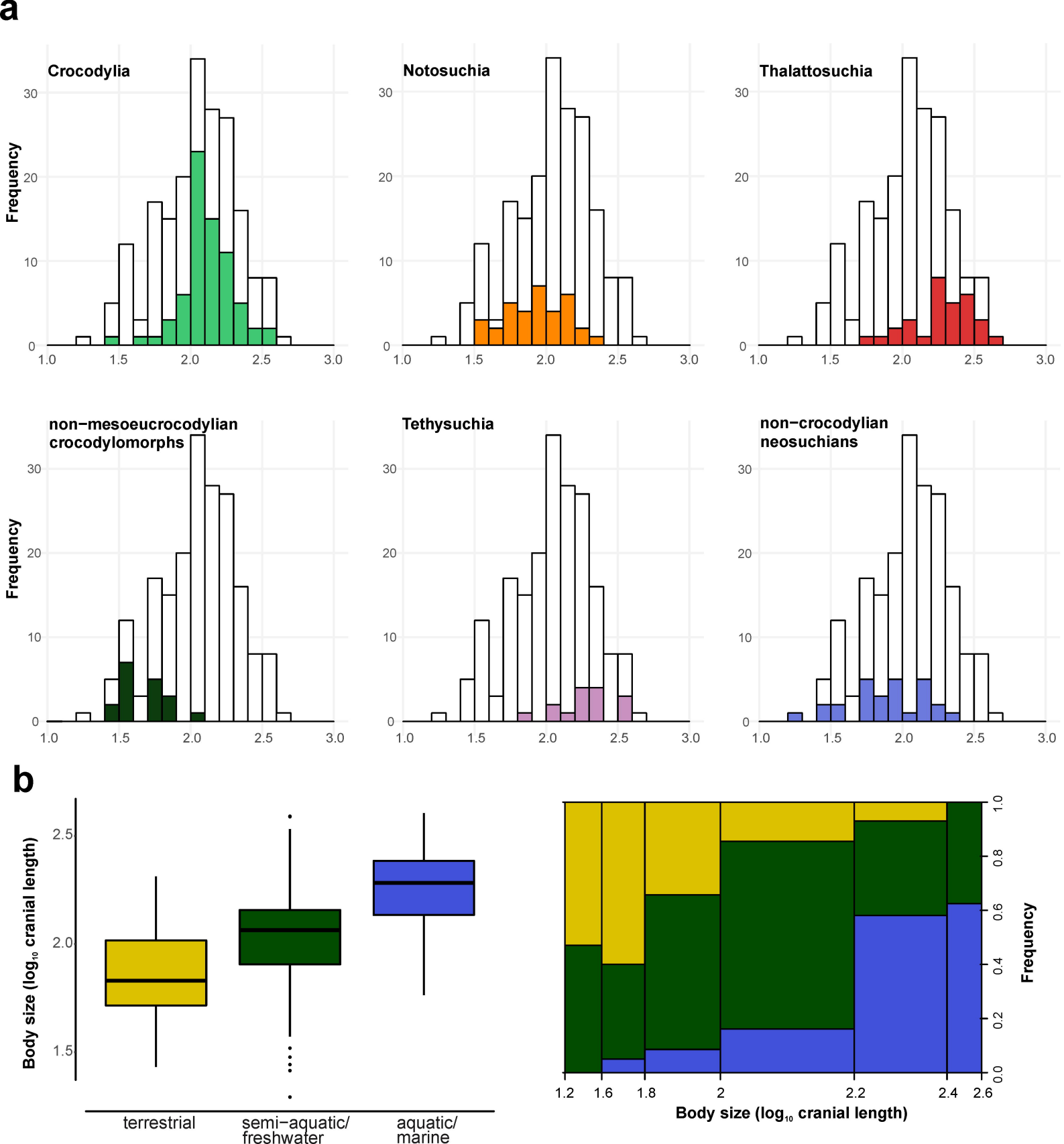

Crocodylia
AICc scores
−100
−75
−50
−25
SURFACE
BM
OU
EB
best trend
BMS
OUMV
OUMA
OUMVA

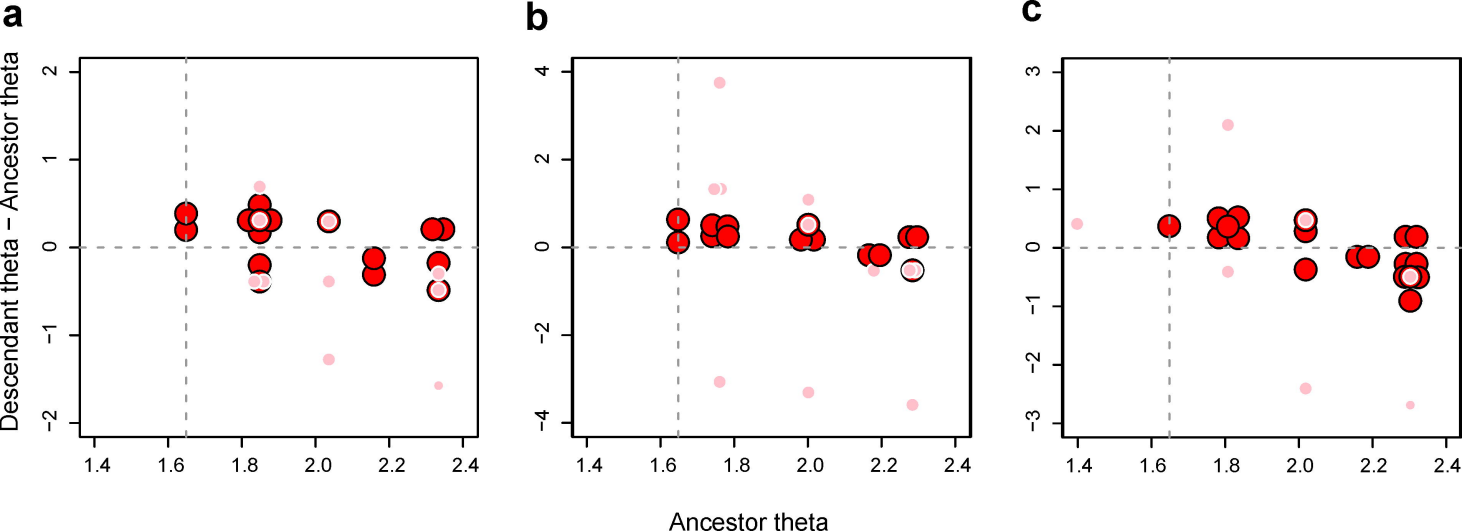

Notosuchia
AICc scores
−40
−20
0
SURFACE
BM
OU
EB
best trend
BMS
OUMV
OUMA
OUMVA


Crocodylomorpha
Neosuchia
Notosuchia
Thalattosuchia
Tethysuchia
Crocodylia
Palaeolatitude (°)
50
0
−50
Triassic
Jurassic
Cretaceous
Cenozoic


a
Crocodylomorpha
Crocodylia
Neosuchia
Notosuchia
Tethysuchia
Thalattosuchia
Log10 cranial length
2.5
2.0
1.5
b
Log10 cranial length
2.5
2.0
1.5
Palaeotemperature δ18O
0.00
1.00
2.00
3.00
c
Disparity
0.35
0.30
0.25
0.20
0.15
0.10
Triassic
Jurassic
Cretaceous
Cenozoic


Neog
Mioce
Palaeogene
Oligo
Eocene
Paleoc
Cretaceous
Upper
Lower
Jurassic
Upper
Middle
Lower
Triassic
Upper
Middle
non-mesoeucrocodylian crocodylomorphs
non-crocodylian neosuchians
Crocodylia
Notosuchia
Tethysuchia
Thalattosuchia
theta / centimetres
900
600
350
250
150
100
50


a
Crocodylia
Notosuchia
Thalattosuchia
non−mesoeucrocodylian crocodylomorphs
Tethysuchia
non−crocodylian neosuchians
Frequency
0
10
20
30
1.0
1.5
2.0
2.5
3.0
b
Body size (log10 cranial length)
2.5
2.0
1.5
terrestrial
semi−aquatic/ freshwater
aquatic/ marine
Frequency
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.6
1.8
2
2.2
2.4
2.6
Body size (log10 cranial length)


a
b
c
Descendant theta − Ancestor theta
Ancestor theta
1.4
1.6
1.8
2.0
2.2
2.4
−2
−1
0
1
2
−4
−3
3
4