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Crocodylomorph cranial shape evolution and its relationship with body size and ecology

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Abstract

Crocodylomorpha, which includes living crocodylians and their extinct relatives, has a rich fossil record, extending back for more than 200 million years. Unlike modern semi-aquatic crocodylians, extinct crocodylomorphs exhibited more varied lifestyles, ranging from marine to fully terrestrial forms. This ecological diversity was mirrored by a remarkable morphological disparity, particularly in terms of cranial morphology, which seems to be closely associated with ecological roles in the group. Here, I use geometric morphometrics to comprehensively investigate cranial shape variation and disparity in Crocodylomorpha. I quantitatively assess the relationship between cranial shape and ecology (i.e. terrestrial, aquatic, and semi-aquatic lifestyles), as well as possible allometric shape changes. I also characterize patterns of cranial shape evolution and identify regime shifts. I found a strong link between shape and size, and a significant influence of ecology on the observed shape variation. Terrestrial taxa, particularly notosuchians, have significantly higher disparity, and shifts to more longirostrine regimes are associated with large-bodied aquatic or semi-aquatic species. This demonstrates an intricate relationship between cranial shape, body size and lifestyle in crocodylomorph evolutionary history. Additionally, disparity-through-time analyses were highly sensitive to different phylogenetic hypotheses, suggesting the description of overall patterns among distinct trees. For crocodylomorphs, most results agree in an early peak during the Early Jurassic and another in the middle of the Cretaceous, followed by nearly continuous decline until today. Since only crown-group members survived through the Cenozoic, this decrease in disparity was likely the result of habitat loss, which narrowed down the range of crocodylomorph lifestyles.

KEYWORDS
adaptive landscape, body size, cranial shape, ecology, geometric morphometrics, macroevolutionary patters, phylogenetic comparative methods

1 | INTRODUCTION

The relationship between form and function has long been recognized (Cuvier, 1817; Lauder, 1981; Russell, 1916), and, given the phenotypic similarities generated by convergence, the incorporation of phylogenetic comparative methods has become almost imperative on analyses of evolutionary shape changes (Bookstein et al., 1985; Felsenstein, 1985; Harvey & Pagel, 1991; Losos, 2011; Monteiro,

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2013; Rohlf, 2001, 2002). Taking this into account, several studies have examined the association between organisms' shape and ecology in a phylogenetic context (e.g. Bhullar et al., 2012; Sidlauskas, 2008; Watanabe et al., 2019). Similarly, another widely studied and documented evolutionary phenomenon is the link between size and shape, which generates allometric shape changes (Gould, 1966; Klingenberg, 2016). Accordingly, with the current expansion of the use of geometric morphometric techniques for analysing shape variation, studies that investigate the relationship between shape and either size or ecology (or both), while also taking a phylogenetic approach, have become increasingly common (Adams, Rohlf, & Slice, 2004; Zelditch, Swiderski, & Sheets, 2012).

In this context, data collected from fossil organisms can yield essential information for a better comprehension of large-scale evolutionary shape changes. Among tetrapods, Crocodylomorpha represent a good system for studying large-scale phenotypic evolution, given the group's long and rich fossil record (Bronzati, Montefeltro, & Langer, 2015; Mannion et al., 2015), as well as extensive recent effort to resolve major phylogenetic uncertainties (e.g. Andrade, Edmonds, Benton, & Schouten, 2011; Brochu, 2011, 2012; Bronzati, Montefeltro, & Langer, 2012; Clark, 2011; Herrera, Gasparini, & Fernández, 2015; Jouve, Iarochene, Bouya, & Amaghzaz, 2006; Larsson & Sues, 2007; Montefeltro, Larsson, França, & Langer, 2013; Pol et al., 2014; Turner, 2015; Wilberg, 2015; Young & Andrade, 2009; Young, Brusatte, Ruta, & Andrade, 2010). Furthermore, previous studies have investigated the relationship between form and function in crocodylomorphs, particularly focusing on the link between ecological roles and skull shape (Brochu, 2001; Busbey, 1995; Taylor, 1987). Historically, the crocodylomorph skull has received substantial attention in anatomical studies (Iordansky, 1973), which might explain the preference for this part of the skeleton as the source of morphological information in most works quantitatively investigating phenotypic evolution in the group (even though some important exceptions exist; e.g. Bonnan, Farlow, & Masters, 2008; Chamero, Buscalioni, & Marugán-Lobón, 2013; Chamero, Buscalioni, Marugán-Lobón, & Sarris, 2014; Stubbs, Pierce, Rayfield, & Anderson, 2013; Walmsley et al., 2013; Toljagić & Butler, 2013; Gold, Brochu, & Norell, 2014).

Previous works that use geometric morphometrics for studying crocodylomorph cranial shape have mostly focused on specific subgroups, especially crocodylians (Bona, Ezcurra, Barrios, & Fernandez Blanco, 2018; Clarac et al., 2016; Fernandez Blanco, Cassini, & Bona, 2018; Foth, Fernandez Blanco, Bona, & Scheyer, 2017; Iijima, 2017; McCurry, Evans, et al., 2017; Monteiro, Cavalcanti, & Sommer, 1997; Morris, Vliet, Abzhanov, & Pierce, 2019; Okamoto, Langerhans, Rashid, & Amarasekare, 2015; Pearcy & Wijtten, 2011; Pierce, Angielczyk, & Rayfield, 2008; Piras, Teresi, Buscalioni, & Cubo, 2009; Piras et al., 2010, 2014; Sadleir & Makovicky, 2008; Salas-Gismondi, Moreno-Bernal, Scheyer, Sánchez-Villagra, & Jaramillo, 2018; Salas-Gismondi et al., 2016; Watanabe & Slice, 2014), but also thalattosuchians (Pierce, Angielczyk, & Rayfield, 2009; Young et al., 2010) and notosuchians (Godoy et al., 2018). One important exception is the recent work of Wilberg (2017), which assessed cranial shape variation across Crocodyliformes (which is only slightly less inclusive than Crocodylomorpha; Irmis, Nesbitt, & Sues, 2013), sampling a large number of species. Nevertheless, the sample size of Wilberg (2017) could still be significantly increased, potentially permitting the assessment of morphospace occupation and morphological disparity among other crocodylomorph subgroups (i.e. not only making a distinction between species within Crocodylia and those outside the crown-group). Furthermore, Wilberg (2017) analysed patterns of cranial shape disparity through time within Crocodylomorpha, but the impact of alternative time sub-sampling methods on disparity-through-time analyses (as recently suggested by Guillerme & Cooper, 2018) was not explored, as well as that of distinct phylogenetic hypotheses. Finally, the potential influence of body size and ecological transitions on crocodylomorph cranial shape can also be quantitatively assessed with phylogenetic comparative methods (Klingenberg & Marugán-Lobón, 2013; Monteiro, 2013; Zelditch et al., 2012). Even though the hypothesis of a link between cranial shape and ecology (mainly feeding strategies) has been previously examined for some groups (e.g. Busbey, 1995; McHenry, Clausen, Daniel, Meers, & Pendharkar, 2006; Young et al., 2010), a wider investigation, including taxa of all crocodylomorph groups, remains to be tested, as well as the role of size in this relationship.

Here, I use geometric morphometric techniques to comprehensively analyse crocodylomorph cranial shape, by combining a previously available landmark dataset (from Wilberg (2017)) with newly digitized specimens. I quantify cranial shape variation and estimate disparity of distinct crocodylomorph subgroups, and also estimate disparity through time. This allowed me to compare my results with those of previous studies, but also to investigate the impact of a variety of alternative methods in disparity-through-time estimation. I further investigate the association between the observed shape variation and two factors: body size and ecology (=lifestyles). For that, I used disparity estimation and morphospace occupation, but also statistical and phylogenetic comparative methods. I also inferred shifts in cranial shape evolutionary regimes, using Bayesian and maximum-likelihood approaches. By doing this, I was able to characterize the patterns of crocodylomorph cranial shape evolution and to test its hypothesized relationship with ecological transitions and size.

2 | MATERIAL AND METHODS

2.1 | Sampling and data collection

The goal of this study was to examine overall cranial shape changes across as many crocodylomorph species as possible. Most crocodylomorph crania are taphonomically deformed, usually by dorsoventral compression, which prevents a comprehensive study from using three-dimensional (3D) data. Thus, I initially used the data published by Wilberg (2017), as this is the most phylogenetically comprehensive 2D landmark dataset to date (i.e. 131 crocodylomorph specimens, most of which were identified to species level). This dataset used only dorsal views of skulls, as this view is less susceptible to

compression and taphonomic distortion across different crocodylomorph groups. For capturing overall cranial shape, Wilberg (2017) digitized four (4) landmarks, each at a key homologous point of crocodylomorph skulls, as well as a semilandmark curve (with 60 semilandmarks) to represent the outline of skulls. It is worth mentioning that the dataset made available by Wilberg (2017) was slightly modified, as in its original version the semilandmark curves were artificially divided into two parts (one rostral to and another caudal to the level rostralmost point of the orbit; see Appendix S1 for description and position of the landmarks and further information on data collection).

To expand this dataset, I digitized landmarks for additional 86 new specimens, representing an increase of nearly 65% over the dataset of Wilberg (2017). Five specimens included in the original dataset were posteriorly removed, and the taxonomy of all specimens was updated following more recent literature (see Appendix S1 for further details). The final expanded dataset includes 212 specimens, representing 209 species (see Appendix S2 for the complete list of specimens sampled). For landmark data collection, I used tpsUTIL version 1.76 (Rohlf, 2015) to compile the images into a single .tps file, then digitizing the landmarks and semilandmarks in tpsDIG2 version 2.30 (Rohlf, 2015).

2.2 | Phylogenetic framework

Within the context of phylogenetic comparative methods, it is fundamental to set a phylogenetic framework, upon which downstream analyses can be performed. For this study, I sought a comprehensive phylogenetic hypothesis (or hypotheses), which enabled the investigation of overall evolutionary patterns within Crocodylomorpha. Thus, I used a modified version of the crocodylomorph informal supertree from Godoy, Benson, Bronzati, and Butler (2019), which is the most recent and comprehensive version of the supertree presented by Bronzati et al. (2012). For the present study, I also added 20 species for which I had landmark data, but were not previously in the supertree (see Appendix S1 for details). The final version of the supertree includes 325 species (316 crocodylomorphs and nine non-crocodylomorph species, as outgroups).

Instead of just a single phylogenetic framework (i.e. supertree), I used three alternative phylogenetic scenarios for dealing with major phylogenetic uncertainties among crocodylomorphs. These major uncertainties mostly concern the relative positions of thalattosuchians (recovered either as neosuchians or as the sister group of Crocodyliformes; Clark, 1994; Pol & Gasparini, 2009; Wilberg, 2015) and that of gavialids in relation to tomistomines and 'thoracosaurs' (Gatesy, Amato, Norell, DeSalle, & Hayashi, 2003; Lee & Yates, 2018). To accommodate these, I created three versions of the supertree, in which the only differences among topologies were the relative positions of Thalattosuchia and the distinct interrelationships within Crocodylia (regarding the relative of gavialids; see Appendix S1 for details). These different versions of the supertree formed the base of the three phylogenetic scenarios used in downstream analyses.

Another important step for macroevolutionary analyses is to time-scale the phylogenetic trees, in order to investigate and characterize deep-time patterns. Therefore, each of these three supertrees/topologies was then time-calibrated using the fossilized birth–death (FBD) model (Didier, Fau, & Laurin, 2017; Didier & Laurin, 2018; Heath, Huelsenbeck, & Stadler, 2014; Ronquist, Klopfstein, et al., 2012; Stadler, 2010; Zhang, Stadler, Klopfstein, Heath, & Ronquist, 2015). I used the protocol within the R package *paleotree* version 3.1.3 (Bapst, 2012), which follows recommendations within Matzke and Wright (2016), to generate an 'empty' morphological matrix and perform Bayesian Markov chain Monte Carlo (MCMC) tip-dating analyses in MrBayes version 3.2.6 (Ronquist, Teslenko, et al., 2012). The three supertree topologies (representing alternative phylogenetic scenarios) were used as topological constraints, and the uniform priors for the age of tips were set based on the occurrence dates' information (i.e. obtained from the literature and the Paleobiology Database). A uniform prior was used for the root of the tree (for all three topologies), constraining it between 245 and 260 Myr ago (given that a crocodylomorph origin older than the Early Triassic is unlikely; Irmis et al., 2013; Turner, Pritchard, & Matzke, 2017; Ezcurra & Butler, 2018). For each alternative phylogenetic scenario, 10,000,000 generations were used in two MCMC runs (with four chains each), after which the parameters indicated that both runs converged (i.e. the potential scale reduction factor approached 1.0 and average standard deviation of split frequencies was below 0.01). In downstream analyses, for each phylogenetic scenario, I used either the maximum clade credibility (MCC) trees or 10 trees randomly sampled from the posterior distribution, both after a burn-in of 25%.

2.3 | Geometric morphometric analyses

I performed a series of geometric morphometric analyses in order to quantitatively investigate cranial shape variation in crocodylomorphs. I was initially interested in observing which differences would arise from adding numerous specimens/species to the dataset of Wilberg (2017), such as in morphospace occupation. I was also interested in statistically testing significant differences in morphospace occupation between crocodylomorph subgroups as well as estimating the phylogenetic signal for the data (which specifically asks how much of the shape variation can be explained by the phylogenetic history of the group). Finally, apart from investigating cranial shape variation between taxonomic groups, I also wanted to explore differences among distinct ecological lifestyle displayed by crocodylomorphs.

All geometric morphometric analyses presented here were performed using the package *geomorph* (version 3.0.7; Adams & Otárola-Castillo, 2013) in R (version 3.5.1; R Core Team, 2018). Generalized Procrustes analysis (GPA) (Gower, 1975; Rohlf & Slice, 1990) was performed prior to all analyses. Semilandmarks were defined using function *define.sliders()*, and the location of sliding semilandmarks during GPA alignment was optimized by minimizing the bending energy between the reference and target specimen

(i.e. argument ProcD = FALSE within in the function *gpagen()*; see Bookstein, 1997). Subsequently, the Procrustes coordinates of specimens were used as the input data for principal component analysis (PCA; Hotelling, 1933). As the landmark data used here were derived from two distinct sources (i.e. the dataset provided by Wilberg, 2017 and the data collected for the present study), particular attention was paid to the potential impact of interobserver error on the cranial shape data. To quantitatively approach this issue, I used Procrustes ANOVA (i.e. linear models; Goodall, 1991; Klingenberg & McIntyre, 1998; Anderson, 2001) to compute the amount of variation caused by interobserver error (see Appendix S1 for further details).

To better visualize the morphospace occupation of different crocodylomorph subgroups (e.g. in PC1 vs. PC2 scatterplots), I used distinct colours and convex hulls (i.e. the area inside the minimum convex polygon; Cornwell, Schwilk, & Ackerly, 2006) for six taxonomic groups: Crocodylia (with 'thoracosaurs'), Tethysuchia, Thalattosuchia, Notosuchia and two paraphyletic groupings of non-crocodylian neosuchians (excluding tethysuchians and thalattosuchians) and non-mesoeucrocodylian crocodylomorphs (excluding thalattosuchians). To statistically assess the differences in the morphospace occupied by these groups, I used nonparametric multivariate analysis of variance (npMANOVA, performed with R package *RVAideMemoire*; Hervé, 2018) with all PC scores (see Appendix S1 for further details). To examine the influence of phylogenetic history on the observed shape variation, I calculated the phylogenetic signal (K_{mult}; Blomberg, Garland, & Ives, 2003; Adams, 2014) using function *physignal()*, with Procrustes coordinates of specimens and the MCC tree of each alternative phylogenetic scenario, performing 1000 iterations.

I also divided crocodylomorph species into three categories representing distinct ecologies (or lifestyles): marine/aquatic, freshwater/semi-aquatic and terrestrial species. For that, I used information available in the literature (Mannion et al., 2015; Wilberg, Turner, & Brochu, 2019), as well as in the Paleobiology Database (see Appendix S2 for the lifestyles assigned to each taxon). I then visually assessed the differences in morphospace occupation using colours and convex hulls and statistically scrutinized these differences using npMANOVA.

2.4 | Estimating disparity

After quantifying cranial shape variation in crocodylomorphs with geometric morphometric analyses, I wanted to explore how the patterns of cranial shape changed through time. For that, I needed to use metric to represent cranial shape disparity. Furthermore, by using this metric, I could also investigate cranial shape disparity within different crocodylomorph groups (taxonomic and ecological groups). For this paper, I selected the sum of variances as the disparity metric, as it seems to be more robust for measuring morphological disparity through time than other metrics (such as range-based measures; see Wills, Briggs, & Fortey, 1994; Butler, Brusatte, Andres, & Benson, 2012; Guillerme & Cooper, 2018), but also because using this metric allows me to compare my results with those from other studies (e.g. Stubbs et al., 2013; Toljagić & Butler, 2013; Wilberg, 2017). Other methods were proposed to measure disparity, and often produce different results, but were not used herein (see Appendix S1 for further discussion).

I performed a series of sensitivity analyses for disparity-through-time estimation, given that previous work demonstrated the susceptibility of these kind of analyses to alternative methods for sub-sampling taxa (Guillerme, 2018; Guillerme & Cooper, 2018) and to different phylogenetic hypotheses (Foth, Ascarrunz, & Joyce, 2017). Thus, I used different sub-sampling procedures (i.e. time-binning and time-slicing methods, *sensu* Guillerme and Cooper (2018)), different numbers of time intervals (10 and 20), and multiple time-scaled phylogenetic trees (randomly sampled from the posterior distribution of tip-dating MCMC analyses) to assess the impact of these alternative approaches on the results. For these analyses, PC scores of all 128 PCs were used, both from terminal taxa and from ancestors (estimated using maximum-likelihood ancestral state reconstruction; see Appendix S1 for further information on disparity-through-time sensitivity analyses). It is worth mentioning that, differently from time binning, time-slicing method is a phylogeny-based approach (i.e. using data from terminal taxa, nodes and branches) and takes into consideration those taxa contemporaneous at specific equidistant points in time (instead of taxa that were present between two points in time), resulting in even sampling (Guillerme & Cooper, 2018).

I also estimated disparity (=sum of variances) among different crocodylomorph subgroups (taxonomic and ecological groups), by subdividing the PC scores for each species into distinct subsets (again, using all 128 PCs). For both disparity through time and between groups analyses, PC scores were bootstrapped 100 times (i.e. resampling all the rows of the matrix and then replacing them with a new random sample of rows). For disparity between groups, the data were also rarefied during each bootstrap replication (i.e. the number of taxa drawn was standardized in all groups). For that, the minimum number of species in a subset was used (which was 18 and 48 taxa for taxonomic and ecological subsets, respectively). Significant differences in bootstrapped median values were statistically assessed using npMANOVA with 10,000 permutations, followed by a Bonferroni correction for adjusted *p*-values (Anderson, 2001; Rice, 1989). All disparity analyses (through-time and between groups) were performed using the R package *dispRity* (Guillerme, 2018).

2.5 | Correlation with body size and ecological factors

An important aspect of this study aimed at examining the association between cranial shape variation and two other factors: body size and ecology. To investigate and visualize allometric changes and how much of shape variation can be explained by body size, I used Procrustes ANOVA, with function *procD.allometry()* in *geomorph*. I used log-transformed centroid size as a proxy for total body size and calculated the regression scores (Drake & Klingenberg, 2008) for plotting purposes. To further inspect and visualize this possible

shape–size relationship, I regressed and plotted my cranial shape data against an independent body size dataset (a comprehensive crocodylomorph dataset of log-transformed dorsal cranial length measurements, made available by Godoy et al. (2019)), using ordinary least square (OLS) and phylogenetic generalized least squares (PGLS) regressions. For PGLS, I incorporated the phylogenetic information from the maximum clade credibility (MMC) trees (of each alternative phylogenetic scenario) and optimized branch length transformations between bounds with maximum likelihood using Pagel's λ (Pagel, 1999) (i.e. argument λ = 'ML' within in the function *pgls()* of the R package *caper*; Orme et al., 2018).

In addition to estimating disparity for distinct ecological categories (see above), I further assessed the influence of ecological factors on crocodylomorph cranial shape by applying Procrustes ANOVA in a phylogenetic framework, using *procD.pgls()* function in *geomorph*. As for allometric Procrustes ANOVA, 10,000 permutations were performed, and I obtained the percentage of variation explained by the independent variables (body size or ecology) by dividing the sum of squares of the variable by the total sum of squares.

2.6 | Identifying regime shifts in crocodylomorph cranial shape evolution

Following the examination of the influence of body size and ecology on crocodylomorph cranial shape, I decided to further investigate these associations by identifying cranial shape regime shifts on the crocodylomorph phylogeny. By doing this, I was specifically able to assess whether major changes in the crocodylomorph skull (represented by cranial shape regime shifts) were associated with ecological transitions and/or accompanied by major changes in body size (represented by previously documented body size regime shifts).

However, some studies have previously indicated intrinsic difficulties of many of the presently proposed methods for automatically detecting regime shifts of phenotypic traits in phylogenies (e.g. Adams & Collyer, 2018; Bastide, Ané, Robin, & Mariadassou, 2018), many of which assume evolution under a nonuniform Ornstein–Uhlenbeck [OU] process (although methods that assume other models/processes are also available; e.g. Rabosky, 2014; Castiglione et al., 2018, 2019; Didier, Chabrol, & Laurin, 2019). In particular, the combination of using multivariate data (such as shape data derived from geometric morphometric methods) and fossils as tips in a time-scaled tree (i.e. a nonultrametric tree) presents a challenge to currently proposed methods, without an appropriate solution to date (Bastide et al., 2018).

Accordingly, for automatically detecting shifts of cranial shape regimes during the evolution of crocodylomorphs, I decided to reduce my analyses to a single (univariate) trait, using only PC1 scores of taxa, since this principal component represents a significant amount of total shape variation (more than 70%) and is biologically meaningful (i.e. translating, predominantly, changes in snout length). Thus, I am ultimately using PC1 scores as a proxy for total cranial shape variation. Using only one dimension (i.e. PC1) allowed me to apply two methods for detecting regime shifts: *bayou* (Uyeda & Harmon, 2014) and *SURFACE* (Ingram & Mahler, 2013). Differently from other methods proposed (e.g. *l1ou* (Khabbazian, Kriebel, Rohe, & Ané, 2016) and *PhylogeneticEM* (Bastide et al., 2018)), *bayou* and *SURFACE* can deal with nonultrametric trees and seem to work better with univariate data (Adams & Collyer, 2018). Even though not ideal (see Polly, Lawing, Fabre, and Goswami (2013), Uyeda, Caetano, and Pennell (2015), Adams and Collyer (2018), and Du (2019) for problems with dimension reduction), by comparing the outputs from both methods (i.e. looking for overall patterns of shift detection) I could visualize patterns of cranial shape variation along the crocodylomorph phylogeny, as well as to compare to body size evolutionary patterns and to ecological transitions in the group.

For *bayou*, which is a Bayesian reversible-jump approach (Uyeda & Harmon, 2014), I ran five MCMC chains of 1,000,000 generations for each of the three phylogenetic scenarios (using the MCC trees), with 30% burn-in and a conditional Poisson distribution as a prior on the number of shifts. For *SURFACE*, which is a stepwise AIC procedure (Ingram & Mahler, 2013), I used phylogenetic Bayesian information criterion (pBIC) as an alternative to AICc in the backward phase of SURFACE (during which 'convergent' regimes are identified), as the former is more conservative than AICc, generating lower rates of false positive identification of regime shifts (Benson, Hunt, Carrano, & Campione, 2018; Ho & Ané, 2014; Khabbazian et al., 2016). Furthermore, given that SURFACE seems to be very sensitive to both topological conformation and branch lengths, instead of MCC trees I used 30 time-scaled crocodylomorph trees for the analyses (i.e. 10 randomly sampled trees of each alternative phylogenetic scenario) and assessed regime shift identification on all trees, looking for overall patterns (see Appendix S1 for more details on *SURFACE* and *bayou* analyses). *bayou* analyses were performed with R package *bayou* (Uyeda, Eastman, & Harmon, 2018), whereas *SURFACE* analyses were performed with *surface* package (Ingram & Mahler, 2013). Implementation of pBIC functions in the backward phase of *SURFACE* model fits used scripts made available by Benson et al. (2018). See Appendix S3 for an R script with the all the analyses performed here (i.e. geometric morphometric, disparity, *SURFACE*, and *bayou* analyses), as well as landmark data and phylogenetic trees.

3 | RESULTS

3.1 | Cranial shape in different crocodylomorph subgroups

Procrustes ANOVA results show that interobserver error accounts for only 1.6% of total shape variation (Appendix S1: Table S1), allowing further analyses using the expanded dataset. The aspects of morphology represented by PC1 and PC2 (Figure 1) are equivalent to those found by Wilberg (2017), with PC1 (71.89% of the variation) mostly describing variation in snout length and PC2 (8.6%) changes in the quadrate condyle, in the position of the orbit in relation to the lateral outline of the skull, and in relative width of the snout with respect to the temporal region (see Appendix S1: Figure S3 for variation in all PCs).

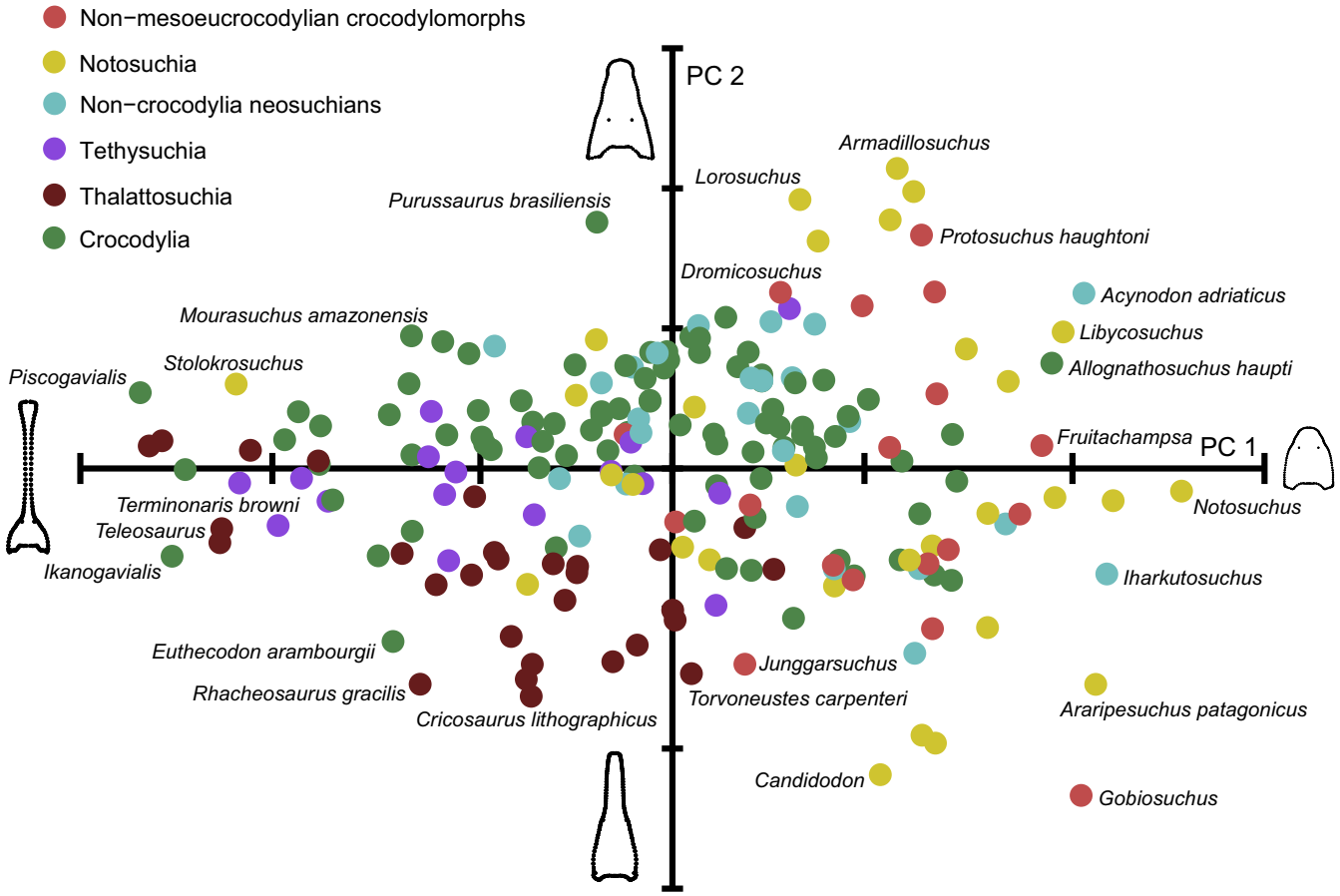

FIGURE 1 Morphospace occupation of crocodylomorphs. PC1 vs. PC2 plot of cranial shape variation, using the expanded dataset, after removing the effect of interobserver error (by standardizing the landmark digitizing protocol). Different colours represent distinct crocodylomorph subgroups: non-mesoeucrocodylian crocodylomorphs (excluding thalattosuchians), Notosuchia, non-crocodylian neosuchians (excluding tethysuchians and thalattosuchians), Tethysuchia, Thalattosuchia and Crocodylia. PC1 and PC2 represent, respectively, 71.89% and 8.6% of total shape variation

Comparisons of the morphospaces occupied by different crocodylomorph subgroups (2a, b, and Appendix S1: Figure S4) reveal a wide distribution of members of the crown group (crocodylians) and notosuchians. Crocodylians exhibit almost the entire range of morphological variation described by PC1 (i.e. long vs. short snouts), whereas most notosuchians occupy the region of short rostra (although the presence of *Stolokrosuchus lapparenti* in the analysis expands the morphospace occupation of the group towards the 'longirostrine region'; Figure 2a, b, and Appendix S1: Figure S4). Pairwise statistical assessment using npMANOVA (Appendix S1: Table S2) reinforces the apparently disparate cranial morphology of these two groups, as it shows that their morphospaces are significantly different to one another (p = .0015), and also from most of the groups tested (see Appendix S1 for further description of morphospace occupation in other crocodylomorph subgroups).

Cranial shape disparity estimated for different crocodylomorph subgroups revealed that Notosuchia has the highest cranial shape disparity among all groups assessed (Figure 2c). Crocodylia exhibits a smaller disparity, although slightly higher than the other four groups (Tethysuchia, Thalattosuchia, non-crocodylian neosuchians and non-mesoeucrocodylian crocodylomorphs), which have comparable median values. Pairwise comparisons (Appendix S1: Table S3) show that disparity in both Notosuchia and Crocodylia is significantly different from that in all other groups analysed, whereas some other groups have statistically equivalent disparities (e.g. thalattosuchians and non-mesoeucrocodylian crocodylomorphs, as well as tethysuchians and non-crocodylian eusuchians). Similar results were recovered when fewer subsets of taxa were analysed (i.e. Notosuchia, Neosuchia, Thalattosuchia, non-mesoeucrocodylian crocodylomorphs), with notosuchian disparity still higher and significantly different from the other groups (Appendix S1: Figure S5 and Table S4).

Even though some crocodylomorph subgroups exhibit morphospaces that are significantly distinct from other groups, the relatively weak to moderate phylogenetic signal estimated for the data (K_{mult} values varied between 0.0866 and 0.2398 with different phylogenetic scenarios; $p < .05$) suggests no strong degree of phylogenetic structure in patterns of cranial shape variation among taxa. This is consistent with the visual representation of phylogenetic information incorporated into tangent space (i.e. phylomorphospace plots of PC1 against PC2; see Appendix S1: Figure S6), with the multiple intersections of branches, even though some caution is advised when

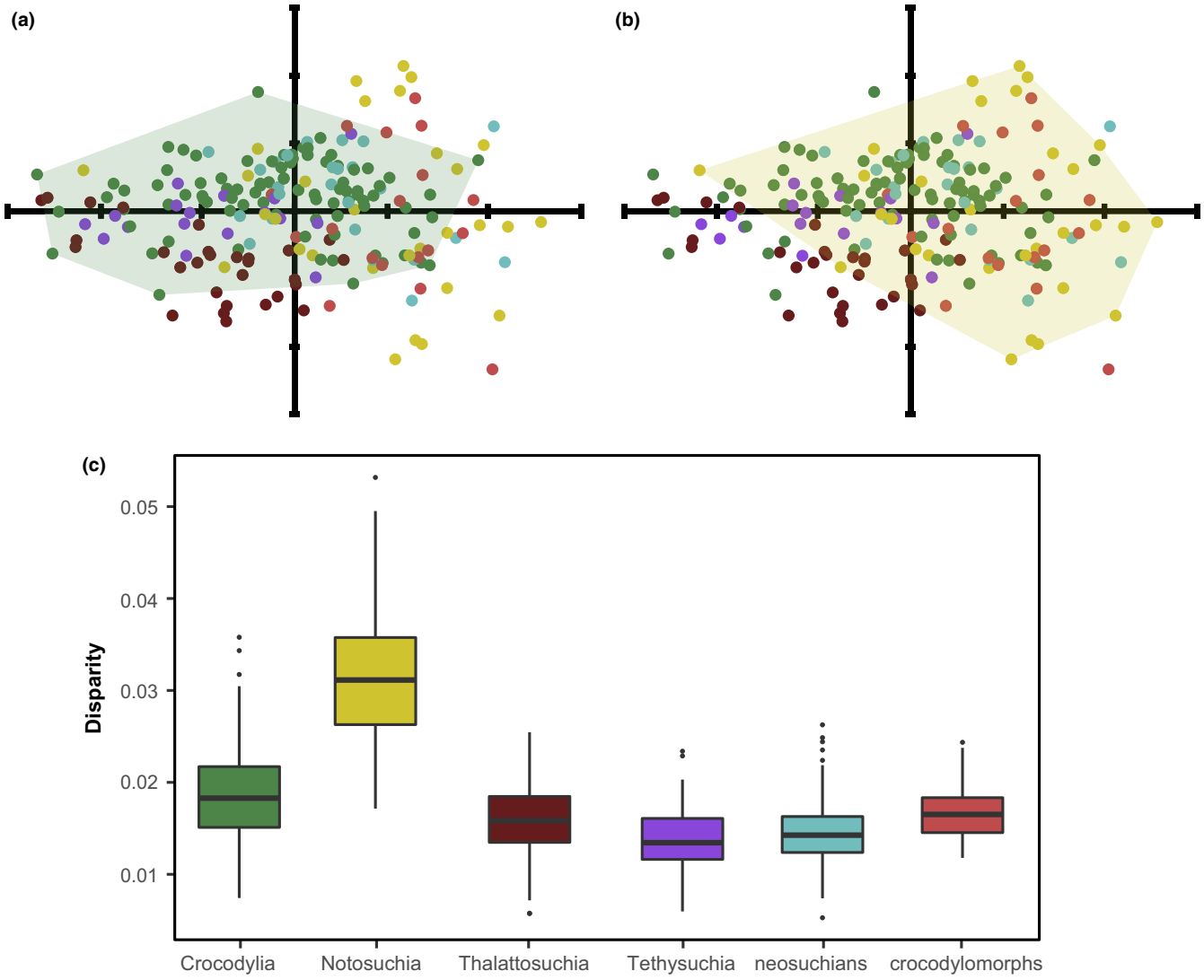

FIGURE 2 Morphospace occupation and cranial shape disparity (sum of variances) of different crocodylomorph subgroups. (a) Morphospace occupied by members of the crown group (Crocodylia). (b) Morphospace occupied by notosuchians. (c) Cranial shape disparity of species divided into six taxonomic subsets ('neosuchians' represent non-crocodylian neosuchians, without tethysuchians and thalattosuchians; 'crocodylomorphs' represent non-mesoeucrocodylian crocodylomorphs, without thalattosuchians). PC scores of specimens were bootstrapped and rarefied for disparity calculation

interpreting K_{mult} values, given that low values could simply be a result of departure from Brownian motion evolution (which is assumed by K_{mult}; Blomberg et al., 2003).

3.2 | Disparity through time

In general, significant impacts on disparity-through-time analyses were observed when distinct tree topologies were used (see Appendix S4 for plots of all disparity-through-time analyses). A number of factors can explain these differences (see Discussion), but most of them are probably arising from age uncertainties of taxa. Even for trees within a same phylogenetic scenario (i.e. same positions of Thalattosuchia and gavialids), taxa ages are drawn from uncertain age ranges, creating differences among them.

Indeed, comparisons between the 10 trees within a same phylogenetic scenario can exemplify these dissimilarities in disparity-through-time analyses (which are usually more marked when a greater number of time intervals are used). For example, for Thalattosuchia sister to Crocodyliformes and gavialids within Gavialoidea, analyses using distinct trees disagree on the timing and magnitude of a disparity peak during the early evolution of the group (Figure 3). Whereas some trees show this peak beginning prior to the Triassic–Jurassic (T–J) boundary, other trees yield a later start, only after the boundary. Other differences include whether there is an increase or a decrease in disparity from the middle of the Neogene (Eocene) to the Recent, as well as if a peak observed during the Early Cretaceous corresponds to the highest disparity seen in the group's entire evolutionary history (Figure 3). Similarly, the use of alternative

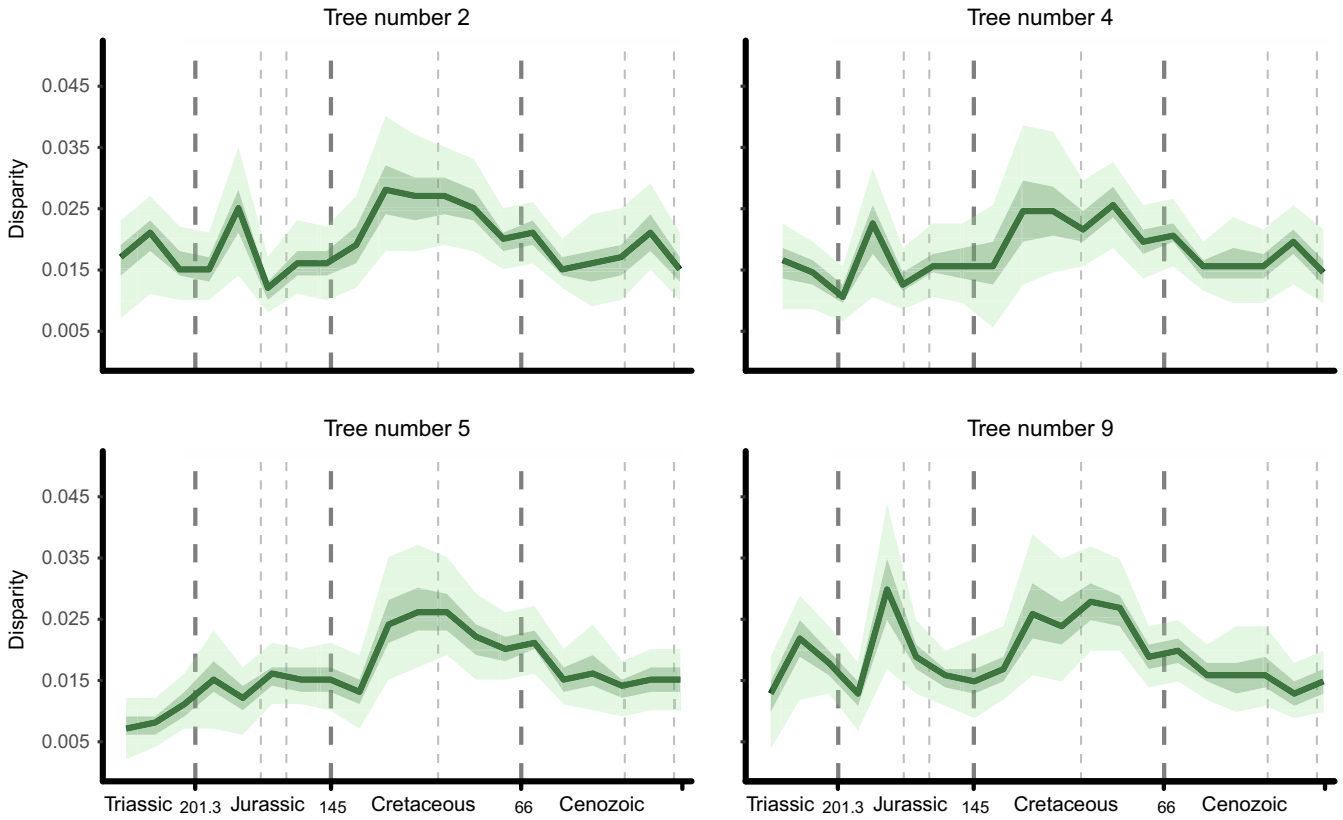

FIGURE 3 Crocodylomorph cranial shape disparity (=sum of variances) through time. Each disparity curve used a different time-scaled trees for disparity-through-time calculation. All trees share the same phylogenetic position of thalattosuchians (as sister to Crocodyliformes) and gavialids (within Gavialoidea) and used the same time sub-sampling method (time-binning method, with 20 equal-length time bins). Discrepancies between results come from differences in branch lengths among trees, which reflect taxa temporal uncertainties. Light and dark green shades represent, respectively, 75% and 97.5% confidence intervals from 1,000 bootstrapping replicates. Analyses used PC scores from all PCs, both from terminal taxa and from ancestors (estimated using maximum-likelihood ancestral state reconstruction)

phylogenetic scenarios also impacted on disparity curves. For example, different positions of Thalattosuchia had greatest impact on disparity estimation during the Jurassic, since this corresponds to the age range of thalattosuchians.

Similarly, distinct time sub-sampling methods (i.e. number of time intervals used and the use of time bins or time slices) also impacted in disparity estimation. The only exception was among analyses that used the time-slicing method but whit different evolutionary models (i.e. punctuated or gradual model), which produced almost identical results (Appendix S1: Figures S7, S8 and S9; see Appendix S4 for all plots). In general, disparity-through-time analyses using more time intervals (either time bins or time slices) reconstruct more nuanced changes in disparity, even though they also often have larger confidence intervals, due to less taxa being included in each time interval (Appendix S1: Figures S7, S8, and S9). When comparing different time sub-sampling methods, similar differences are observed to those seen when different tree topologies are compared (i.e. variation in the timing and magnitude of disparity peaks). For example, the magnitude estimated for the peak seen at the end of the Early Cretaceous was usually greater when using the time-slicing method.

Despite these dissimilarities arising from different time-scaled trees and time sub-sampling methods, most analyses seem to agree on some overall patterns of crocodylomorph cranial shape disparity through time (3; Appendix S1: Figures S7, S8 and S9). An early peak in disparity is frequently observed, most often during the Early Jurassic (although sometimes even prior to the Triassic–Jurassic boundary). Following a sharp decrease during the Middle Jurassic, disparity undergoes a continuous increase until the middle of the Cretaceous (Aptian–Albian), when maximum disparity is reached in most analyses. Subsequently, a near constant decline is observed during the Late Cretaceous and the Paleocene, with analyses only disagreeing whether it continues until the Recent or ceases during the Eocene. In these latter cases (more frequently seen in analyses using the time-slicing method), a sharp increase in disparity is seen in the Eocene, but is frequently followed by an equally sharped decrease until the Recent.

These overall patterns resemble those found by Wilberg (2017) in that a clear peak is observed in the Cretaceous, followed by a nearly continuous decline towards the Recent. Some differences, however, are also noted. Since Wilberg (2017) used different disparity metrics in his analyses, the comparisons made here focused on variance-based disparities. The first discrepancy arises from the fact that Wilberg (2017) restricted his study to Crocodyliformes (with the exception of thalattosuchians) and did not include any Late Triassic

TABLE 1 Proportion of crocodylomorph cranial shape variation explained by body size (=centroid size)

Effect	SS	MS	% of variation	*F*	*p*
Total shape variation (all PCs)					
Centroid size	1.8246	1.82461	33.70073	105.22	.0001*
Residuals	3.5895	0.01734			
Total	5.4142				
Shape variation represented by PC1					
Centroid size	1.8097	1.80967	46.49398	179.87	.0001*
Residuals	2.0826	0.01006			
Total	3.8923				

Note: Procrustes ANOVA results: SS, sum of squares after 10,000 permutations; MS, mean squares; % of variation, obtained by dividing the sum of squares of the independent variable (centroid size) by the total sum of squares; *F*, *F*-statistic; *p*, *p*-value.
*Significant at alpha = 0.05.

species, resulting in an absence of information about crocodylomorph disparity prior to the Jurassic. When using stratigraphic intervals as time bins for his disparity-through-time analyses (resulting in 36 time bins), Wilberg (2017) found two significant disparity peaks during the Jurassic (one in the Pliensbachian and another in the Aalenian–Bajocian), whereas in most of my analyses, a single Jurassic peak was estimated, usually occurring from the Sinemurian to the Toarcian (Figure 3; Appendix S1: Figures S7, S8 and S9). The timing of the disparity peak in the Cretaceous is another divergence between the two studies, with the analyses performed by Wilberg (2017) indicating a Late Cretaceous peak (Cenomanian), whereas most of my analyses show a slightly earlier peak (Barremian–Albian). Finally, another difference was found in the pattern of disparity from the Eocene to the Recent. Whereas many of my analyses (particularly when using the time-slicing method) indicate a disparity increase starting in the Eocene, this increase is not identified by the variance-based analyses in Wilberg (2017).

3.3 | Allometric changes in cranial shape

Body size (=centroid size) has a significant ($p < .005$) effect on crocodylomorph cranial shape, representing nearly 35% of the total observed variation (this is increased to more than 45% when only PC1 is considered; Table 1). This relationship can be visualized in a shape vs. size plot, using the regressions scores (which shape variation represented is very similar to that of PC1) and log-transformed centroid size (Figure 4b). Mapping PC1 (which represents more than 70% of all observed shape variation) into crocodylomorph phylogeny indicates that many of the largest taxa (such as some thalattosuchians and tethysuchians) also exhibit PC1 values associated with longer rostra, whereas most of the predominantly small-bodied notosuchians show PC1 values related to shorter snouts (Figure 4a). Further examination of this relationship using an independent body size dataset (from Godoy et al., 2019) provided very similar results, with a significant correlation between shape and size (using untransformed and phylogenetically corrected data; Appendix S1: Table S5 and Figure S10). These results indicate that body size is a strong predictor of cranial shape in the group. Consequently, the morphospace occupation of distinct crocodylomorph subgroups using 'allometry-free' shape data (i.e. from size-adjusted residuals, Figure 4c) reveals different patterns from that of uncorrected data (Figure 1 and Appendix S1: Figure S4), even though some general patterns can still be recognized. For example, crocodylian morphospace is comparatively more restricted, without exploring the region of extreme longirostrines (which is mainly dominated by thalattosuchians), whereas tethysuchians are more widespread, expanding their morphospace to that of more short-snouted taxa.

3.4 | Cranial shape and ecology

Procrustes ANOVA results show a significant, although small (~3%, $p < .05$), influence of ecology (=lifestyles) on crocodylomorph cranial shape (Table 2). Consistently, npMANOVA results indicate that all three ecological categories have significantly different morphospace occupation (i.e. $p < .001$). The PC1 vs. PC2 scatterplot (Figure 5a) reveals that most terrestrial taxa are restricted to the region of short-snouted skulls along PC1 axis, although they have a wider distribution along PC2 axis. Conversely, aquatic crocodylomorphs, represented by some of the most extreme longirostrine forms (such as the gavialid *Ikanogavialis gameroi*), are mainly confined to the region of more elongated snouts (left side of PC1 axis; Figure 5a). Semi-aquatic species are more widespread along the PC1 axis (Figure 5a), even though their distribution along the PC2 axis seems to be similar to that observed for aquatic forms. In terms of disparity (=sum of variances), terrestrial crocodylomorphs show significantly higher disparity than the other two categories, whereas aquatic and semi-aquatic species exhibit similar median disparity (Figure 5b and Appendix S1: Table S6).

3.5 | *SURFACE* and *bayou* analyses

In general, a clear consistency is observed in regime shift detection across different methods (6; see Appendix S5 for plots of all *SURFACE* and *bayou* results). In both *SURFACE* and *bayou* results, regime shifts are usually associated with ecological transitions and body size regime shifts in crocodylomorphs, which were previously presented by other studies (Godoy et al., 2019; Wilberg

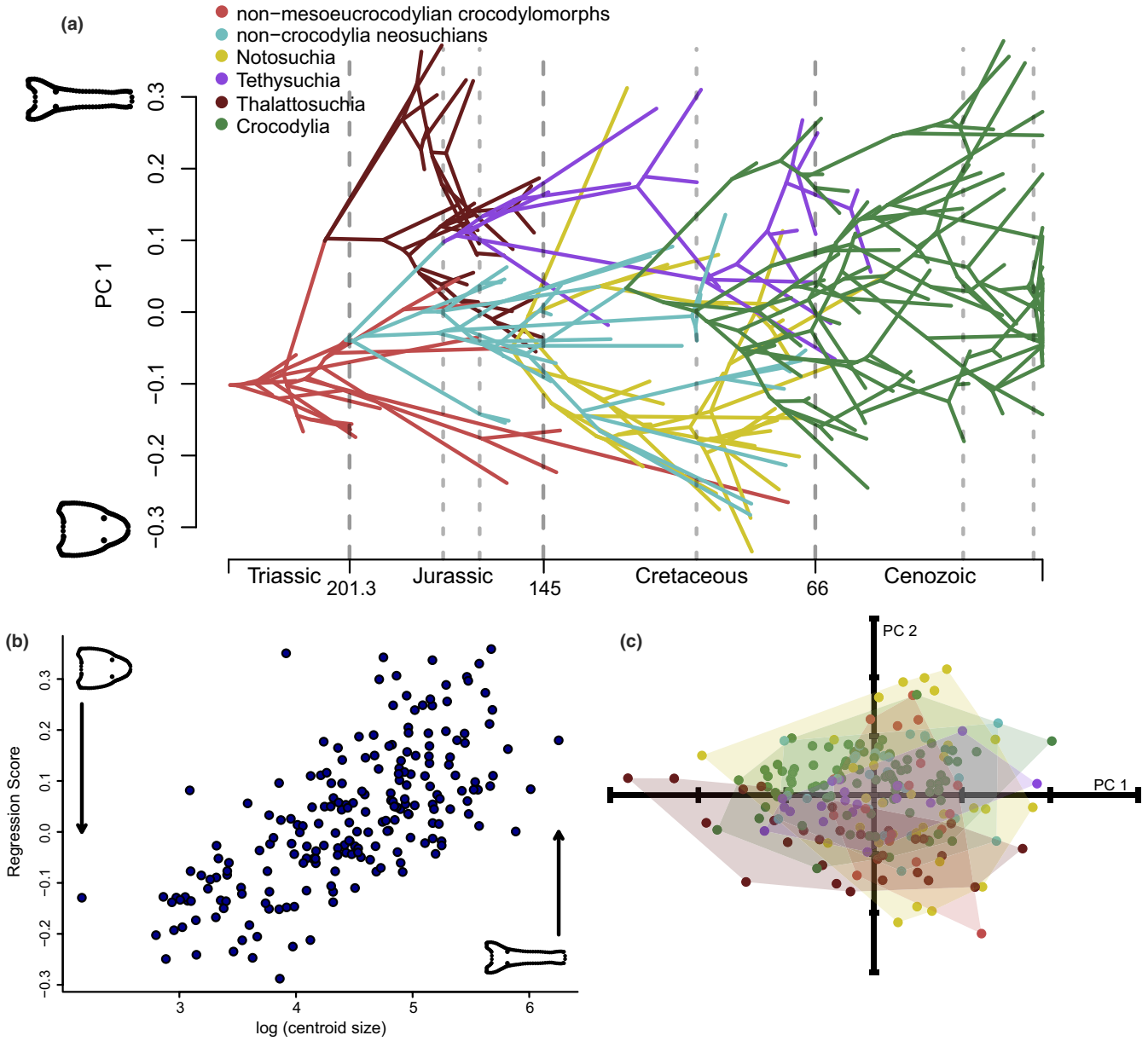

FIGURE 4 Influence of body size on crocodylomorph cranial shape. (a) Phenogram mapping cranial shape (PC1 scores) onto crocodylomorph phylogeny (topology from the MCC tree with Thalattosuchia sister to Crocodyliformes and gavialids within Gavialoidea). Different colours represent distinct mono- and paraphyletic crocodylomorph subgroups. (b) The relationship between cranial shape (regression scores) and body size (log-transformed centroid size) in crocodylomorphs. (c) PC1 vs. PC2 plot showing crocodylomorph subgroups morphospace occupation using 'allometry-free' shape data (i.e. from size-adjusted residuals). Colour key as in (a)

et al., 2019). In particular, regime shifts to longer snouts (i.e. PC1 scores trait optima values, θ, >0.1) are frequently detected in groups of aquatic or semi-aquatic species, which are usually large-bodied animals, such as thalattosuchians, tethysuchians, gavialids and 'thoracosaurs'. The opposite is commonly true for terrestrial taxa, mostly associated with regimes of short rostra (θ < −0.1), even though some exceptions exist (such as the large-bodied terrestrial sebecosuchians). The ancestral cranial shape regime was frequently associated with shorter snouts (with values of ancestral trait optimum for all crocodylomorphs, Z_0, ranging from −0.16 to −0.07), which is consistent with some of the oldest known crocodylomorph taxa, such as 'sphenosuchians' and protosuchids. The use of different phylogenetic scenarios did not cause significant impacts on these overall results, with a consistent association between trait optima values and crocodylomorph subgroups across different analyses.

It is worth mentioning, however, that some minor discrepancies were noted between *SURFACE* and *bayou* results. For example, *SURFACE* analyses usually identified more regime shifts (usually more than 15 shifts) than *bayou*, which found <15 shifts with highly supported posterior probabilities (i.e. signal-to-noise ratio ≫ 1; Cressler, Butler, & King, 2015; Smaers, Gómez-Robles, Parks, & Sherwood, 2017) in all three phylogenetic scenarios. However, as the backward phase of *SURFACE* lumps together regimes with similar values of θ

TABLE 2 Proportion of crocodylomorph cranial shape variation explained by ecology (=lifestyles)

Total shape variation (all PCs)					
Effect	**SS**	**MS**	**% of variation**	***F***	***p***
Lifestyle	0.007586	0.0037932	3.098517	3.2935	.0079*
Residuals	0.237256	0.0011517			
Total	0.244842				

Note: Procrustes ANOVA results: SS, sum of squares after 10,000 permutations; MS, mean squares; % of variation, obtained by dividing the sum of squares of the independent variable (lifestyle) by the total sum of squares; *F*, *F*-statistic; *p*, *p*-value.
*Significant at alpha = 0.05.

(creating 'convergent' regimes; Ingram & Mahler, 2013), most of my *SURFACE* model fits ended up identifying <10 regimes (i.e. 'convergent' regimes *sensu* Ingram and Mahler (2013)). Despite these slight differences in the number of regime shifts, the magnitudes of θ values associated with different crocodylomorph subgroups were consistent across methods. Additionally, the magnitudes of alpha (α, the strength of attraction) and sigma square (σ^2, the rate of stochastic evolution) were also very similar across most of the better supported *SURFACE* analyses and all three *bayou* analyses (see Appendix S5 for all plots).

Another minor discrepancy was that some *SURFACE* analyses, more frequently those with Thalattosuchia placed outside Crocodyliformes, exhibited significantly simpler model fits (i.e. with much fewer regime shifts and usually unrealized low or high values of theta). This could be the results of the inability of the *SURFACE* algorithm to deal with certain tree topologies and branch lengths (similar to the unsuccessful/suboptimal model fits identified and demonstrated by Benson et al., 2018). This does not undermine the *SURFACE* results presented here, but stresses the importance of using multiple time-scaled trees for *SURFACE* analyses.

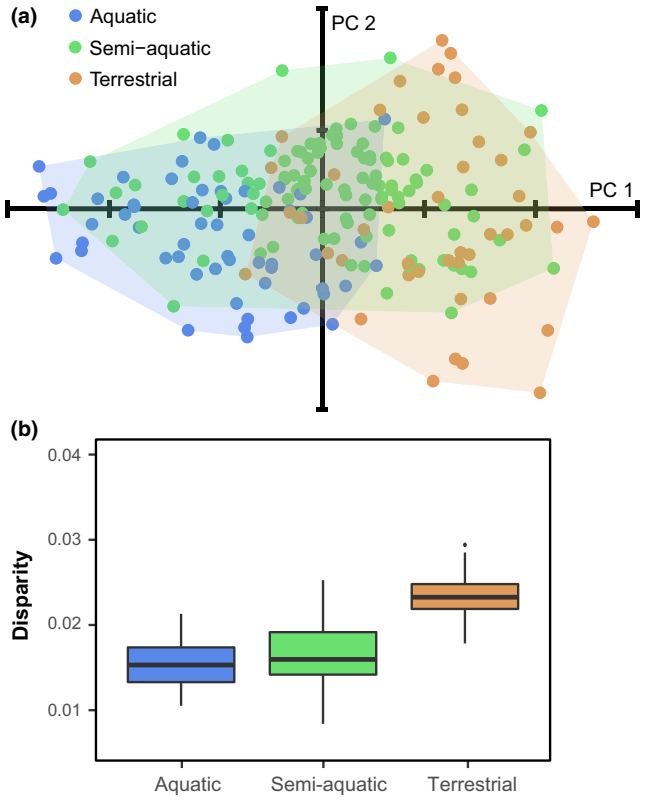

FIGURE 5 Crocodylomorph cranial shape within different ecological categories (a) Morphospace occupation (PC1 vs. PC2 plot) of crocodylomorphs divided into three ecological categories: aquatic/marine (*n* = 54), semi-aquatic/freshwater (*n* = 107) and terrestrial (*n* = 48). (b) Boxplots showing cranial shape disparity (=sum of variances) with crocodylomorphs subdivided into the same three categories. PC scores of specimens (all PCs) were bootstrapped and rarefied for disparity calculation

4 | DISCUSSION

4.1 | Crocodylomorph snouts and feeding ecology

Most of the shape variation in crocodylomorph skulls is represented by changes in the snout, particularly in its length and width (Figure 1). This is consistent with what was found in previous geometric morphometric studies (e.g. Foth, Ascarrunz, et al., 2017; Godoy et al., 2018; Pierce et al., 2008, 2009; Piras et al., 2009; Sadleir & Makovicky, 2008; Wilberg, 2017; Young et al., 2010), indicating that this region of the skull has the highest morphological variation. High variability in crocodylomorph snout length has long been acknowledged (Brochu, 2001; Busbey, 1995; Langston, 1973), even leading early taxonomists (e.g. Lydekker, 1888) to erroneously classify crocodylomorphs into different groups (Pierce et al., 2008). More recently, however, cladistic studies (e.g. Clark, 1994; Jouve et al., 2006; Pol & Gasparini, 2009; Wilberg, 2015) have suggested that convergences of crocodylomorph snouts during their evolutionary history have created a 'longirostrine problem', in which clades that are not necessarily closely related tend to be grouped together in phylogenetic analyses. In this context, the high plasticity of crocodylomorph snouts could explain the weak to moderate phylogenetic signal found for my dataset, as well as datasets of other crocodylomorph subgroups (such as crocodylians and thalattosuchians; Pierce et al., 2008, 2009).

Snout length can provide useful insights into ecological specializations (Brochu, 2001; Busbey, 1995; McHenry et al., 2006; Pierce et al., 2008; Taylor, 1987; Walmsley et al., 2013), and recent examinations of crocodylomorph cranial functional morphology further indicate strong ecological selective pressures on the snout, particularly

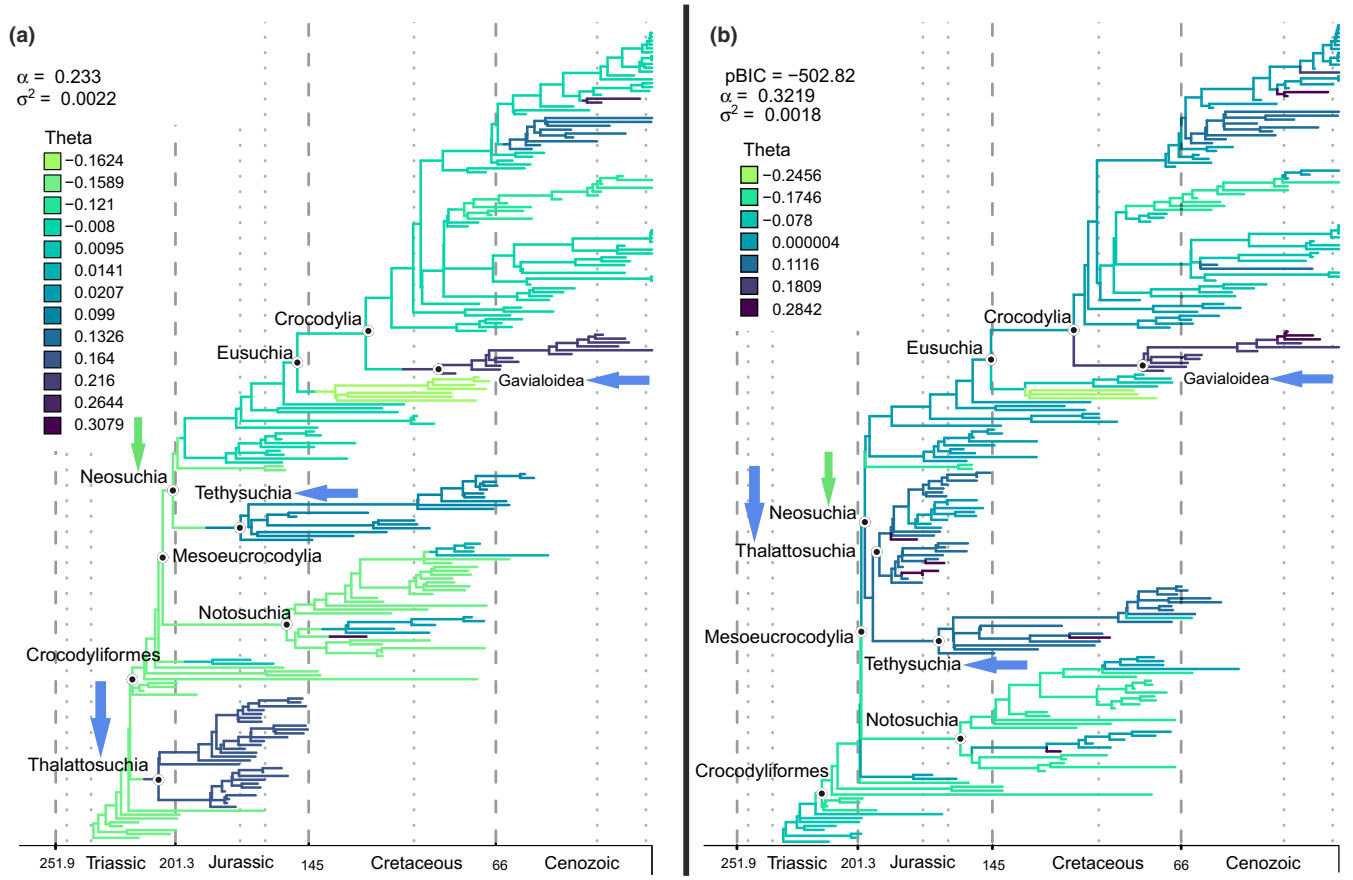

FIGURE 6 Cranial shape regime shifts during crocodylomorph evolutionary history. Plots with results of bayou and SURFACE analyses using PC1 scores (as a proxy for skull shape). Branches are coloured according to different values of regime trait optima/theta (θ), with lighter colours associated with regimes of shorter snouts and darker colours representing regimes of more longirostrine taxa. Arrows show ecological transitions and body size regime shifts in some major crocodylomorph subgroups. Blue and green arrows indicate, respectively, transition to marine and freshwater lifestyles. Relative sizes of arrows represent different magnitudes of body size regime shifts (i.e. larger arrows are used for shits to regimes of larger sizes). Note that at the base of Crocodylomorpha, species are terrestrial and relatively small. (a) Results from bayou analysis using the MCC tree with Thalattosuchia sister to Crocodyliformes and gavialids within Gavialoidea. Parameter estimates alpha (α, strength of attraction) and sigma square (σ2, rate parameter) are mean values from all MCMC analyses with this tree topology (after 30% burn-in). Only theta (θ) values with posterior probability higher than 0.5 are shown. (b) Results from SURFACE analyses using tree number 10 with Thalattosuchia within Neosuchia and gavialids within Gavialoidea. Likelihood information criterion (pBIC) and parameter estimate values are shown only for this tree topology. Theta values shown are those of 'convergent' regimes. Information on ecological transitions and body size regime shifts was derived from Wilberg et al. (2019) and Godoy et al. (2019), respectively

those arising from feeding behaviour (Ballell, Moon, Porro, Benton, & Rayfield, 2019; Gignac & O'Brien, 2016; Gignac, O'Brien, Turner, & Erickson, 2019; McCurry, Evans, et al., 2017; McHenry et al., 2006). Longer snouts are traditionally associated with a piscivorous diet, since the tip of the snout moves faster through water, facilitating the capture of small prey such as fish (McCurry, Walmsley, Fitzgerald, & McHenry, 2017; McHenry et al., 2006; Thorbjarnarson, 1990; Walmsley et al., 2013). Thus, the widespread presence of longirostry in different crocodylomorph subgroups is presumably related to the numerous transitions to aquatic and semi-aquatic lifestyles during crocodylomorph evolutionary history (Wilberg et al., 2019), which are more directly connected to piscivory, highlighting the influence of ecology on the group's cranial shape evolution.

Furthermore, snout width also has important biomechanical implications, such as impacting on hydrodynamic pressure drag (e.g. longirostrine animals compensate the higher pressure from drag with narrower snouts; McHenry et al., 2006; Walmsley et al., 2013). Similarly, other regions of the crocodylomorph skull that vary significantly also have important implications for biomechanics and feeding strategies, such as the changes in quadrate condyle width, which are presumably associated with the craniomandibular joint (Kley et al., 2010; Ősi, 2014; Stubbs et al., 2013), even though relatively less variation is observed in these regions when compared to the snout.

4.2 | Cranial shape and size linked to ecology

Interpreting crocodylomorph cranial shape evolution within the concept of a Simpsonian Adaptive Landscape (Simpson, 1944, 1953) can be useful for characterizing macroevolutionary changes, since this concept includes ideas such as adaptive zones invasion and quantum evolution (Hansen, 1997, 2012; Stanley, 1973). This is consistent

with the methodological approach used here for characterizing cranial shape evolution (i.e. *bayou* and *SURFACE* methods), which assumes evolution under an OU process (even though the fit of alternative evolutionary models, such as those under Brownian motion, was not investigated here). Within the paradigm of adaptive landscapes, the different regimes of nonuniform OU models (such as *bayou* and *SURFACE*) can be interpreted as adaptive zone (Mahler & Ingram, 2014; Uyeda & Harmon, 2014). Accordingly, taking into account the selective pressures associated with these adaptive zones, shifts between macroevolutionary regimes can possibly drive large-scale patterns of phenotypic evolution.

In crocodylomorphs, the clear relationship between ecology and cranial shape and size is evidenced by the significant effects of size and lifestyle on cranial shape demonstrated here (Tables 1 and 2; Figures 4b and 5; Appendix S1: Table S6 and Figure S10). Furthermore, the evolutionary patterns of cranial shape, which were characterized here by the *bayou* and *SURFACE* results (Figure 6), display similarities with those of body size (analysed by Godoy et al. (2019)) as well as with ecological transitions (demonstrated by Wilberg et al. (2019)). For example, shifts to regime of more longirostrine skulls are usually associated with shifts to larger-sized regimes and transitions to aquatic or semi-aquatic lifestyles. Previous studies investigating a link between larger body sizes and a more aquatic lifestyle have mostly focused on mammals (e.g. Downhower & Blumer, 1988; Smith & Lyons, 2011; Gearty, McClain, & Payne, 2018, although there are exceptions, such as for lissamphibians; Laurin, Girondot, & Loth, 2004; Laurin, Canoville, & Quilhac, 2009), but a similar pattern was also documented for crocodylomorphs (Godoy et al., 2019). Within the concept of adaptive landscapes, this intricate relationship between cranial morphology, body size and ecology could be related to adaptations to an aquatic life, with selective pressures originated from intrinsic (e.g. physiological constraints associated with aquatic life) and/or extrinsic factors (e.g. resources availability, such as a predominance of fish as possible preys).

The association between cranial shape and diet can also provide insights on the higher disparity seen in terrestrial taxa (Figure 5b). Although aquatic and semi-aquatic species also explore distinct feeding strategies other than piscivory (such as durophagy; Ősi, 2014; Melstrom & Irmis, 2019), a higher variability is exhibited by terrestrial crocodylomorphs, with strategies such as herbivory, omnivory, insectivory and hypercarnivory (Godoy et al., 2018; Melstrom & Irmis, 2019; Ősi, 2014). The greatest contribution to this higher disparity seen in terrestrial crocodylomorphs comes from notosuchians, most of which were terrestrials and displayed exceptionally high cranial disparity (Figure 2c), mirroring their rich fossil record (Mannion et al., 2015; Pol & Leardi, 2015) as well as their high morphological and body size disparities (Godoy et al., 2019; Stubbs et al., 2013; Wilberg, 2017). The drivers of such remarkable taxic diversity and morphological disparity in the group are only poorly explored, but some hint can be provided by their occurrence temporal and geographically constrained, since most notosuchians were confined to the Cretaceous of Gondwana (Mannion et al., 2015; Pol & Leardi, 2015), with specific environmental conditions (hot and arid climate; Carvalho, Gasparini, Salgado, Vasconcellos, & Marinho, 2010). Indeed, Godoy et al. (2019) found evidence for more relaxed modes of body size evolution in the group, which could also be the case for other phenotypic aspects.

Apart from notosuchians, other crocodylomorph subgroups contribute to the higher disparity of terrestrial forms, mainly non-mesoeucrocodylian crocodylomorphs (such as protosuchids, gobiosuchids and shartegosuchoids; Pol & Norell, 2004; Clark, 2011; Irmis et al., 2013; Buscalioni, 2017; Dollman, Clark, Norell, Xing, & Choiniere, 2018), for which a series of cranial specializations have been previously reported (Buscalioni, 2017; Dollman et al., 2018). Among these, modifications related to brachycephaly (e.g. snout length reduction, rounded neurocranial shape, dorsal rotation of the mandibles, mandibular asymmetry and tooth loss and/or orientation change; Buscalioni, 2017) are possibly associated with feeding behaviour and might represent the result of ecological selective pressures.

4.3 | Cranial shape through time

Overall, disparity-through-time results were highly sensitive to changes in the time sub-sampling method and particularly in the phylogenetic hypothesis used (Figure 3; Appendix S1: Figure S7, S8 and S9). The considerable variation seen in these results has multiple causes. First, distinct time-scaled trees vary in assuming different stratigraphic dates for the occurrences of individual taxa (reflecting the uncertainties in the stratigraphic occurrences of most taxa used in these analyses, with many taxa known from point occurrences but with stratigraphic uncertainty often spanning two or more stages), as well as in different resolutions for polytomies (which were randomly resolved in each tree). Foth, Fernandez Blanco, et al. (2017) have previously investigated the influence of temporal and topological uncertainty on disparity though time in turtles (Testudinata) and reported comparable impacts. Similarly, although not tested here, it is very likely that alternative time-scaling methods (e.g. *a posteriori* time-scaling approaches *sensu* Lloyd, Bapst, Friedman, & Davis, 2016) would also impact on disparity-through-time estimation (see Bapst, 2014 for further discussion). Furthermore, as distinct trees were used for estimating the ancestral states (i.e. landmark coordinates of hypothetical ancestors), they presumably produce distinct PC scores for ancestors, which were subsequently used in disparity estimation. Similarly, distinct approaches to estimate ancestral states could also potentially impact on the results (see Ekman, Andersen, & Wedin, 2008; Slater, Harmon, & Alfaro, 2012). Finally, the use of distinct time sub-sampling methods, as well as different numbers of time intervals (either time bins or time slices), results in different taxa being sampled in each time interval, since the rates of sedimentation (and fossilization) are uneven in space and time (Butler et al., 2012; Guillerme & Cooper, 2018).

These results shed light on the importance of using multiple time sub-sampling methods for these analyses (as previously highlighted by Guillerme & Cooper, 2018), but also of multiple phylogenetic hypotheses, especially for groups with major uncertainties in

stratigraphic occurrence dates and phylogenetic relationships (as previously acknowledged by Foth, Fernandez Blanco, et al., 2017). However, many other previous studies have ignored this issue, often presenting results based on one time-scaled phylogeny and one time sub-sampling approach (e.g. Brusatte, Benton, Ruta, & Lloyd, 2008a; Brusatte, Benton, Ruta, & Lloyd, 2008b; Foth & Joyce, 2016; Stubbs et al., 2013). In fact, the discrepancies noted between the results presented here and in Wilberg (2017) could at least partially be explained by the use a single tree in the latter study (as well as by the different sample sizes and time sub-sampling methods used). Accordingly, rather than using a single analysis, perhaps a better way to report the results might be by describing shared patterns among multiple outputs, as done here as well as in Foth, Fernandez Blanco, et al. (2017).

Regarding the overall disparity-through-time results, the peaks and declines observed are presumably associated with the appearance and extinction of distinct crocodylomorph subgroups, such as thalattosuchians in the Jurassic and notosuchians in the Cretaceous, as already pointed out by previous studies (Stubbs et al., 2013; Wilberg, 2017). Some of these peaks can be more securely be linked to abiotic factors, such as palaeotemperature. For example, as suggested by Wilberg (2017), the Eocene peak could be related to the Early Eocene Climatic Optimum (Zachos, Dickens, & Zeebe, 2008), reflecting an increase in diversity (Mannion et al., 2015). However, although this relationship was not quantitatively investigated here (i.e. through statistical correlation test), it is difficult to draw more general conclusions, such as that palaeotemperature (or other environmental factor) drives overall patterns of crocodylomorph cranial disparity through time. Similarly, other large-scale investigations of crocodylomorph evolution (such as species diversity and body size evolutionary patterns; Mannion et al., 2015; Godoy et al., 2019) found more significant influence of abiotic factors only at smaller temporal and phylogenetic scales. This would be consistent with the different biological and physiological characteristics presumed for distinct crocodylomorph subgroups (which range from species highly adapted to a fully aquatic life to terrestrial and nearly cursorial forms), for which different responses to environmental changes are expected. Accordingly, within the paradigm of adaptive landscapes (Hansen, 1997, 2012; Simpson, 1944, 1953), overall patterns of phenotypic evolution (such as cranial shape) are more likely to reflect clade-specific adaptations related to the invasion of new adaptive zones (with in turn involve new specific environmental conditions), particularly when analysing large-scale events, across numerous subgroups.

This could also help to understand the nearly continuous decline in crocodylomorph disparity since the Late Cretaceous, which is mainly represented by members of the crown-group Crocodylia. With few exceptions, crocodylians are predominantly semi-aquatic species (Wilberg et al., 2019), what could explain their relatively low cranial disparity (Figure 2c) despite being the most specious crocodylomorph subgroup in my analyses (n = 89). The extinction of other subgroups, which were occupying a wider variety of ecological niches, combined with the presence of predominantly semi-aquatic forms during the Cenozoic, could be a consequence of differential responses to environmental changes (such as global cooling; Zachos et al., 2008), which potentially led to a reduced niche availability. A similar rationale was outlined by Godoy et al. (2019) to explain the decrease in body size disparity seen for crocodylomorphs since the Late Cretaceous. Regarding body size, Godoy et al. (2019) argued that the pattern of global cooling documented for the last 66 million years would be related to a more restricted geographical distribution of crocodylomorphs (that became more confined to the tropics), and that this probably led to the selective extinction of small-bodied species. Therefore, the current scenario of most modern crocodylian species being piscivorous semi-aquatic animals, within relatively limited variability of body sizes (i.e. large animals) and cranial shapes, could be the result of a long-standing pattern of habitat loss in crocodylomorphs, leading to a narrower range of ecologies and morphologies.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vb6s1r4

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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