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Macroevolution of the Crocodylomorpha

Maximilian T. Stockdale

A dissertation submitted to the University of Bristol in accordance
with the requirements for award of the degree of Doctor of
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Abstract:

The Crocodylomorpha are an ancient clade with origins in the Late Triassic, however their extant diversity is meagre in comparison with their fossil forebears. Fossil Crocodylomorpha includes hundreds of morphologically disparate species, including herbivorous, marine and semi-fossorial forms. How has the diversity and rate of crocodylomorph evolution changed through time? What are the driving factors of evolutionary rate and diversity? Do living crocodiles deserve status as living fossils?

This project presents a phylogenetic hypothesis of the crocodylomorpha based on meta-analysis of the literature. This hypothesis is utilised as a framework for comparative phylogenetic approaches to test for models of body size evolution, and for variable evolutionary rates. The phylogenetic hypothesis is applied as a phylogenetic correction to diversity through time and disparity through time data. Time-series datasets are analysed for relationships with environmental and preservation variables using univariate and multivariate linear modelling approaches.

The analyses presented here support a well-resolved phylogenetic hypothesis, supporting the monophyly of several established clades. Supertree approaches may be biased by the literature, but this architecture is also supported by supermatrix approaches. However, large supermatrices are limited by a build-up of inapplicable characters. The low evolutionary rate and diversity of extant Crocodylomorpha identifies them as living fossils. Climate is found to be a crucial factor in crocodylomorph evolution. Crocodylomorph body size and rates of body size evolution increase during periods of cooling, in accordance with Bergmann's rule. Diversity is limited by temperature, decreasing during periods of cooling but recovering during periods of stability. Crocodylomorph morphological disparity is decoupled from diversity, resembling a 'disparity-first' model.The crocodylomorphs show strong support for a punctuated equilibrium model of evolution driven by environmental change, as defined by the court Jester hypothesis. The vulnerability of living crocodylomorphs to environmental change and their status as living fossils makes their conservation a priority.

Acknowledgements

I am indebted to Michael Benton for supervising my work on this project, making suggestions and critiquing manuscripts. I would like to give thanks to Mario Bronzati for contributing data to chapter 2 of this thesis. I also wish to acknowledge the considerable contributions by Mark Puttick and Tom Stubbs for introducing me to R, and to Armin Elsler for introducing me to Python and Bayestraits. I would like to give additional thanks to James Fleming and Gareth Coleman for teaching me to use MrBayes. I am obliged to Emily Rayfield and Daniela Schmidt for reviewing my progress and for all their advice, support and encouragement. Finally I would like to give my thanks to Polly Russell, Agata Staniewicz, Catherine Klein, Carla Bardua, Robert Brocklehurst, Evan Saitta, Rachel Frigot and Neil Brocklehurst for their comments and discussion.

Dedications

This thesis is dedicated to my mother Judith, for giving me the freedom to pursue what has my passion for as long as I can remember. You either failed to spot the symptoms of palaeontology, or chose not to cure me. I am indebted to you for giving me an education at home, I am sure my dyslexia would have prevented me from progressing as far academically had I gone to school. This thesis is also dedicated to my sister Charlotte, for always encouraging me but also giving me perspective and keeping my feet on the ground. You are also the only non-palaeontologist in my life who would have the faintest idea what a *Sarcosuchus* is! Meine Liebe zu Mike Taverne und Laura Speich, Du warst mein Bruder und meine Schwester in Bristol, und Du hast zwei Wohnungen mein Zuhause gemacht. Lots of love to Rosie Lane, Becca Ellis, Ben Rackauskas, Phil Bogucki, Jodie Hunt, Rachel Dunn, Ally Jones, Rhys Charles, Emma Landon, Melisa Morales Garcia, Susana Gutarra Díaz, and Rose Bradshaw. I enjoy my research immensely, but the last four years has had its share of low points; you always spared a thought for me, and your friendship always brought me sanity, comfort and respite when I needed it. I would like to give a special thank you to David Mountain, who played a huge role in keeping my creativity alive. You reminded me not to lose sight of my other passions for the sake of one. Finally, I would like to send a big thank you to each of my project students, Suresh Singh, Elsa Panciroli, Sofia Schiavo, Luke Britton and Coral Billingham. Teaching you was a fantastic opportunity in developing my own career as well as building my technical skills. It was also hugely enjoyable and I hope you are justly proud of both your projects and the achievements you have made since.

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: DATE:

Contents

Figures & Tables

Chapter 1 figures:

Chapter 2 figures:

Chapter 3 figures:

Chapter 4 figures:

Chapter 3 tables

Chapter 4 tables

Chapter 1: Introduction

The Crocodylomorpha are a clade of pseudosuchian archosauromorph diapsids, with fossils occurring in rocks from the Late Triassic (Allen *et al.* 2013). They are represented by 23 extant species belong to nine genera. *Crocodylus* includes 11 species occurring throughout the tropics. *C. acutus, C. intermedius, C. moreletii* and *C. rhombifer* occur in the Americas and the Caribbean (Grigg 2015). *C. niloticus* is the only member of the genus to occur in Africa. India is home to *C. palustris; C. porosus, C. novaeguineae* and *C. siamensis* occur throughout south Asia and Indonesia (Grigg 2015). *C. porosus* is also known from Australia, together with *C. johnstoni. C. mindorensis* is found in the Philippines (Grigg 2015). The family Crocodylidae includes two further extant genera, *Mecistops* and *Osteolaemus,* both peculiar to central and eastern Africa. The number of species represented by *Mecistops* is disputed, with molecular analyses supporting a distinction between *Mecistops* in different biogeographic zones (Shirley *et al.* 2013). For the purposes of this study I shall consider *Mecistops* a single species, *Mecistops cataphractus,* since no proposed species of *Mecistops* are distinguishable from using the morphological data attainable from fossils. Likewise the genus *Osteolaemus* may also be polytypic according to molecular data (Eaton *et al.* 2009). Again, in this study I will consider it a single species, *Osteolaemus tetraspis,* since any other species show a conservative morphology that is difficult or impossible to determine from fossils. Closely affiliated with the Crocodylidae are the genera *Tomistoma* and *Gavialis,* each comprising of a single species, known from Indonesia and India respectively. The Alligatoridae represent a separate major clade of extant crocodylomorphs. The genus *Alligator* is known from two species found in North America and China, *A. mississippiensis* and *A. sinensis* (Grigg 2015). The Alligatoridae also includes a subclade, the Caimaninae, which includes the genera *Caiman, Melanosuchus* and *Paleosuchus*. *Melanosuchus* is the least diverse caiman genera, including a single species, *M. niger. Palaeosuchus* includes two species, *P. trigonatus* and *P. palpebrosus* (Grigg 2015)*.* The genus *Caiman* is the most specious of the caimans including three species, *C. yacare, C. crocodilus* and *C. latirostris*. All three genera of Caiman are peculiar to south America (Grigg 2015).

The extant members of the Crocodylomorpha are distributed in a band 30 degrees north and south of the equator (Markwick 1998) in fluvial, lacustrine, estuarine and marine habitats. They share a common morphology, featuring long snouts, powerful tails, osteoderms, short limbs and a sprawling gait. Their feeding ecology is varied, ranging from ichthyophagy to hypercarnivory (Cott 1961). The crocodylomorphs have great cultural significance, having been worshipped by the ancient Egyptians (Faulkner 1985, Hekkala *et al.* 2011) and possibly mentioned in the bible (Job 41:13-31). They have been observed and documented in early academic works, including the writings of Pliny the elder (translated 1938) and Marco Polo (Marsden & Wright 2004). The crocodylomorpha have significant commercial value, being farmed for skins used in the fashion industry. Meat from crocodiles and alligators is also widely consumed.

The fossil record of the Crocodylomorpha began to emerge during the enlightenment. In 1758 two manuscripts were published in the *Philosophical Transactions of the Royal Society,* documenting the remains of a crocodile-like animal found in the oolite cliffs near Whitby in Yorkshire. Chapman (1758) decided that it was an alligator, while Wooller (1758) concluded that it was an Indian gharial. The principle of uniformitarianism, formulated by James Hutton in 1785 (Lyell 1837), made it clear that these fossil remains are extremely old. In 1825 Geoffroy Saint-Hilaire assigned these specimens to a new taxon, *Teleosaurus.* While he was correct to distinguish *Teleosaurus* from both alligators and gharials, he was puzzled by its morphology and concluded incorrectly that it was related to mammals (Le Guyader 1998). Reconstructions of *Teleosaurus* were included in the Crystal Palace exhibition in 1854. Richard Owen concluded that *Teleosaurus* represented the most primitive member of the crocodile lineage (Owen 1854). He surmised that the *Teleosaurus* had a marine mode of life, despite its superficial resemblance to the extant gharial (Owen 1854).

The evolution of the Crocodylomorpha is of specific relevance to the geological history of the British Isles. *Goniopholis kiplingi*, from the Durlston Bay formation in Dorset, has a familiar alligator-like morphology (Andrade *et al.* 2011). This contrasts with *Torvoneustes* (Andrade *et al.* 2010) and *Plesiosuchus* (Parrilla-Bel & Canudo 2015), both from the Kimmeridge Clay formation, also in

Dorset. *Torvoneustes* and *Plesiosuchus* show a derived marine-adapted morphology with tail flukes and reduced fin-like limbs. These marine crocodylomorphs from Dorset lack the dermal armour of *Teleosaurus, Goniopholis* or their extant relatives, and exhibit a derived hypercarnivorous dentition (Andrade *et al.* 2010). *Terrestrisuchus,* from the Late Triassic rocks of Cromhall quarry in Gloucestershire, differs still further from extant forms. *Terrestrisuchus* is small, under a meter in length, and lacks dermal armour. It has an ostensibly terrestrial morphology, with long limbs positioned under the body in an erect posture similar to mammals (Allen *et al.* 2003). From these examples it is clear that morphological disparity is considerably higher in fossil crocodylomorphs than in their extant relatives (Fig. 1.1).

There is a strikingly higher diversity of crocodylomorph taxa in the fossil record than is represented today. As of January 2018, the paleobiology database (pbdb.org) contains almost 800 entries for species attributed to the Crocodylomorpha. However, a large number of them are junior synonyms and other *nomen dubium,* with many taxa described multiple times under different names. Further, there are many examples of crocodylomorph fossils that have not been attributed to a described taxon, such as the “Kayenta form” (Benton & Clark 1988). The Crocodylomorpha may also be victim to phylogenetic inflation, with some individuals of described species being reassigned to entirely new genera (Foffa *et al.* 2017). Despite this abundance of invalid taxa, a conservative estimate of the number valid described species still amounts to nearly 400.

The tempo and mode of large-scale evolutionary processes (Simpson 1944) is an ongoing controversy (Benton 2015). Evolution of major clades may follow one of a number of models. Such models may be dynamic, for example adaptive radiations or directional trends in phenotype. Alternatively evolutionary models may be stable or subject to constraining factors. Similarly character evolution on individual branches of a phylogenetic tree may be variable, with some branches showing above or below average phenotypic change per unit time. A second major controversy surrounds the drivers of evolution (Benton 2015). The red queen hypothesis proposes that evolution is driven by constant pressure from biological interactions such as predation pressure, sexual selection, competition and an arms race with parasites (Van

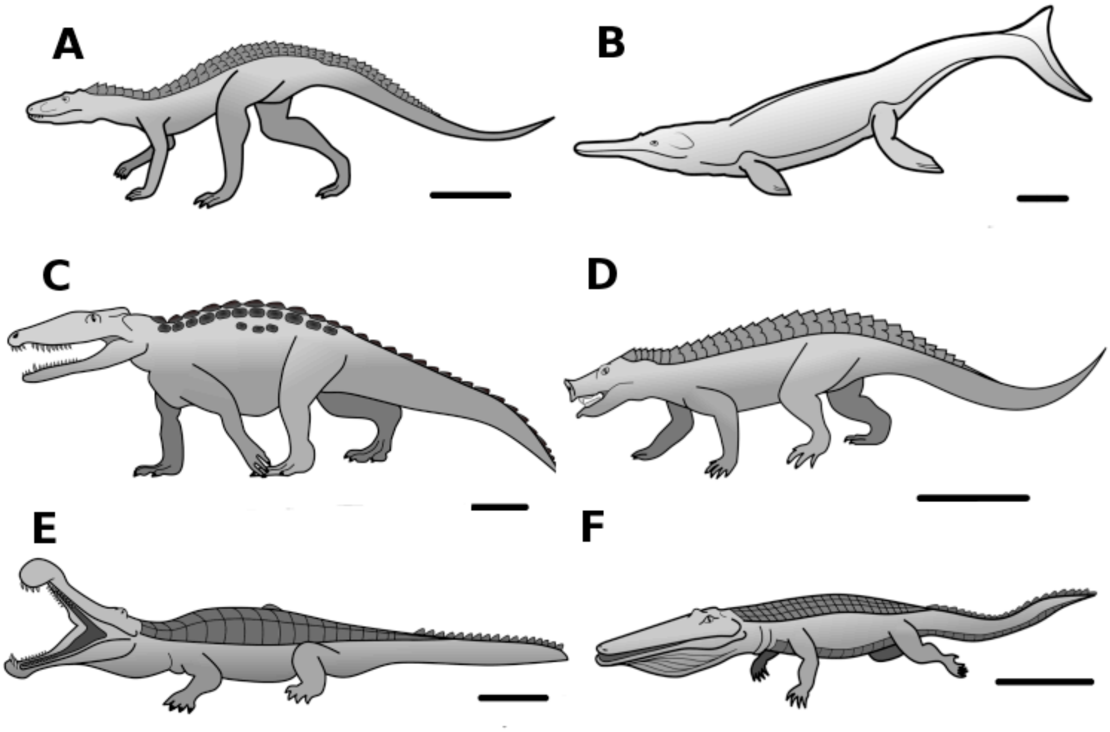

Figure 1.1. Examples of novel crocodylomorph ecomoropholgy. **A)** A fully terrestrial insectivorous sphenosuchian with a cursorial gait. Scale bar approx. 10cm. **B)** A fully marine ichthyophagous metriorhynchid thalattosuchian. Scale bar approx. 10cm. **C)** A terrestrial hypercarnivorous baurusuchid. Scale bar approx. 10cm. **D)** A heterodont omnivorous Notosuchian, with a muscular snout. Scale bar approx. 10cm. **E)** A giant amphibious longirostrine pholidosaur, *Sarcosuchus imperator.* Scale bar approx. 100cm. **F)** An amphibious laganosuchid with a aberrant platyrostral skull morphology*.* Scale bar approx. 100cm.

Valen 1979). The alternative court jester hypothesis proposes that evolution is driven by environmental changes such as climate shifts or mass extinctions (Barnosky 1999).

Any systematic analysis of phenotypes in the fossil record present a fundamental problem in that data points are not independent, since they share evolutionary heritage (Felsenstein 1985). Therefore the phenotype of any given taxon cannot be attributed to an independent variable, since the phenotype of a taxon is limited by that of its common ancestor with other taxa. The formulation of phylogenetic hypotheses enables the reconstruction of character states in deep time through the inference of common ancestors. Taking common ancestors in to account allows phenotype data to be phylogenetically corrected and analysed in a systematic framework. The phenotypic pathways of morphological characters through time can also be modelled numerically using statistical approaches.

Since the year 2000 there have been significant advances in technology enabling testing of increasingly sophisticated evolutionary hypotheses. Phylogenetic methods have enabled the rigorous analysis of cladistic relationships (Wright & Hillis 2014; O'Reilly *et al.* 2016; Puttick *et al.* 2017). The number of phylogenetic analyses in the literature has accumulated sufficiently that meta-analytical supertree approaches can be used to estimate increasingly large and comprehensive topologies (Pisani *et al.* 2002, Ruta *et al.* 2003, Ruta *et al.* 2007, Lloyd *et al.* 2008, Bronzati *et al.* 2012, Bronzati *et al.* 2015, Lloyd *et al.* 2016). While trees can be combined informally, the selection of source trees from the literature to represent parts of a supertree becomes a subjective exercise and subject to author bias. Formal approaches to estimating supertree toplogy have been devised to mitigate this problem, attempting to create a comprehensive synopsis of previously published trees sampled from the literature (Baum 1992, Regan, 1992, Akanni *et al.* 2014). Estimates of the temporal range of fossil occurrences and the branch lengths of phylogenetic trees are now possible through advances in radiometric dating and geological mapping of geological formations. Dated phylogenetic topologies can be used to reconstruct diversity in deep time, helping to mitigate the effects of preservation biases on the fossil record. However, despite these technological advances, there is not yet a single consensus on the phylogeny of the Crocodylomorphs, with multiple different phylogenetic hypotheses being proposed by various authors (Fig. 1.2).

Analyses of morphological data from fossil vertebrates hold great importance in understanding large-scale evolutionary trends. The majority of life on earth is extinct and beyond the scope of molecular methods, therefore morphological data is the only feasible way to quantify past diversity.

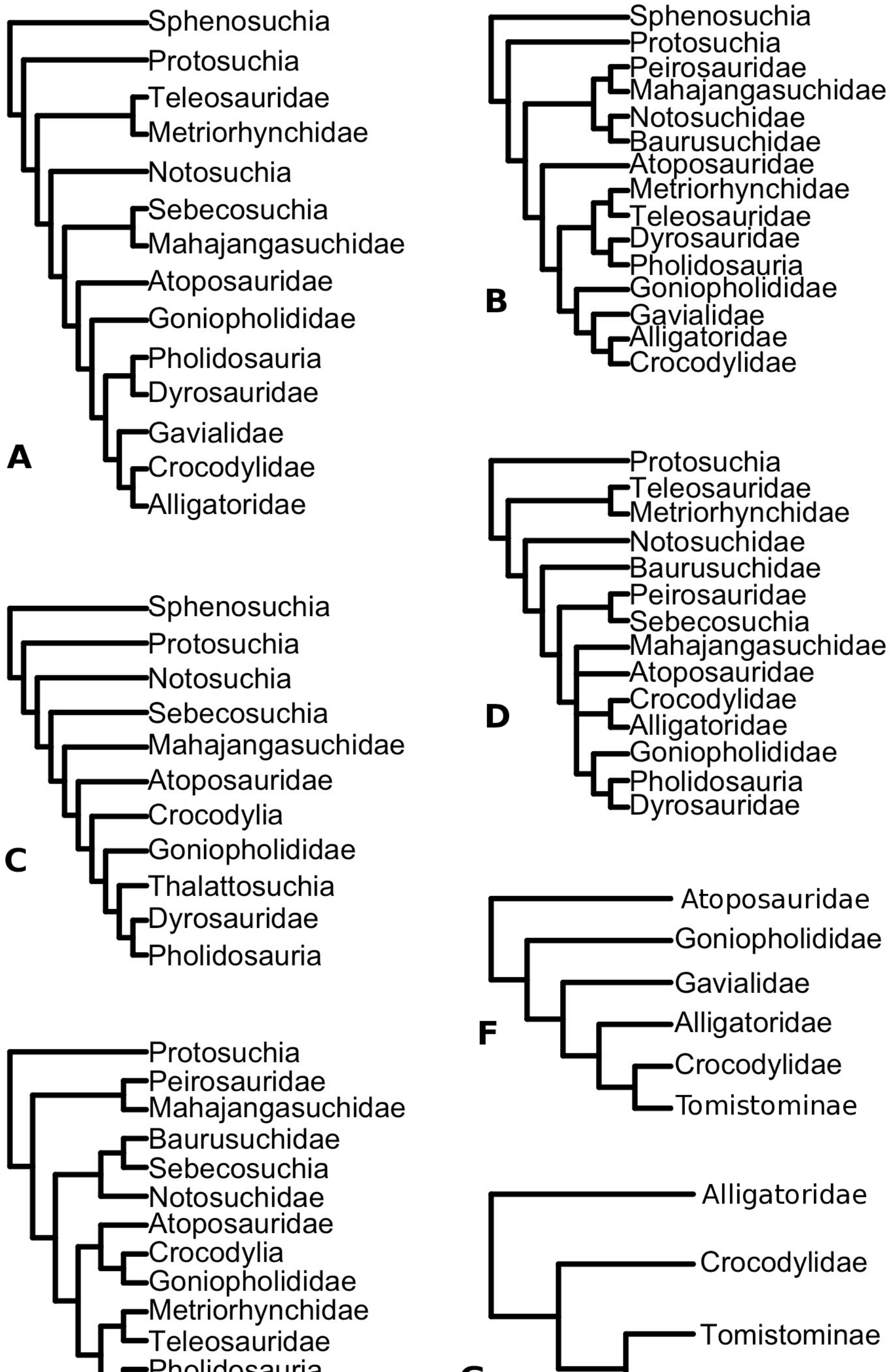

Figure 1.2. Simplified trees illustrating some different accounts of crocodylomorph phylogeny in the literature: **A)** Young & Andrade 2009; **B)** Adams 2013 ; **C)** Andrade *et al.* 2014; **D)** Larsson & Sues 2007; **E)** Bronzati *et al.* 2012; **F)** Buscalioni *et al.* 2011; **G)** Oaks *et al.* 2011.

Vertebrates have hard skeletal elements, giving them a considerably greater preservation potential than many invertebrate groups (Behrensmeyer & Kidwell 1985). Vertebrates also have great richness of morphological and ecological diversity, making phylogeny and morphological distinctiveness easier to determine than in other groups. The evolution of functional characters that are subject to selection pressure gives insight into the impacts of long-term environmental shifts and short-term extinction events. Understanding the impacts of environmental changes and mass extinctions on biodiversity is a topic of great concern in the light of anthropogenic climate change.

The Crocodylomorpha are ideal subjects to test models of character evolution. The crocodylomorphs have endured great environmental change since their inception in the Late Triassic, including prolonged climate change in the Cenozoic (Lear 2000) and three major extinction events. Crocodylomorph skeletal elements often include robust skulls and osteoderms resistant to decay and diagenesis. Further, crocodylomorphs often exhibit an amphibious or aquatic mode of life. High sedimentation rates in these environments increase the probability of burial post mortem (Behrensmeyer & Kidwell 1985). Therefore the crocodylomorph fossil record may be superior to other clades of a similar antiquity. The difference between fossil and extant crocodylomorph biodiversity presents a number of key questions that this project will aim to resolve:

- What do previous analyses conclude about the phylogenetic relationships of crocodylomorph taxa? This question will be addressed in Chapter 2 using supertree and supermatrix approaches to draw conclusions on the topology of Crocodylomorph phylogeny from published analyses.
- Are innovations in probabilistic approaches to phylogeny applicable to very large datasets? The practical application of established parsimony-based methods and innovative probabilistic methods will be tested in Chapter 2.

  Do living examples qualify as 'living fossils'? This question will be addressed in Chapter 3, using comparative phylogenetic methods and body size data to test for the status of crocodylomorphs as living fossils according to a range of definitions. This will utilise the phylogenetic hypothesis derived in Chapter 2.

- Is crocodylomorph evolution driven by long-term environmental change, or by biological interactions such as predation and competition? What model best describes the evolution of major crocodylomorph clades? These questions will be addressed in Chapter 3, using phylogenetic modelling approaches and body size data. This topic will be analysed further in Chapter 4, by comparing the time-series of diversity and disparity with that of range of other time-series variables in a systematic framework.
- Are evolutionary rates stable or subject variation? Does the low diversity of extant crocodylomorphs indicate a decline in evolutionary rates? Relative evolutionary rate will be established using comparative phylogenetic models of body size data in Chapter 3. These rates will then be further explored in a temporal context.
- How has the taxic and morphological diversity of crocodylomorphs changed through time? Are morphological and taxic diversity coupled, or can they change at different rates? Taxic diversity and morphological disparity through time are quantified and visualised in Chapter 4 using the phylogenetic hypothesis and cladistics character matrix from chapter 2. These time-series illustrate relative shifts in diversity and disparity through time.

The characterisation of crocodylomorph evolution in deep time will offer insight in to the diversity of extant crocodylomorphs, their conservation and how they may be impacted by environmental changes in the future. This study opens new avenues of research to determine interactions between different climate variables on crocodylomorph diversity, and the impact of climate change on the macroevolution of other clades.

Chapter 2: Meta-analytical approaches to the phylogeny of the Crocodylomorpha

Abstract:

The last decade has seen dramatic advances in the use of probabilistic approaches to phylogenetic analyses. These advances have so far centred on molecular analyses, but recent simulation studies have demonstrated that application to morphological data can also be advisable. Understanding evolutionary patterns on a geological timescale requires large, comprehensive phylogenies, but using morphological data from fossils presents practical challenges. Meta-analyses including supertree and supermatrix analyses attempt to circumvent these problems, but they are not without limitations. The Crocodylomorpha, crocodiles and their relatives, present an excellent opportunity to evaluate these methods. Since their emergence in the Triassic, the Crocodylomorpha diversified substantially in the Mesozoic, but has since reduced to only 24 species today. The Crocodylomorpha have a higher preservation potential than many vertebrate groups of similar antiquity, and are relatively well represented in the fossil record. Since 2000, there have been over 120 systematic analyses attempting to resolve aspects of crocodylomorph phylogeny, but a comprehensive tree has yet to be assembled. This previous research effort offers a means of determining a phylogeny using existing data, a more achievable prospect than encoding and analysing the entire clade anew. Here is presented a comprehensive phylogenetic analysis of the Crocodylomorpha using both supertree and supermatrix approaches and utilising parsimony and probabilistic methods. Supertree approaches are found to be the most practical means of summarising previous research effort. From these analyses, it can be concluded that while Bayesian approaches to phylogeny are a more rigorous means of analysing character data than parsimony, their application to highly incomplete supermatrices is hampered by the abundance of inapplicable and homoplastic characters.

INTRODUCTION

Phylogenetic methods attempt to estimate a likely null hypothesis describing the evolutionary relationships between groups of taxa. Phylogenetic trees represent evolution as a distribution of splitting events, where new taxa form through cladogenesis. Phylogenetic methods use optimisation criteria and morphological or molecular data to estimate the relative timing of branch separations.

Since the year 2000, there has been a growing effort to create ever larger and more inclusive phylogenetic trees. The Crocodylomorpha are not exceptions to this rule, with the number of tips in published trees roughly doubling in the last ten years (Fig. 2.1). Published data on the fossil record is cumulative in nature, with the number of specimens available for phylogenetic analysis increasing over time. Increasing tree size may also be a reflection of the increase in available computer processing power over time. Such huge trees lie behind many practical endeavours – for example, global issues such as anthropogenic climate change, loss of biodiversity and interspecies transmission of disease demand an understanding of evolution on a global scale. Computational methods such as phylogenetic comparative methods, morphometrics, and combined Bayesian analyses are now available to test macroevolutionary hypotheses. Advances in gene sequencing technology have enabled the rapid generation of large, high-quality data sets, while increases in computer processing power have enabled thorough analysis of ever more inclusive phylogenetic trees. The statistical power of any statistical analysis is contingent on the number of points in a data set, therefore comparative phylogenetic methods demand increasingly comprehensive phylogenetic hypotheses.

The importance of fossil data to phylogenetic analyses cannot be overstated (Quental & Marshall 2010; Benton *et al.* 2015; Ezard *et al.* 2016). The vast majority of life is extinct and beyond the scope of molecular analyses. Fossil taxa are elementary in studying evolution through time, currently presenting the only effective means of calibrating molecular clock analyses or estimating branch lengths.

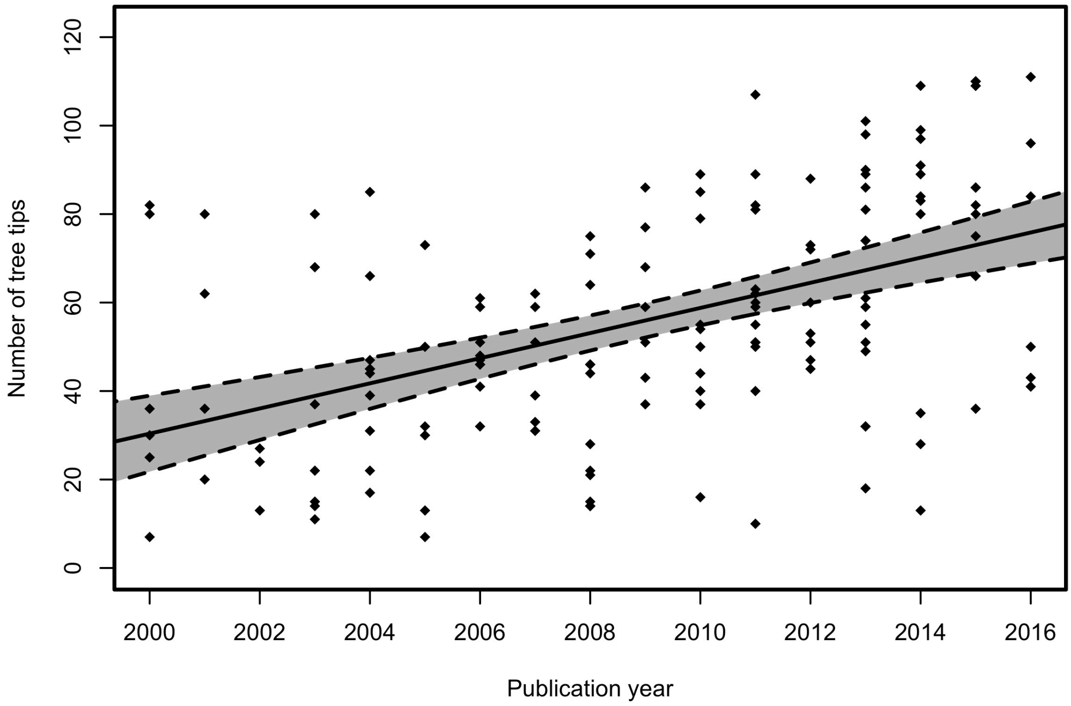

Figure 2.1. Representation of crocodylomorph tree size through time. Tree size is denoted by the number of terminal branches (tips) per tree, and the timing of each tree is indicated by its publication year.

Further, they can massively supplement our inferences of the scope and topology of phylogenetic trees based solely on extant taxa, and this is certainly true of Crocodylomorpha. However, fossil data present a number of challenges to building large phylogenies. Morphological characters of any given taxa are subject to selection pressure, and therefore cannot be assumed to be independent from one another due to coevolution and modularity. This places phylogenetic analysis of morphological characters at a disadvantage compared to analyses of molecular data. Non-coding DNA has no manifestation in a phenotype, therefore variations are not subject to selection pressure. DNA sequences will be subject to selection pressure, but to a far lesser extent than morphology. Any given amino acid in a protein may be encoded by multiple different codon triplets. Therefore, coding DNA may sustain a considerable degree of interspecies variation without expressing any change in function for selection to act upon. Phylogenetic analysis of morphology is further hampered due to taxon completeness, and homoplastic characters make resolving topology difficult. Similarly, clades with large stem-groups cannot be effectively constrained to topologies generated from molecular studies. Molecular data matrices can be expected to have greater completeness than morphological data from fossils. The decay of the fossil record results in continual loss of data over time. Since molecular data is limited to recent taxa it is not vulnerable to the effects of taphonomy. Further, DNA is common to all organisms, giving less scope for inapplicable character states to emerge. Molecular data may present a further advantage in the quantity of character states attributable to a single taxon. Diagnosing sufficient morphology to distinguish taxa can be difficult, especially in examples where morphological disparity is low. Molecular data can include orders of magnitude more character states, irrespective of how disparate the sample taxa are. The accuracy of phylogenetic analyses has been shown to increase with the number of characters in the analysis (O'Reilly *et al.* 2016). For the purposes of this study, molecular analyses will be considered methodologically superior.

Throughout the late 20th century, maximum parsimony has been the most practical and widespread means of estimating phylogeny. Parsimony makes an assumption that the phylogeny representing the smallest number of character state changes must be correct (Hennig 1966). This approach seems intuitive, and will usually return a well-resolved phylogeny. Parsimony analyses are fast and mathematically simple enough that they can be performed easily on a desktop computer with limited processing power. However, parsimony cannot take convergent and other homoplastic characters into account. This could theoretically result in an underestimate of the number of character state changes along tree branches. Further, it tends to force a maximum resolution, even when support for many nodes is modest (O'Reilly *et al.* 2016).

Maximum likelihood approaches to reconstructing phylogeny is a probabilistic approach that returns the phylogenetic tree most likely to explain the distribution of data according to a pre-determined model. Tree likelihood models are defined by a range of parameters, such as the rate of character substitutions on a branch and the number of character states. Bayesian approaches methods are similar to that of maximum likelihood approaches, frequently using the same model parameters. However, Bayesian approaches use Markov Chain Monte Carlo (MCMC) methods to iteratively update priors within the model. Bayesian implementations of probabilistic models return a posterior probability of a tree given a prior probability set by the model. This posterior probability is then used as a revised prior probability in the next iteration of the MCMC chain.

Models of molecular evolution have advanced sufficiently for prior probabilities to be imposed on a phylogenetic analysis. Tests of probabilistic approaches using simulations have suggested that their application increases the accuracy of molecular phylogenetic analyses. Models of molecular evolution enable these probabilistic analyses to cope with homoplastic and non-independent characters, which occur in molecular data. However, despite these advances, such methods are time-consuming, computationally expensive, and so far a probabilistic model of morphological character substitution has yet to be described (O'Reilly *et al.* 2016).

In the absence of a model of morphological character evolution to inform Bayesian analyses of morphological data, parsimony has remained a mainstream method of analysing morphological data from fossils. Recent simulation studies have begun to shift this paradigm by demonstrating that a Bayesian implementation of the Lewis MK model (Lewis 2001) resolves topology with greater accuracy than parsimony (Wright & Hillis 2014; O'Reilly *et al.* 2016; Puttick *et al.* 2017). These studies have also demonstrated that the parsimony approach may result in false precision, a type 1 statistical error. Such findings suggest that published phylogenetic analyses using morphological data need to be revised using the Lewis MK model in a Bayesian framework. The Lewis Mk model is a variant of the Jukes and Cantor, or JC69 model (Lewis 2001). It is a very simple model that assumes the rate of character substitution is constant. The Lewis Mk model is an advance on the former JC69 model in that it can withstand more than two character states. The Lewis Mkv model refers to a specific implementation of the Lewis Mk model that does not permit invariant constant characters (Lewis 2001). Since coding an invariant morphological character would yield no phylogenetic information, most morphological character matrices contain only variant characters. Therefore both Lewis Mk and

Mkv models are appropriate for most analyses of morphological data matrices. The Lewis Mk and Mkv models are not models of morphological character evolution, more a model of evolution that can be applied to morphological data. These models are extremely simplistic and cannot determine the relative probability of two different character substitutions (Lewis 2001).

The Crocodylomorpha presents a number of qualities that makes it an ideal clade for examining the application of phylogenetic methods on large-scale fossil datasets. The Crocodylomorpha are better represented in the fossil record than many other tetrapod groups of similar antiquity because of their often-robust skeletal elements, aquatic ecology and subsequent improved preservation potential (Behrensmeyer & Kidwell 1985). The Crocodylomorpha are extremely ancient, with fossil remains from the Late Triassic onwards, spanning over 200 million years. Unlike many clades of that age, such as the Ornithischia, Sauropodomorpha (Sues *et al.* 2011) and Pterosauria (Hone & Benton 2007), the Crocodylomorpha are represented by a number of extant genera. The Crocodylomorpha have a diverse stem-group, featuring several exotic ecomorphologies not represented in living taxa (Fig. 1). Crown crocodylomorphs are limited to amphibious ambush predators, while the stem-group is represented by terrestrial, marine, cursorial, omnivorous and herbivorous forms. The diversity of extant Crocodylomorpha is low, comprising just 24 species (Fig. 1). This contrasts starkly with the crocodylomorph sister group, the birds, which have achieved a diversity of over 10,000 extant species. Assembling sufficient data for phylogenetic analyses of large clades presents a formidable task. This has given rise to meta-analytical approaches to phylogeny, using the findings of existing research as a foundation of larger studies. Formal supertree approaches combine multiple smaller source trees in to a single larger topology (e.g, Pisani *et al.* 2002, Ruta *et al.* 2003, Ruta *et al.* 2007, Lloyd *et al.* 2008, Bronzati *et al.* 2012, Bronzati *et al.* 2015, Lloyd *et al.* 2016). Therefore, the purpose of a supertree is not to resolve phylogenetic topology, but to derive a synopsis of previous phylogenetic analyses. As such an effective supertree method will represent the literature representatively, but this not necessarily a model of biological reality.

There is not yet a single definition of a supermatrix, or what distinguishes it from simply a large matrix of phylogenetic data. For the purposes of this study a supermatrix is defined to be a collection of morphological character data taken from the literature and representing members of a taxon as comprehensively as possible. This study will draw a distinction between supermatrices and total evidence matrices. Total evidence matrices are defined in this study as matrices that include all possible data attributed to a taxon, be it molecular or morphological, but are not necessarily comprehensive in their coverage of taxa. Better coverage makes for more representative trees, which is essential for phylogenetic comparative methods.

Meta-analytical approaches to phylogeny are controversial, with different authors promoting different views. Supertree methods are subject to limitations, with different methods being biased towards different tree shapes (Wilkinson *et al.* 2005), and may find phylogenetic relationships not supported by character data (Hone & Benton 2008). Gatesy *et al.* (2002) have contended that the limitations of supertree methods are so severe that they should be avoided altogether. A rebuttal by Beninda-Emonds *et al.* (2003) concluded that these problems could be mitigated through careful source tree selection protocols, and stated that supertrees are a necessity due to the inherent impracticality of supermatrices for large clades. Gatesy *et al.* returned with a counter-rebuttal (2004), rejecting the findings of Beninda-Emonds *et al.* It must be considered that the analyses of Gatesy *et al.* focused entirely on molecular data of living taxa. As stated previously, large matrices of molecular are inherently less susceptible to homoplasy and convergence because of non-functional variation in DNA sequences. Furthermore, the molecular matrices of Gatesy *et al.* will enjoy far greater completeness than their morphological counterparts, since DNA samples from living organisms is not subject to diagenesis. Therefore perhaps in the context of molecular data, supermatrix approaches may represent a significantly superior approach to supertrees. However, the majority of life is extinct and beyond the scope of molecular data, necessitating the use of morphological data. A comparison of supermatrices of fossil morphology with supertrees by Hone and Benton (2008) also concluded that supermatrix approaches are superior to supertree methods. Hone and Benton concede that assembling large supermatrices represents a formidable task and is potentially impractical for the largest clades. Instead, the authors recommend that efforts be made to improve supertree methods. An essay by von Haeseler (2012) concluded that the ideal solution is to apply both methods and explore common relationships between the two.

Attempts to implement meta-analytical approaches to the Crocodylomorpha have been made before. A meta-phylogeny of the stem Crocodyliformes was assembled using a supertree approach (Bronzati *et al.* 2012), but this analysis excluded the crown-group. An informal supertree of the Crocodylomorpha was assembled by combining the data of Bronzati *et al.* 2012 with that of Brochu 2012 (Bronzati *et al.* 2015). However, a comprehensive supermatrix of the Crocodylomorpha has yet to be published.

Accounts of crocodylomorph phylogeny vary, with the position and monophyly of major groups being contentious. The topology of the stem Crocodylomorpha is represented by a diverse array of conflicting phylogenetic hypotheses in the literature. The Peirosauridae have been resolved as a sister clade to the Neosuchia (Bronzati *et al.* 2015), a subclade of the Sebecosuchia (Benton & Clark 1988), a subclade of the Neosuchia (Turner & Calvo 2005), and a sister group to the Notosuchia (Turner & Sertich 2010). The Sebecosuchia has been resolved as both monophyletic (Turner & Calvo 2005) and paraphyletic (Larsson & Sues 2007). A monophyletic Sebecosuchia has been considered a member of the Notosuchia (Turner & Calvo 2005; Bronzati *et al.* 2015) or a sister group of the Notosuchia (Turner & Sertich 2010). The marine Thalattosuchia have been resolved as a derived clade within the Neosuchia (Clark 1994; Pol & Gasaprini 2009; Andrade *et al.* 2011), a basal sister clade to the Crocodyliformes (Jouve 2009), or an intermediate clade within the Mesoeucrocodylia but outside the Neosuchia (Sereno & Larsson 2009, Young & Andrade 2009). The position of the marine crocodylomorphs clade has important implications for the origins of the aquatic mode of the crocodylomorph crown-group. Within the crown group, a consistent disagreement emerges in the position of *Gavialis gangeticus* when analysed using morphological (Brochu 1997) and molecular data (Oaks *et al.* 2011). Total evidence approaches support the topology found by molecular analyses, with branch support being improved with the addition of morphological data (Gatesy *et al.* 2003).

This study, attempts to resolve a comprehensive phylogeny of the Crocodylomorpha using both established parsimony and innovative probabilistic approaches. Supertree analyses are employed to find a synopsis of the current phylogenetic consensus. Alternative supermatrix approaches factor in all the available data, and may allow the recovery of previously unobserved phylogenetic relationships. The validity of supertree and supermatrix approaches in practice will be tested using fossil morphology, and estimate a sample of treespace that will include a likely representation of phylogenetic relationships. This treespace will have utility in the reconstruction of character states through time, tempo and mode of character evolution, and reconstructing biodiversity through time.

MATERIALS AND METHODS

Supertree approaches

The Matrix Representation with Parsimony (MRP) method is a means of concatenating published phylogenetic analyses into a single topology. This method is classified as a liberal formal supertree approach. Formal supertrees represent a more rigorous approach to supertree construction than informal trees, which are assembled from select branches taken from the literature. Informal supertrees are subjective, and represent the opinions of the researcher assembling them. An informal supertree cannot represent the literature comprehensively, especially if there is a lack of consensus on the phylogenetic topology of a taxon. While branches may be added to an informal tree *ad infinitum*, authors frequently use discrete phylogenetic analyses to represent large clades (e.g. Benson *et al.* 2014, Button *et al.* 2017). These source analyses may not be comprehensive in their taxonomic coverage. Therefore, the comprehensive approach of a formal supertree may achieve much better taxon coverage. MRP virtual character data presents a further advantage over discrete character data, since by definition MRP virtual characters cannot be secondarily lost. Therefore among virtual characters there is no homoplasy. This mitigates a major problem with the parsimony method, which cannot account for homoplasy (O'Reilly *et al.* 2016).

A liberal supertree approach enables a greater phylogenetic resolution to be estimated by favouring more common source topology. The frequency of a given source topology in the literature can be considered an indication of its robusticity. A conservative supertree approach would return nodes incongruent between source trees as a polytomy (McMorris & Wilkinson 2011), irrespective of relative frequency. Greater phylogenetic resolution is required for comparative phylogenetic methods, which mostly require fully resolved trees.

The MRP method represents a practical advantage over other supertree methods since it can be performed using widely-available and unspecialised tools. Source trees can be encoded manually from graphically presented phylogenetic trees, and it is therefore easy to derive MRP data from a range of different sources. This contrasts with other methods, which require source trees in a specific digital format (e.g. Steel & Penny 1993). The resulting MRP data can be analysed using widely available phylogenetic analysis software. The MRP method is a well-established approach and has been applied in many examples using fossil data, including early tetrapods (Ruta *et al.* 2003, 2007), dinosaurs (Lloyd *et al.* 2008, 2016) and crocodyliforms (Bronzati *et al.* 2012, 2015). The analysis presented here uses the Baum (1992) and Regan (1992) implementation of the MRP method, which encodes a virtual character as present in the descendant tips for each given node, and absent in all taxa outside that node. This differs from the Purvis (1995) implementation of the MRP method, which defines a virtual character as present in all descendants of a given node, but absent only in the sister taxon to that node, with the remaining tips on the source tree being classified as unknown. The Purvis method has a tendency to return less well-resolved trees than the Baum and Regan method (Purvis 1995). The Purvis method was devised in an attempt to limit data redundancy in MRP data, but Ronquist (1996) concluded that the data removed by the Purvis method was non-redundant.

The MRP method is subject to limitations. Like any supertree method, it is dependent on the correctness of its source trees. The MRP method must be implemented carefully, since it allows informal or erroneous trees to be included as source data. The analyses presented below include only source trees derived from formal phylogenetic analyses, in accordance with the guidelines proposed by Bininda-Edmonds (2003). Supertree methods, including the MRP approach, may also be biased by the opinions of prolific authors. Author bias can be analysed by testing for a relationship between author proficiency with distance between source trees and the supertree (below). Analyses affected by author bias can be corrected through the weighting of virtual characters, or by being selective in the source trees included. The MRP method may also be biased towards asymmetric trees (Wilkinson *et al.* 2005). This does not put it at a disadvantage compared to other supertree methods, which may be biased towards other tree shapes (Wilkinson *et al.* 2005). However, in a demonstration of a likelihood-based Bayesian supertree approach, Akanni *et al.* (2015) found that the MRP method outperformed other non-likelihood based methods in its representation of source trees. Therefore bias in the MRP method may be inherent to the parsimony method, and therefore shared with parsimony-based source trees.

A dataset of 146 source phylogenies was assembled from the literature. The literature was searched using online tools including Google Scholar (google.com/scholar), Web of Science (webofknowledge.com) and the Paleobiology Database (pbdb.org). The source phylogenies sampled from the literature were all estimated using formal optimisation criteria, including parsimony, maximum likelihood and Bayesian approaches (Supplementary information 1). All the selected source analyses were published with their original character data. Previous meta-analyses, such as Bronzati *et al.* (2012, 2015) and analyses using molecular data were excluded. Source trees were sampled from publication dates between 2000 and 2016. 2000 was set as a lower margin since the late 1990s and early 2000s saw the advent of consumer-level phylogenetic analysis software. These applications made phylogenetic methods, particularly parsimony, available to researchers in fields outside bioinformatics. Some titles from this period, such as TNT (Goloboff 1999), have seen widespread use throughout the literature and are still available as of 2018. Therefore it seems reasonable to suppose that the standard of phylogenetic analyses improved, or at least became more consistent, around the time of the new millennium.

Supertrees were assembled using the MRP method (Baum 1992; Regan 1992; Bininda-Emonds *et al.* 1999, 2004). This method uses source trees to infer a matrix of virtual characters. A virtual character is generated from each node of each source tree, with the exception of the root. A virtual character derived from the root would be present in all the tips of the source tree, rendering it invariant and therefore meaningless. The virtual character is encoded as present in all the descendants of that node, and absent in all taxa outside that node. Taxa not represented in the source tree are encoded as unknown.

This supertree analysis was assembled to species-level resolution. Greater phylogenetic resolution ensures more comprehensive coverage of the fossil record, increasing the statistical power of comparative phylogenetic methods. Species-level phylogenies present a further advantage in that the phylogenetic resolution can be reduced to genus- or family- level *post hoc.* However, source phylogenies were sometimes assembled to genus-level resolution, or did not use a consistent phylogenetic resolution throughout, representing higher-rank taxa with a single tip. Furthermore, source phylogenies often did not use a consistent taxonomic nomenclature, including synonyms and *nomina dubia.* To mitigate these problems in this analysis, tip labels in the source trees were standardised according to the Palaeobiology Database (Supplementary information 1). The one exception is *Crocodylus depressifrons,* which was updated to *Asiatosuchus depressifrons* as per Delfino and Smith (2009). Tips not attributed to a described species were excluded to reduce the risk of duplicate taxa in the data set. Higher-rank terminal taxa were replaced with a polytomy comprising all undisputed members of that clade according to the Palaeobiology Database (Supplementary information 1). In order to limit author bias, only one tree was taken from any source analysis. Where multiple trees were provided in an analysis, source trees were selected according to consensus criteria, taxic inclusiveness and resolution of topology. Therefore the source tree taken from each study was the highest-resolution strict consensus tree with the greatest number of tips.

The source phylogenies were digitised using the hand-drawing tools in Mesquite (Maddison & Maddison 2016). Mesquite was then used to generate a matrix of standard MRP data from the digitised source trees and exported in TNT format. An artificial taxon was added to the matrix to serve as an artificial outgroup, with all characters marked as absent (0). The MRP data was then analysed using TNT for Windows version 1.5 (Goloboff 2016). Treespace was searched using the TNT new technology search using the tree bisection and reconnection algorithm. The new technology search was set to find 25 hits, with memory set to a maximum of 200 trees. The output MRP supertrees were then tested for author bias. This was performed using a regression of two variables, metrics for author proficiency and tree distance (Fig. 2.2). The author proficiency for each source tree was denoted by the number of source trees in the analysis that had the same author. Tree distance was estimated using the mean Robinson-Foulds metric for all supertrees and 10 random resolutions of each source tree (supplementary information 1).

Published analyses using morphological data greatly outnumber those using molecular data. Virtual characters scored from molecular source trees are likely to be overwhelmed by those scored from morphological source trees. Therefore, including topologies derived from molecular data as source trees in an MRP analysis will not adequately represent the findings of these studies. To mitigate this problem, the MRP analysis was repeated with the application of a topological constraint taken from analysis of molecular data. Extant species were constrained to the topology of Oaks *et al.* (2011), a current molecular phylogeny. This replicates the approach of Salisbury *et al.* (2006).

A third supertree analysis was performed following the methodology of Akanni *et al*. (2015). This is a maximum-likelihood based approach to supertree assembly, implemented using a Bayesian MCMC framework. Supertree likelihood is estimated using the likelihood equation derived by Steel and Rodrigo (2008), which models the likelihood of a supertree representing a source tree according to an exponential distribution. The equation states that:

$$P = \alpha \exp[-\beta d(T', T \mid Y)] \tag{2.1}$$

Where *P* = the tree likelihood, α = a normalising constant, β =the quality and quantity of the source tree data, *d* = Robinson-Foulds distance, *T'* = a given source tree and *T|Y* = the subtree of the sampled supertree matching T'. This equation calculates the likelihood of a given supertree in representing the topology of a given source tree. A likelihood is calculated from each source tree, and these likelihoods are then summed to create a total likelihood for each sampled supertree. A Bayesian interpretation of this method is implemented in the Python library P4 (Foster 2004). This approach omits α while β is maintained at a low value, which the authors claim improves the speed of the algorithm without harming the accuracy of the tree (Akanni *et al.* 2015). This Bayesian supertree method does not yet have the capacity to interpret unresolved source tree data; to mitigate this problem the polytomies were replaced with a single tip representing the member species of that polytomy which occurs most frequently in source tree dataset (Supplementary information 1), therefore maximising overlap between source trees. Each source tree dataset was analysed in two runs of 500 million replicates each. The analysis was run on a server cluster with 258GB of RAM. The functions implemented in P4 cannot be parallelised, so performance was limited to one core per run. Convergence was identified using the profile of likelihood values and estimates of estimated sample size calculated in P4.

Supermatrix approaches

The supermatrix approach, where multiple source matrices of character data are combined into a single matrix, appears to be a straightforward and rigorous means of analysing large numbers of taxa. Using actual rather than virtual character data theoretically allows for the calculation of branch support values. Supermatrices have been analysed successfully using both parsimony (Hill 2005; Hone & Benton 2007) and Bayesian frameworks (Dembo *et al.* 2015).

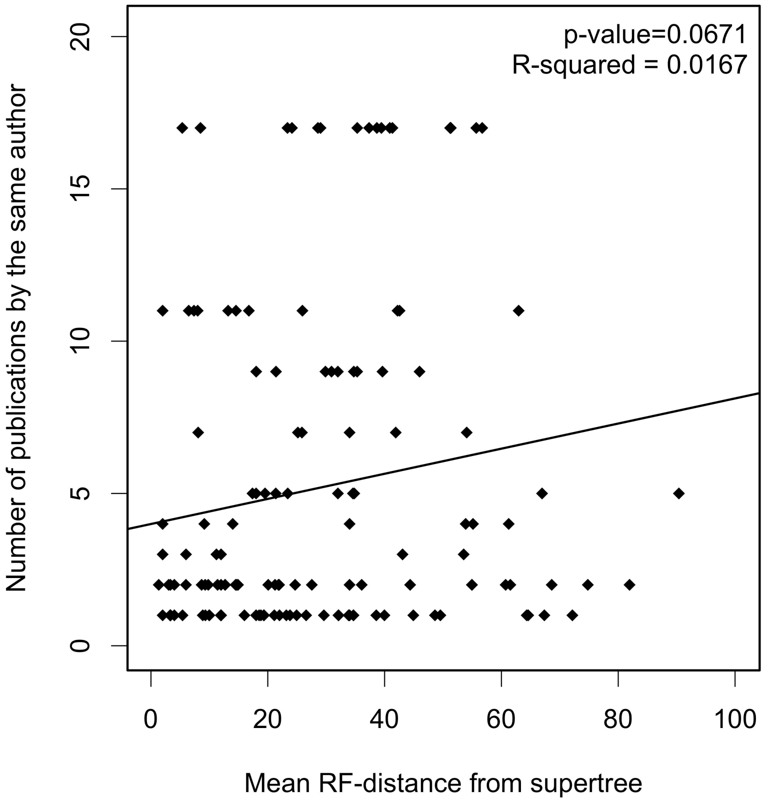

Figure 2.2. Testing for author bias using a regression of author productivity against distances between source trees and supertrees. Author productivity is indicated by the number of source trees included in the analysis by the same author. Source tree distance from supertrees was calculated using a mean Robinson-Foulds distance between all the supertrees returned by the analysis and 10 random resolutions of each source tree.

The supermatrix approach does present drawbacks. As matrices become more inclusive, there is a build-up of inapplicable characters. An inapplicable character is one that cannot meaningfully be applied to a taxon. For example, Brochu (2011) included six characters defining the character of osteoderms in the Crocodylia. These characters are only applicable to crocodylomorph taxa that possess crocodylian- like osteoderms. However, many crocodylomorphs lack osteoderms, such as the Metriorhynchidae (Young *et al.* 2011) and certain Sphenosuchia (Clark & Sues 2002). Brochu (2011) character 39 describes crocodylian dorsal midline osteoderms as either square, denoted 0, or rectangular, denoted 1. A metriorhynchid cannot be encoded as either 0 or 1, since it lacks dermal armour, making this character inapplicable.

Character inapplicability presents further problems for taxa that are excluded from source analyses that are not comprehensive. For example, a character present in two taxa might be assumed to be present in all descendants of their common ancestor. However, assigning character states in this manner requires a predetermined understanding of phylogeny. This presents particular difficulty when there is not a consensus on the position of a taxon, for example *Gavialis gangeticus* (Gatesy *et al.* 2003, Brochu 2007). The only solution to this problem would be to examine the morphology directly from specimens. This would be incredibly time-consuming for a large supermatrix, perhaps to the point of impracticality, and would defeat the purpose of a literature-based meta-analysis. The effects of inapplicable and incomplete characters mean that supermatrices may be highly incomplete. Further, many characters may not be encoded in similar terms between matrices, resulting in incomplete or duplicate characters and redundancy. Previous supermatrices have attempted to reconcile matrices to eliminate redundant characters manually, for example Hill *et al.* (2005). However, the matrix of Hill *et al.* includes 80 taxa, a fraction of the number of taxa included in this study. The matrix of Hill *et al.* also includes only 3 source analyses. Checking and modifying characters across hundreds of taxa and dozens of source matrices may require the re-examination of specimens on a scale that may be impractical. Not reconciling characters from source matrices will result in duplicate characters in a supermatrix. Multiple non-independent characters threatens to over-weight potentially incorrect phylogenetic relationships (O'Keefe & Wagner 2001), therefore simply concatenating matrices presents a major obstacle to resolving trees accurately. This over-weighting of relationships due to redundant characters presents a further problem in resolving the confidence of nodes, artificially inflating branch support values (O'Keefe & Wagner 2001). However, morphological characters do not necessarily evolve in isolation, and changes may occur in a correlated manner (O'Keefe & Wagner 2001). Therefore it must be considered that character independence cannot be guaranteed in any phylogenetic analysis.

The analyses sourced in the MRP analysis were scraped for the character data from which their topologies were estimated. The row names of the source matrices were standardised according the same taxonomic nomenclature as the MRP supertree (supplementary information 1). Rows attributed to higher-rank taxa were removed, and their character states replicated in all species previously attributed to that taxon in the Paleobiology Database (supplementary information 1). This matrix is highly incomplete. If completeness is measured as the percentage of cells in the matrix not occupied by a question mark, the matrix assembled here has a meagre completeness of 13.4%. This compares with a mean completeness of 63.7% among the source matrices (supplementary information 1). The large difference between these two values offers an indication of the numbers of inapplicable characters in the matrix. This is unsurprising since the number of taxa represented in the matrix is large, and character states will pertain to morphological features that are not ubiquitous among crocodylomorphs. This estimate makes the assumption that cells marked with a question mark in the source matrices are attributable to missing data, due to the loss of morphology to taphonomic processes. It should be noted that this is a rough estimate, since inapplicable characters may be present within source matrices as well. Differences in completeness suggest that this supermatrix is missing around 35% of data due to absences in the fossil record, and as much as 50% due to the accumulation of inapplicable characters.

The supermatrix was analysed using a New Technology search in TNT (Goloboff 2016) using the tree bisection and reconnection algorithm, set to 25 hits with memory for 200 trees. *Venaticosuchus rusconii* was used as an outgroup to root the analysis. Since the number of redundant characters in the matrix is high, branch support values could be inaccurate and were not calculated. As noted previously, the discrepancies between phylogenetic analyses of morphological and molecular analyses must be taken in to account. To account for differences in topology between different data types the supermatrix analysis was repeated with the application of a topological constraint. As in the MRP analysis, extant species were constrained to the topology of Oaks *et al.* (2011) (Fig. 5).

The supermatrix was subjected to further analysis in a Bayesian framework using an Mk-model (Lewis 2001), implemented in MrBayes (Ronquist 2012). The model was set to withstand invariant characters, rendering this an implementation of the Mk, rather than Mkv, versions of the model. The tree was rooted and prior probability of branch lengths was set to a uniform distribution. The analysis was rooted on *Venaticosuchus rusconii*. 100 million tree generations were searched in two runs and eight MCMC chains, sampled once in every 10000 generations. A start tree for the MCMC chain was set in order to reduce the treespace to be searched. This is based on the assumption that the trees recovered in the analyses so far are closer in tree space to the true tree than a tree generated at random. The start tree was randomly drawn from the sample of trees resolved by the constrained MRP analysis. This analysis was selected because it was derived from source tree data rather than the supermatrix being analysed. The constrained version of the supertree reflects the phylogeny recovered from molecular analyses, and a supertree also maintains support from previous work. It is important to note that while the start tree may not be correct, it does not serve as a constraint and the MCMC chain can migrate away from it if posterior probability values permit it. The Bayesian analysis of the supermatrix was run on a cluster with 258 gigabytes of RAM and using eight cores, with one core per chain. Testing for convergence was performed using measures of effective sample size (ESS), implemented in Tracer (Rambaut *et al.* 2013), with a target ESS of 200. Again, the analysis was repeated with an enforced topological constraint taken from the Oaks *et al.* (2011) phylogenetic analysis.

Evaluating analysis performance

As noted previously, the purpose of a supertree analyses differ from that of other phylogenetic methods. The goal of a supertree is to represent the topology of a given set of source trees. This distinguishes it from other phylogenetic methods, which seek to identify evolutionary relationships that explain the distribution of character or sequence data. Trees can be evaluated for representation of the literature using tree distance metrics and source tree data.

Multiple methods have been devised for this purpose, notably the V1 index (Wilkinson *et al.* 2005), which has been applied to supertrees of fossil taxa in previous work (Lloyd *et al.* 2008). A more recent development is the supertree likelihood equation derived by Steel and Rodrigo (2008), which has utility in Bayesian and maximum-likelihood supertree methods (Akanni *et al.* 2014, 2015). The trees returned by analyses in this study were tested for representation of the literature using the Rodrigo and Steel equation (equation 2.1). This was implemented in the manner described in Akanni *et al.* (2014), where α and β were both set to 1. The source trees were resolved in the same manner as those used in the Bayesian supertree analysis. A Rodrigo and Steel likelihood was calculated for each source tree, and these likelihoods were then summed to create an overall likelihood for each sampled supertree or supermatrix tree (Fig. 2.3A).

While the purpose of a supertree is to represent source tree data, for the purposes of many macroevolutionary analyses the best supertree is that which best represents true evolutionary relationships. A phylogeny of the Crocodylomorpha is a representation of a past event, therefore this study will assume that there is a single tree which is correct. The challenge of different phylogenetic approaches is to get as close to this hypothetical true tree as possible, but without the ability to empirically test it. Evaluating how realistic the trees are in evolutionary terms can be achieved through the application of character data and optimisation criteria, such as maximum likelihood or parsimony. Supertrees derived from MRP data will be the most parsimonious with respect to that MRP data, but they are not necessarily the most parsimonious trees for a given matrix of character data. Similarly, trees returned from analysis of a supermatrix will be the most parsimonious trees for that supermatrix, but subtrees of sampled supermatrix trees corresponding to source matrices may not be equally parsimonious. For this analysis, a novel approach to estimating the relative parsimony of each sampled tree was implemented using the source matrices. Copies of each sampled tree were subset to correspond to the species profile of each source matrix. The parsimony scores of subtrees corresponding to each source matrix were recovered using the R package Phangorn (Schliep *et al.* 2018). These parsimony scores (Supplementary information 1) were then summed to give an overall score for each sampled tree (Fig. 2.3B). This distributed approach to tree parsimony has the benefit of being based on real character data, but is independent of caveats associated with the supermatrix, for example inapplicable and redundant characters. The approach implemented gives only a relative indicator of parsimony, and the summed scores are not meaningful in isolation. The effectiveness of this method is conditional on the sampled supertrees being fully resolved and representing an identical distribution of taxa, and that they be evaluated using an identical distribution of source matrices.

The limitations of parsimony as an optimisation criterion invite concerns about the best-performing trees. O'Reilly *et al.* (2016) conclude that parsimony may result in artificially short trees due to the effects of homoplastic characters and character state reversions. Therefore parsimony methods may be vulnerable to false precision and poorer accuracy. The Mk model (Lewis 2001) is less vulnerable to these phenomena since it is based on substitution rates, rather than the number of state changes. The trees sampled in these analyses were further evaluated using the Mk model as an optimisation criterion. A likelihood for each tree was calculated using the supermatrix, using the default Mkv model implemented in Paup* (Swofford 2003). Likelihood estimation in Paup* estimates initial branch lengths using the methodology of Rogers and Swofford (1998). The Rogers and Swofford method uses parsimony to approximate branch lengths, rather than using an arbitrary value, which increases the speed of likelihood estimation. This returned differing distributions of likelihood values for each analytical approach (Fig. 2.3C). These likelihoods may be based on a superior optimisation criterion to parsimony, but they may be subject to bias from the high incompleteness and redundancy in the supermatrix. Therefore in this study Mk-model likelihood compliments, but does not supplant, source matrix parsimony for evaluating trees.

RESULTS AND DISCUSSION

Performance of phylogenetic approaches

Regression of author productivity with source tree distance from sampled trees found no significant relationship (Fig. 2.2). Therefore, the supertree topologies in this analysis are not significantly more or less similar to the source trees of productive authors. This is plausible, since authors frequently update their source matrices with new taxa and modified characters, which in turn changes the source tree topology over time. Based on these observations, it would seem that author bias is not a major contributor to supertree topology. However, the issue of author bias is somewhat intractable for the Crocodylmorpha, since even less prolific authors adapt the matrices and characters defined by their more prolific colleagues.

The unconstrained MRP analysis returned 92 most parsimonious trees. The strict consensus of these 92 trees has a poor resolution, with only 138 nodes out of a possible 382 nodes (Appendix 1, Supplementary Fig. 1). The constrained MRP analysis returned 97 most parsimonious trees. The resolution of the strict consensus is similarly poor, recovering 182 nodes common throughout the sample (Appendix 1, Supplementary Fig. 1). This poor resolution can be attributed to incongruence in the source trees. Source trees show considerable variation in the position of major groups, for example Pol and Gasparini (2009), Young and Andrade (2009) and Andrade *et al.* (2011) all position the Thalattosuchia in different places. This inconsistency is reflected in the differing RF distances between each supertree and source trees with a similar distribution of branch tips (Fig. 2.2).

The Bayesian supertree approach used by Akanni *et al.* (2015) failed to reach convergence. After their considerable running time, none of the runs returned an effective sample size (ESS) value more than 10, out of a target sample size of 200. Theoretically if the analysis was allowed to run indefinitely it would converge, however it seems that this is not in a practical time-span for the data presented here. Comparing the datasets of this analysis and that of Akanni *et al.* sheds light on the slow rate of convergence. The dataset of carnivoran source trees used by Akanni *et al.* included 274 trees, significantly more than the number of crocodylomorph supertrees used in this analysis. Similarly, in the Akanni dataset there is an average of 5 taxa in common between all the source trees, while among the crocodylomorph source trees presented here there is an average of 25 common taxa. Therefore the number of source trees and the degree of overlap between them is not an obstacle to convergence in this case. The source trees used in this analysis had an average of 76 tips, in comparison with an average of 26 tips in the carnivoran dataset used by Akanni *et al.* Since the calculation of Robinson-Foulds distances increases in complexity with the number of taxa, it is conceivable that the size of source trees may inhibit the speed of the Bayesian supertree algorithm. The tree dataset used by Akanni *et al.* is also more internally congruent than the crocodylomorph data presented here. The mean RF distance between source trees in the Akanni data set is 33 steps, while the mean distance between the crocodylmorph source trees used here is 94 steps (Supplementary information 1).

A further problem with the Akanni *et al.* method is that it has no means of imposing constraints on topology. In this case, had the analysis reached convergence it would undoubtedly have reflected the crown-group topology inferred by morphological data. The analysis would have demonstrated itself quite ineffective had it returned a topology comparable with molecular analyses. Representing morphological analysis is an accurate representation of the literature, but arguably not of evolutionary reality. The number of molecular analyses is limited and would likely be overwhelmed by the volume of contrary source topologies. Alternative solutions would be to vet the source-tree characters for homoplasy, which would require major revision of fossil material, or by the application of constraints to source trees. Both solutions would require large-scale reanalysis of existing data. It seems that while the method of Akanni *et al.* represents a theoretical advance, there are factors that constrain its utility with respect to real data taken from the literature.

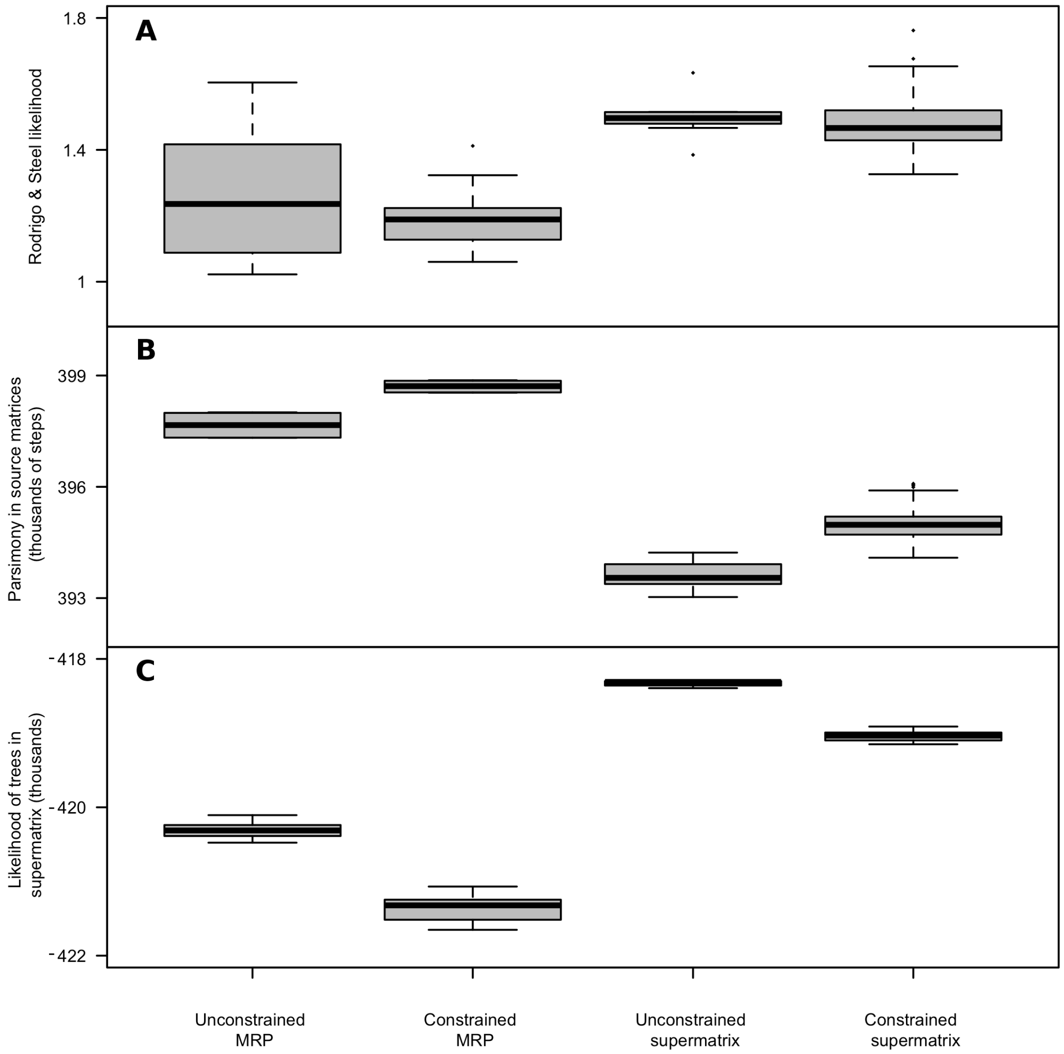

Figure 2.3. Performance of supertree and supermatrix tree analyses according to various criteria. **A.** Performance of trees in representing source tree topology, according to Rodrigo & Steel likelihood. **B.** Performance of trees in representing character data, according to total parsimony of subtrees in each source matrix. **C.** Performance of trees in representing character data, according to the likelihood of trees in context of the supermatrix according to the Mkv model.

The unconstrained parsimony analysis of the supermatrix returned 95 trees. The strict consensus of this analysis is the best resolved of all the analyses performed, finding 215 common nodes out of 381 (Appendix 1, Supplementary Fig. 3). The constrained supermatrix analysis returned 93 trees. The strict consensus of these 10 trees was less than the unconstrained analysis, finding 178 nodes out of 382 (Appendix 1, Supplementary Fig. 4). The low resolution of the consensus trees in these analyses is due to multiple solutions to the shortest possible tree. This variability comes about through the convergent acquisition or secondary loss of characters.

Analysis of the supermatrix using a Bayesian implementation of the Lewis Mk model ran for ten weeks. The sample runs failed to converge on a single topology, and likelihood profiles did not achieve a uniform distribution. It is possible that if left to run indefinitely a topology would converge, but this is clearly not on a practical timescale. The number of characters is not a direct obstacle to convergence. In the simulation studies of O'Reilly *et al.* (2016) the accuracy and resolution of Bayesian analyses increases proportionally with the number of characters. The impact of missing data on phylogenetic analyses, including Bayesian methods, is a matter of controversy. Simulation studies by Huelsenbeck (1991) concluded that incomplete taxa make resolving phylogenetic hypotheses accurately more difficult. Contrary to this, Wiens (2006) concluded that far from having a deleterious effect, missing data improved the accuracy of phylogenetic analyses by helping to mitigate long-branch attraction. Wiens contended that data matrices are often optimised for completeness, which may adversely affect topology due to the characters that are present. However, the analysis by Wiens, unlike that of Huelsenbeck, was simulated to replicate molecular, rather than morphological, data. Further, Wiens considered the completeness of individual taxa, with the assumption that some taxa were more complete than others. They concede that high levels of incompleteness may still have a deleterious effect on the outcomes of phylogenetic analyses, whether by Bayesian, maximum-likelihood or parsimony-based methods.

Bayesian implementation of the Lewis Mk model can theoretically tolerate homoplastic characters (Lewis 2001). However, this does not preclude the possibility that homoplastic characters could frustrate a Bayesian analysis if they are present in sufficient quantity. Wiens (2006) suggested that homoplasy and incompleteness may interact to reduce the accuracy of phylogenetic analyses. Conflicting phylogenetic signals from different characters may make convergence in an MCMC run difficult to achieve. Homoplasy has been demonstrated to be a problem with crocodylomorph character data; Gatesy (2003) identified multiple convergent characters contributing to the incongruence between morphological and molecular analyses of crocodylians.

The supertree and supermatrix analyses did not perform equally in representing the literature. The constrained analyses consistently performed less well than their constrained counterparts (Fig. 2.3A); this is to be expected, as the constraint topology isn't represented in the source tree data. The constrained and unconstrained supermatrix analyses overall outperform the supertree analyses in representing the source tree topologies (Fig. 2.3A). This is surprising, since the supertrees were resolved from data that was scored directly from source tree topology. However, the supermatrix trees were estimated from the same characters as the source trees. Therefore, supermatrix tree and source tree topology are not independent, and so this result is not implausible. Further, one of the best performing single trees in the entire sample is in the unconstrained MRP analysis (Fig. 2.3A). The unconstrained MRP analysis shows the widest variation in supertree likelihood, perhaps due to the effects of incongruent source trees.

The sampled trees were not equally parsimonious in the source matrices between analytical approaches. Constrained analyses have higher parsimony scores than unconstrained analyses (Fig. 2.3B). This is unsurprising, since the source matrices consistently return topologies more similar to the unconstrained analysis. The supermatrix analyses have lower scores than the supermatrix analyses (Fig. 2.3B). This is also to be expected, since the supermatrix trees are estimated from the character data in the source matrices. Sampled trees were also not equally parsimonious within analyses, even when estimated from the supermatrix (Fig. 2.3B). Therefore, the variation in source matrix parsimony between supermatrix trees can only be attributed to the effects of redundant characters and missing data in the supermatrix.

The MK likelihoods of the sampled trees are concordant with the findings of the source matrix parsimony evaluation. Again, constrained analyses perform less well than their unconstrained counterparts (Fig. 2.3C). The supermatrix trees return higher supermatrix likelihoods than the supertrees. This is unsurprising since the supermatrix and its trees a non-independent (Fig. 2.3C). The range in likelihood values is also smaller in trees estimated from the supermatrix than in supertrees (Fig. 2.3C).

These evaluations favour the supermatrix analyses over the supertree. While the MRP supertree analyses can return trees that are competent synopses of the literature, the sample is highly variable, returning trees which represent the literature less well than the supermatrix analyses. Therefore, based on these findings it is advisable for samples of MRP supertrees to be evaluated according to another criterion such as supertree likelihood in order to find the most representative tree. The supermatrix trees consistently outperform the supertree in explaining the distribution of character data. This was to be expected, since the supermatrix trees are estimated directly from the same character data. The concordant results between source matrix parsimony and supermatrix likelihood suggests that the greater performance of the supermatrix tree is not a result of inapplicable or redundant characters in the supermatrix.

It is clear that the incongruence between topologies estimated from morphological and molecular data cannot be explained through optimisation criteria. Analyses constrained to match molecular topology perform less well in explaining the distribution of character data than unconstrained analyses, irrespective of methodology. Parsimony methods may be susceptible to the effects of convergence and character-state reversions (O'Reilly *et al.* 2016), but apparently substitution models are not invulnerable to them either. This supports the findings of Gatesy (2003), who attributed the incongruence of morphological and molecular trees to homoplastic characters, and casts doubt on the accuracy of crown-group phylogenetic analyses such as those by Brochu (2013). In this analysis, I will consider molecular topology and therefore the constrained analyses to be more robust than analyses of morphology alone.

Phylogeny of the Crocodylomorpha

This section will compare the topology of the supertree most representative of the literature with the highest performing tree overall. The most representative supertree is defined as a tree returned by an unconstrained MRP analysis that has the highest Rodrigo and Steel likelihood (Fig. 2.4). This is a supertree in its truest sense, and functions only as a representation of the source tree data. The highest performing tree overall is defined as the tree which matches molecular topology and has the highest likelihood according to the Lewis MK model using real character data. This corresponds to the highest likelihood tree returned by the constrained supermatrix analysis (Fig. 2.5).

The supertree analysis finds *Venaticosuchus rusconii* to be the sister taxon to all other taxa represented in the tree (Fig. 2.4A). This suggests that *V. rusconii* was a suitable choice of outgroup for the supermatrix analysis. The supertree and supermatrix analyses agree that *Gracilisuchus stipanicicorum* lies outside the Crocodylomorpha (Fig. 2.4A, 2.5A). This is concordant with the literature, which positions it within a sister taxon to the Paracrocodylomorpha, and therefore the Crocodylomorpha itself (Butler *et al.* 2014). The supermatrix and supertree analyses find the giant *Carnufex carolinensis* to be the most basal crocodylomorph. This conforms with the topology of previous analyses of *C. carolinensis,* which found it to be a sister taxon to the Sphenosuchia (Zanno *et al.* 2015).

Both supertree and supermatrix analyses return a monophyletic Sphenosuchia, forming a sister taxon to the Crocodyliformes (Fig. 2.4A, 2.5A). The membership and topology of this group differs slightly between the two approaches. The supertree analysis places *Kayentasuchus* and *Saltoposuchus* as a sister taxon to the other Sphenosuchia. By contrast, the supermatrix finds *Saltoposuchus* to be embedded within the Sphenosuchia, while *Kayentasuchus* and *Litargosuchus* represent basal stem-group Crocodyliformes. Monophyly in the Sphenosuchia has some support in the literature (Clark & Sues 2002), but not exclusively (Nesbitt 2011).

Protosuchians do not form a monophyletic clade in either the supertree or supermatrix analyses, instead forming a paraphyletic grade of basal

Crocodyliformes (Fig. 2.4A, 2.5A). This is in agreement with the literature (Pol *et al.* 2004, Fiorelli & Calvo 2007). *Junggarsuchus* is found by the supermatrix to be a sister group to all other Crocodyliformes, but the supermatrix finds it to be a member of a small clade along side *Almadasuchus, Hoplosuchus* and *Macelognathus* (Fig. 2.5A). The supertree shows *Almadasuchus* and *Macelognathus* as a small subclade in a comparable position. The supertree resolves *Macelognathus* in a more derived position, forming a monophyletic Protosuchidae alongside *Protosuchus, Hemiprotosuchus* and *Orthosuchus* (Fig. 2.4A). These three genera also form a small subclade in the supermatrix analysis.

Both supertree and supermatrix analyses find *Gobiosuchus* and *Zaraasuchus* to form a small subclade crownward of the Protosuchidae. This contrasts with the findings of Fiorelli and Calvo (2007), who concluded that *Gobiosuchus* and *Zaraasuchus* together form a sister group to the Protosuchidae. These results compare more favourably with the findings of Pol *et al.* (2004), who recovered *Gobiosuchus* as crownward of the Protosuchidae. Supertree and supermatrix analyses agree that *Neuquensuchus*, *Shangungosuchus* and *Sichuanosuchus* form a monophyletic clade crownward of *Gobiosuchus* and *Zaraasuchus,* and that *Fruitiachampsa* is a separate, more derived taxon (Fig. 2.4A, 2.5A). This differs slightly from work by Pol *et al.* (2004) and Fiorelli and Calvo (2007), which resolved *Fruitiachampsa* as a member of the same clade of stem Crocodyliformes as *Neuquensuchus, Shangungosuchus* and *Sichuanosuchus.* The supertree and supermatrix tree disagree in the placement of *Zosuchus*; the supermatrix tree places it in a small clade with *Fruitiachampsa* and *Edentosuchus,* while the supertree positions it in the same clade as *Neuquensuchus, Shangungosuchus* and *Sichuanosuchus* (Fig. 2.4A, 2.5A). The supertree places *Edentosuchus* in a much more basal position among the Protosuchidae (Fig. 2.4A).

Both supertree and supermatrix analyses return *Hsisosuchus* as a sister taxon to the Mesoeucrocodylia, comparable with the topologies of Pol *et al.* (2004) and Fiorelli and Calvo (2007) (Fig. 2.4A, 2.5A). The topology of major mesoeucrocodylian groups is a point of significant disagreement between the supertree and supermatrix approaches. The supermatrix tree units the terrestrial Notosuchia, Sebecosuchia, Peirosauridae and Mahajangasuchidae into

Figure 2.4. MRP supertree of the Crocodylomorpha that performs highest under Rodrigo and Steel supertree likelihood. **A.** Shows topology of non-neosuchian Crocodylomorpha, **B.** Includes topology of Peirosauridae and stem-group Neosuchia (excluding the Goniopholididae). Artificial all-zero outgroup not shown.

Figure 2.4. MRP supertree of the Crocodylomorpha that performs highest under Rodrigo and Steel supertree likelihood. **C.** Shows topology of Goniopholididae, Paralligatoridae, Stem Eusuchia and Gavialidae. **D.** Includes topology of Crocodylidae and stem-group Alligatoridae.

a single clade, forming a sister group to the Neosuchia (Fig. 2.5A). This relationship has been returned in previous analyses (Turner & Sertich 2010). The supertree finds the Notosuchia to separate first from the common ancestor of all Mesoeucrocodylia (Fig. 2.4A). The Peirosauridae and Mahajangasuchidae lie crownward of the Notosuchia, forming a sister clade to the Neosuchia (Fig. 2.4B). This relationship has support in the literature (Leardi & Pol 2009) and has been recovered in previous supertree analyses (Bronzati *et al.* 2015). Uniting the Peirosauridae with the Notosuchia is arguably more parsimonious than with the Neosuchia, since it implies less missing data. The Peirosauridae are limited to the Cretaceous and are contemporaries of the Notosuchia (Leardi & Pol 2009). The Neosuchia are of considerably greater antiquity, with examples known from the Early Jurassic (Tykoski *et al.* 2002). Therefore a peirosauarid sister group to the Neosuchia would imply their presence throughout the Jurassic, which is currently unknown. However, the Peirosauridae includes the subfamily Trematochampsidae, a group featuring amphibious examples of a mode of life comparable with many neosuchians (Rogers *et al.* 2007). Supertree and supermatrix analyses place the subfamily Mahajangasuchidae within the Peirosauridae (Fig. 2.4B, 2.5A). The inclusion of Mahajangasuchidae within the Peirosauridae has been observed in previous analyses (Pol *et al.* 2012) but other studies have positioned them as a sister clade to the Peirosauridae (Sereno & Larsson 2009; Andrade 2011).

The fundamental topology of the Notosuchia is similar between the supertree and supermatrix analyses. Both supertree and supermatrix analyses agree that *Anatosuchus* is the sister taxon to all other notosuchians (Fig. 2.4A, 2.5A). *Araripesuchus* is similarly basal compared to other notosuchians (Fig. 2.4A, 2.5A). This relationship has some support in the literature (Turner & Sertich 2010) but this support is not universal (Turner & Calvo 2005). Both supertree and supermatrix analyses find the Baurusuchidae and the Sebecosuchidae form a sister clade to the Notosuchidae (Fig. 2.4A, 2.5B). Affiliation between the Baurusuchidae and the Sebecosuchidae has support in the literature (Turner & Sertich 2010, Pol & Powell 2011), but contrasts with Benton and Clark (1988) and Sereno and Larsson (2009), who positioned the Sebecosuchia crownward of the Notosuchia. The supertree and supermatrix trees agree on a paraphyletic grade of basal Notosuchia, including *Malawisuchus, Candidodon, Pakasuchus, Uruguaysuchus, Libycosuchus* and *Simosuchus* (Fig. 2.4A, 2.5B). The supertree positions *Notosuchus, Comahuesuchus* and *Mariliasuchus* in this group (Fig. 2.4A), while the supermatrix tree places them in a more derived position among the Notosuchidae (Fig. 2.5A). Supertree and supermatrix trees agree that *Pehuenchesuchus* is a sister taxon to all other Sebecosuchia and Baurusuchidae (Fig. 2.4A, 2.5A). The supermatrix positions *Doratodon* outside these groups as well (Fig. 2.4A), however the supertree places it in a more derived position as a basal sebecosuchian (Fig. 2.4A). The supertree also identifies *Caririsuchus* as a basal sebecosuchian (Fig. 2.4A), while the supermatrix tree places it among the Peirosauridae (Fig. 2.4B).

The supertree and supermatrix analyses show congruent topology for the major lineages of the Neosuchia. Both analyses return a clade comprising of the Thalattosuchia and the Tethysuchia (Fig. 2.4B, 2.5B). This clade is sister group to a clade including the Atoposauridae, Goniopholididae, Paralligatoridae and Eusuchia (Fig. 2.4B, 2.5B). Positioning the Thalattosuchia within the Neosuchia has some support in the literature (Pol & Gasparini 2009, Andrade *et al.* 2011) but is incongruent with other analyses that place it in basal positions within the Mesoeucrocodylia (Jouve 2009, Sereno & Larsson 2009, Young & Andrade 2009, Montefeltro *et al.* 2013).

The Tethysuchia are found to include two major subtaxa, corresponding to the Elosuchidae and the Dyrosauridae (Fig. 2.4B, 2.5B). The genus *Pholidosaurus* is found to the sister genus to all other Tethysuchia, making the group Pholidosauria paraphyletic (Fig. 2.4B, 2.5B). This excludes *Pholidosaurus decepiens,* which the supertree analysis returns as an elosuchid (Fig. 2.4B). Aspects of this topology have been recovered previously; Andrade *et al.* (2011) identified a separation of *Pholidosaurus* from the Elosuchidae, however their analysis positioned *Pholidosaurus* in a more derived position closer to the Dyrosauridae.

Supertree and supermatrix analyses agree on the large-scale structure of the Thalattosuchia. Both analyses find a monophyletic family of basal Thalattosuchia, the Teleosauridae, forming the sister group to Metriorhynchidae.

Figure 2.5. Supermatrix tree with the highest likelihood under the MK model. **A.** Shows topology of non-neosuchian Crocodylomorpha. **B.** includes topology of stem-group Neosuchia.

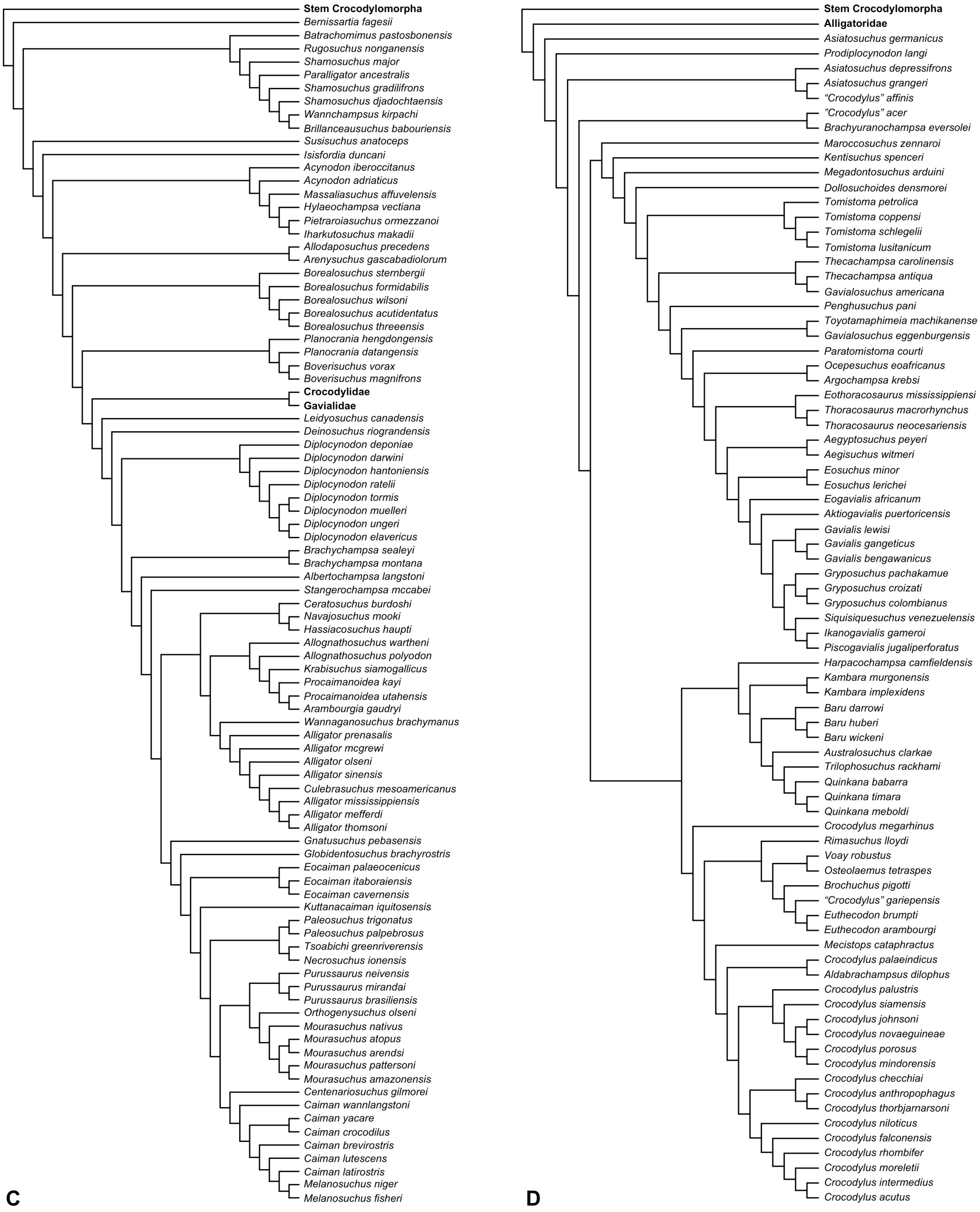

Figure 2.5. Supermatrix tree with the highest likelihood under the MK model. **C.** Shows topology of Paralligatoridae, stem-group Eusuchia, Alligatoridae. **D.** Shows topology of the Gavialidae and Crocodylidae, constrainted to the topology of Oaks *et al.* (2011).

This contrasts with some previous analyses, which found the Teleosauridae to be paraphyletic (Young *et al.* 2011), but a monophyletic Teleosauridae has been recovered as well (Young *et al.* 2012, Turner 2015). Both supertree and supermatrix analyses further subdivide the Metriorhynchidae into the Metriorhynchinae and the Geosaurinae (Fig. 2.4B, 2.5B). The supermatrix tree finds *Pelagosaurus* to be sister taxon to all other Thalattosuchia (Fig. 2.4B). The supertree analysis finds *Pelagosaurus* to be in a more derived position, as sister taxon to the Teleosauridae (Fig. 2.4B). Neither analysis returns the genus *Steneosaurus* as monophyletic (Fig. 2.4B, 2.5B). Many supposed species of *Steneosaurus* have been proposed, and it may be an inflated 'dustbin taxon'. The supermatrix analysis supports monophyly in the genus *Machimosaurus*. Both analysis return similar topology for the Metriorhynchinae. *Cricosaurus* is found to be a monophyletic genus with a clade including *Maledictosaurus* and *Rhacheosaurus.* This forms a sister clade to the genus *Gracilineustes* (Fig. 2.4B, 2.5B)*.* Neither supertree nor supermatrix analyses find *Metriorhynchus* to be a monophyletic genus. The analyses agree that *M. moreli* and *M. superciliosus* lie within a sister clade to all other Metriorhynchidae (Fig. 2.4B, 2.5B). However, the analyses distribute other *Metriorhynchus* species differently. The supertree identifies *Metriorhynchus* as a paraphyletic grade of basal metriorhynchids (Fig. 2.4B). The supermatrix finds other Metriorhynchus in a more derived position, as a paraphyletic grade close to the Geosaurinae (Fig. 2.5B). Both trees find *Eoneustes* to be a sister taxon to the Metriorhynchidae (Fig. 2.4B, 2.5B). Perhaps therefore *Eoneustes* represents a transitional form between basal amphibious Thalattosuchia to derived fully marine forms. Both analyses find *Geosaurus*, *Dakosaurus*, *Neptunidraco*, *Plesiosuchus* and *Tyrannoneustes* to lie within the Geosaurinae.

Both supertree and supermatrix analyses find the Atoposauridae to be a monophyletic sister group to the Goniopholididae and Eusuchia (Fig. 2.4B, 2.5B). The Atoposauridae represent a problem taxon, with previous analyses placing it in different positions, either as a sister group to the Neosuchia (Adams 2014) or together with the Paralligatoridae forming a sister group of the Eusuchia (Rogers 2003). A review of atoposaurid phylogeny (Tennant *et al.* 2016) found the topology to vary depending on the ordering and weighting of characters and the optimisation criteria applied. However, this review consistently found the Atoposauridae to be a paraphyletic grade of basal neosuchians, with goniopholidid and tethysuchian taxa within the group. Tennant *et al.* (2016) notably did not include any crown group taxa in their analysis. The supertree and supermatrix topologies presented here resemble that of Turner and Pritchard (2015), who also recovered the Atoposauridae as a monophyletic sister group to the Eusuchia and Goniopholididae. However, unlike the analyses presented here, the analysis of Turner and Pritchard (2015) included the Tethysuchia within the Eusuchia. The supertree and supermatrix analyses agree that *Atoposaurus* and *Alligatorellus* form sister genera. The supermatrix analysis finds *Alligatorium* to be a monophyletic sister genus to *Atoposaurus* and *Alligatorellus* (Fig. 2.5B), but the supertree finds it to be paraphyletic (Fig. 2.4B). *Theriosuchus* is found by both analyses to be a sister clade to all other Atoposauridae (Fig. 2.4B, 2.5B), but the supertree positions *T. sympiestodon* and *T. ibericus* outside the Atoposauridae as memebers of the Paralligatoridae (Fig. 2.4B).

Both supertree and supermatrix analyses find the Goniopholididae to form a monophyletic group positioned crownward of the Atoposauridae (Fig. 2.4C, 2.5B). Monophyly of the Goniopholididae has support in the literature (Adams 2014; Andrade *et al.* 2011). These analyses agree *Koumpiodontosuchus* is the sister taxon to all other gonipholidids (Fig. 2.4C, 2.5B). *Calsoyasuchus* and *Sunosuchus* form a monophyletic clade, which is in turn sister to a larger clade including *Goniopholis, Anteophthalmosuchus, Hulkepholis, Nannosuchus* and *Siamosuchus* (Fig. 2.4C, 2.5B). This is supported by Adams (2014) but contrasts with Andrade *et al.* (2011), who recovered *Calsoyasuchus* as the sister taxon to all other goniopholidids. The supertree places *Chalawan* closer to *Goniopholis* than *Calsoyasuchus* (Fig. 2.4C), unlike the supermatrix which places it as a sister taxon to *Sunosuchus miaoi* (Fig. 2.5B). Neither the supermatrix nor supertree analyses find the genus *Goniopholis* to be monophyletic (Fig. 2.4C, 2.5B). Paraphyly and polyphyly have been observed in *Goniopholis* in previous analyses (Andrade *et al.* 2011, Adams 2013, Halliday *et al.* 2013, Adams 2014). Perhaps *Goniopholis* is a ‘dustbin’ taxon, and is in need of reclassifying as multiple genera.

Alternatively the Goniopholididae may be victim to phylogenetic inflation, with members of *Goniopholis* being attributed to non-existent genera.

The genus *Bernissartia* is found by both analyses to be a sister taxon to the Paralligatoridae and Eusuchia (Fig. 2.4C, 2.5C). This relationship has some support in the literature (Adams 2014,) but not universally. Some previous analyses have placed *Bernissartia* crownward of this position, as a sister clade to crown-group Crocodylomorpha (Andrade *et al.* 2011, Halliday *et al.* 2015). The Paralligatoridae form a monophyletic clade lying crownward of *Bernissartia* in both the supertree and supermatrix analyses (Fig. 2.4C, 2.5C). This position reflects the findings of previous analyses (Montefeltro *et al.* 2013; Adams 2014). The supertree finds *Wannachampsus* and *Brillanceausuchus* in a sister clade to other Paralligatoridae (Fig. 2.4C). This clade also includes two species of *Theriosuchus* usually associated with the Atoposauridae (Tennant *et al.* 2016). The supermatrix analysis agrees that *Wannachampsus* and *Brillanceausuchus* are sister genera, but places them closer to *Shamosuchus* (Fig. 2.5C). The supertree finds *Batrachomimus* and *Rugosuchus* to form a monophyletic subclade within the Paralligatoridae (Fig. 2.4C), but this monophyly is not supported in the supermatrix analysis (Fig. 2.5C). Neither analysis finds *Shamosuchus* to be monophyletic.

The supertree analysis finds that *Isisfordia* and *Susisuchus* form a monophyletic sister clade to the Eusuchia. This topology matches that of Salisbury *et al.* (2006) and Turner and Pritchard (2015). The supermatrix analysis finds these taxa to form a paraphyletic grade of stem-group Eusuchians, similar to the topology of Fortier and Schultz (2009). The Hylaeochampsidae are found to form a monophyletic clade of stem-group Eusuchia in both the supertree and supermatrix analyses (Fig. 2.4C, 2.5C). This clade includes *Hylaeochampsa, iharkutosuchus* and *Pietraroiasuchus.* This is consistent with the literature (Delfino *et al.* 2008, Martin *et al.* 2016). Both analyses also include *Acynodon* in this group (Fig. 2.4C, 2.5C). This position reflects the findings of some previous studies (Brochu 2013, Martin *et al.* 2016), but *Acynodon* has also previously been associated with the Alligatoridae (Delfino *et al.* 2008).

The fundamental topology of the crown-group in the supermatrix is defined by the topological constraint. This places the Gavialidae and

Tomistominae on a single branch, forming a sister group to the Crocodylidae (Fig. 2.5D). Together these form a sister group to the Alligatoridae (Fig. 2.5C). The supertree is unconstrained, and so reflects the topology of morphological trees in the literature (e.g. Buscalioni *et al.* 2001, Brochu 2013). This places the Gavialidae as the sister group to all other crocodilians (Fig. 2.4C). The Tomistomidae and Crocodylidae together form a sister group to the Alligatoridae (2.4D).

Both supertree and supermatrix analyses agree that *Borealosuchus* is a monophyletic taxon (Fig. 2.4C, 2.5C). The supermatrix analysis resolves *Borealosuchus* as a stem-group eusuchian (Fig. 2.5C), congruent with the findings of Gatesy *et al.* (2003). The supertree finds it to be within the crown-group as a stem-group 'Brevirostres' (Fig. 2.4C), comparable with other analyses of morphology (Brochu 2013). The supertree and supermatrix analyses also agree on the monophyly of the Planocraniidae, and find it to be more derived than *Borealosuchus* (Fig. 2.4C, 2.5C). The unconstrained supertree finds it to be a stem 'Brevirostres' (Fig. 2.4C), conforming to the topology of Brochu (2013). The supermatrix finds it to be a stem crocodylian (Fig. 2.5C), congruent with the total evidence approach of Gatesy *et al.* (2003).

Both supertree and supermatrix analyses include *Leidyosuchus, Deinosuchus, Diplocynodon, Brachychampsa, Albertochampsa* and *Stangerochampsa* as members of a paraphyletic grade of stem-group Alligatoridae (Fig. 2.4D, 2.5C). The supertree analysis finds *Stangerochampsa* to be the most derived of this grade and is the sister taxon to the crown-group Alligatoridae. The supermatrix analysis finds a more inclusive sister clade of the crown-group Alligatoridae (Fig. 2.5C). This sister clade includes *Stangerochampsa, Brachychampsa* and *Albertochampsa.* The total-evidence analysis of Gatesy *et al.* (2003) was not able to resolve the stem-group Alligatoridae, so does not favour either topology. The supertree and supermatrix analyses agree on a paraphyletic grade of stem-group alligators. Both analyses find *Ceratosuchus, Hassiacosuchus* and *Navajosuchus* to form a monophyletic subclade (Fig. 2.4D, 2.5C). Crownward of this is a second monophyletic subclade including *Allognathosuchus, Arambourgia* and *Procaimanoidea* (Fig. 2.4D, 2.5C). This topology is supported by previous analyses of morphology (Brochu 2013), but analyses of combined morphological and molecular data have left these nodes unresolved (Gatesy *et al*. 2003). The supermatrix includes *Krabisuchus* in this group (Fig. 2.5C), while the supertree considers it a stem-group caiman (Fig. 2.4D). Both supertree and supermatrix analyses find *Wannaganosuchus* to be the sister taxon to the extant genus *Alligator* (Fig. 2.4D, 2.5C), similar to the findings of Brochu (2013). The supermatrix considers *Alligator* to be paraphyletic and includes *Culebrasuchus* (Fig. 2.5C)*,* however the supertee analysis places this as a stem-group caiman (Fig. 2.4D). *Culebrasuchus* is found to be a stem caiman in the analysis of Hastings *et al.* (2013).

Gnatusuchus, Globidentosuchus, Eocaiman and *Kuttanacaiman* are found in both supertree and supermatrix analyses to form a paraphyletic grade of stem caimans (Fig. 2.4D, 2.5C). This topology was also found by Salas-Gismondi *et al.* (2015). The position of *Eocaiman* is congruent with the findings of combined morphological and molecular analyses (Gatesy *et al.* 2003) and with morphology-only studies (Brochu 2013). Supertree and supermatrix find the novel platyrostrine *Mourasuchus* and the giant *Purussaurus* to lie with the crown-group caimans. Together with *Orthogenysuchus* they form a sister clade to a clade of derived caimans including *Centenariosuchus* and the extant *Caiman* and *Melanosuchus* (Fig. 2.4D, 2.5C)*.* The extant *Paleosuchus,* together with *Tsoabichi,* form a sister clade to all other crown-group caimans (Fig. 2.4D, 2.5C). The supermatrix analysis places *Necorsuchus* as a sister genus to *Tsoabichi* (Fig. 2.5C)*,* while the supertree places it on a separate branch closer to *Caiman* and *Melanosuchus* than to *Palaeosuchus* (Fig. 2.4D)*.* This topology is congruent with multiple previous analyses of both morphological (Brochu 2013, Salas-Gismondi *et al.* 2016) and combined morphological and molecular data (Gatesy *et al.* 2003). However, this congruence is not universal; an analysis by Salas-Gismondi (2015) found *Purussaurus* and *Mourasuchus* to form a sister clade to the crown-group caimans.

The supertree analysis finds *Tomistoma* to be polyphyletic, appearing in a clade of 'tomistomines' including *Gavialosuchus, Thecachampsa, Toyotamaphimeia, Penghusuchus* and *Paratomistoma* (Fig. 2.4C)*.* This clade of 'tomistomines' is preceded by a paraphyletic grade of basal taxa including *Maroccosuchus*, *Kentisuchus*, *Dollosuchoides* and *Megadontosuchus* (Fig. 2.4C).

This topology is congruent with the findings of Brochu (2013) and Salas-Gismondi *et al.* (2016). The supermatrix finds these taxa to be a paraphyletic grade of stem-group gavialids (Fig. 2.5D). The combined molecular and morphological analysis by Gatesy *et al*. (2003) placed *Dollosuchoides* in a congruent position to the supermatrix analysis, however *Kentisuchus* and *Megadontosuchus* were not included. The supermatrix positions the extant *Tomistoma* as a monophyletic sister genus to all other crown-group Gavialidae (Fig. 2.5D). The supermatrix unites *Gavialosuchus, Thecachampsa, Toyotamaphimeia, Penghusuchus* and *Paratomistoma* with *Argochampsa, Ocepesuchus, Eothoracosaurus, Thoracosaurus, Eosuchus, Eogavialis,* and *Akitogavialis* to form a paraphyletic grade of crown-group Gavialidae (Fig. 2.5D). The topology of the crown-group Gavialidae is mostly unresolved in the analysis of Gatesy *et al.* (2003), but *Gryposuchus, Eogavialis* and *Thoracosaurus* are resolved in congruent positions to the supermatrix. *Argochampsa, Ocepesuchus, Eothoracosaurus, Thoracosaurus, Eosuchus, Eogavialis,* and *Akitogavialis* are returned by the supertree analysis as a paraphyletic grade of stem-group Gavialidae (Fig. 2.4C), similar to the topology of Brochu (2013) and Salas-Gismondi *et al.* (2016). The supermatrix identifies an extinct clade of crown-group Gavialidae including *Gryposuchus, Ikanogavilis, Piscogavialis,* and *Siquisiquesuchus*. This clade is the sister taxon to the extant *Gavialis* (Fig. 2.5D). The supertree analysis finds these taxa to be a paraphyletic region of the gavialid stem-group (Fig. 2.4C). The supertree analysis does not support the monophyly of *Gryposuchus,* finding *G. colombianus* and *G. croizati* to be more closely related to *Gavialis* than *Gryposuchus pachakamue* (Fig. 2.4C).

The supertree and supermatrix analyses agree that the Mekosuchinae represent a monophyletic clade of stem-group crocodiles, including *Australosuchus, Baru, Trilophosuchus, Quinkana, Harpacochampsa* and *Kambara* (Fig. 2.4D, 2.5D). The monophyly of this group is supported by palaeogeography, since all members of this group occur in Australasia and the South Pacific (Willis 1993). Both supertree and supermatrix analyses find *"Crocodylus" megharinus* to lie crownward of the Mekosuchinae, and is the sister taxon to the crown-group crocodiles (Fig. 2.4D, 2.5D). Both analyses agree on a clade of crown-group crocodiles that is distinct from *Mecistops* and *Crocodylus* (Fig. 2.4D, 2.5D).

Members of this clade are limited to Africa (Conrad *et al.* 2013), including *Rimasuchus, Brochuchus, Euthecodon, Voay* and the extant *Osteolaemus.* Analysis by Conrad *et al.* (2013) identified a similar monophyletic group including *Osteolaemus, Voay, Brochuchus* and *Rimasuchus,* which they named the Osteolaeminae. However, the topology of both trees contrast with that of Conrad *et al.* (2013) in other respects; Conrad *et al.* (2013) placed *Mecistops*, *Euthocodon* and *"Crocodylus" gariepensis* in a separate sister clade to *Crocodylus.* The supertree and supermatrix analyses include "*Crocodylus" gariepensis* in the Osteolaeminae (Fig. 2.4D, 2.5D). The supertree also includes *Aldabrachampsus* in this clade (Fig. 2.4D), while the supermatrix identifies it as a sister genus to *Crocodylus palaeindicus* (Fig. 2.5D)*.* Analysis by Brochu (2006) did not resolve *Aldabrachampsus* as being closer to either *Crocodylus* or *Osteolaemus.* Both supertree and supermatrix analyses agree on the monophyly of extant *Crocodylus* (Fig. 2.4D, 2.5D). The affiliation with of *C. palaeindicus* with Asian and Australasian *Crocodylus* shown by the supertree is supported by more recent analysis by Brochu and Storrs (2012).

The supertree considers *Mecistops* to be the sister taxon to valid members of *Crocodylus* (Fig. 2.4D)*.* The supermatrix places *Mecistops* as the sister genus to a clade which includes all valid members of *Crocodylus,* but as noted previously also includes *Aldabrachampsus* (Fig. 2.5D)*.* Both analyses find a subgenus of *Crocodylus* with members limited to India, Indochina, Indonesia and Australasia, including *C. johnsoni, C. novaeguineae, C. porosus, C. mindorensis, C. siamensis,* and *C. palustris* (Meredith *et al.* 2011) (Fig. 2.4D, 2.5D)*.* The supertree analysis also includes *C. palaeindicus* in this group (Fig. 2.4D). A second subgenus unites new-world *Crocodylus* taxa, including *C. intermedius, C. acutus, C. moreletii, C. rhombifer* and *C. falconensis* (Meredith *et al.* 2011) (Fig. 2.4D, 2.5D)*.* The supermatrix includes the African *C. niloticus* in this group, and finds the African *C. checchiai, C. thorbjarnarsoni* and *C. anthropophagus* to form sister clade (Fig. 2.5D). The supertree positions *C. checchiai* within this clade of new-world taxa, as a sister species to *C. palaeindicus* (Fig. 2.4D)*. C. thorbjarnarsoni* and *C. anthropophagus* are found to form a sister clade to new world *Crocodylus* and *C. checchiai* (Fig. 2.4D). A monophyletic clade including *C. thorbjarnarsoni* and *C. anthropophagus* was identified by Brochu & Storrs (2012), but its exact relationship to other African and new-world Crocodylus was not resolved. The supertree finds *C. niloticus* to be a sister taxon to all African and new-world *Crocodylus* taxa (Fig. 2.4D). The topology of extant in both supertree and supermatrix analyses is congruent with analysis of mitochondrial DNA (Meredith *et al.* 2011). Meredith *et al.* (2011) hypothesize an African origin for new-world *Crocodylus* taxa*.* The position of *C. thorbjarnarsoni* and *C. anthropophagus* may differ slightly between the supertree and supermatrix analysis, but both positions are congruent with this hypothesis.

CONCLUSION

The MRP supertree method is highly capable of producing effective synopses of source tree topology. However, in the case of the Crocodylomorpha, this method returns other trees that perform less well in representing previous work. The supertree likelihood methods devised by Rodrigo and Steel (2008) present a means to evaluate individual supertrees, and can be used to eliminate trees returned by an MRP analysis. However, there are factors in some real-world data that affect the utility of Bayesian supertree approaches that use the Rodrigo and Steel supertree likelihood as an optimality criterion.

Assembling a supermatrix presents a formidable undertaking. The accumulation of inapplicable characters is inevitable, and therefore supermatrix data cannot be expected to equal the standard of less taxically inclusive matrices. However, in this example, crudely concatenating matrices for analysis using parsimony can yield results that are at least as good, or arguably better, than supertrees at representing the distribution of character data. This is despite the very high incompleteness of the matrix and the number of redundant characters. While this approach performs well under parsimony, it is difficult to successfully analyse such a large and incomplete matrix using Bayesian implementation of the Lewis MK model, which is argued to be a superior method to parsimony.

The best-performing supertree and best-performing supermatrix tree find considerable agreement in the overall topology of crocodylomorph phylogeny. They both support the monophyly of many established groups, including the Notosuchia, Thalattosuchia, Tethysuchia, Neosuchia and Eusuchia.

Incongruences between the two methods are not implausible and reflect incongruence in the source data. However, it is only through the application of a topological constraint that analyses of morphological data will return a topology which matches that of molecular analyses. With the application of a topological constraint, the supermatrix can return a topology of fossil taxa which matches that of combined morphological and molecular analyses. Tree likelihoods in the supermatrix, and the parsimony of subtrees in the source matrices, both agree that the supermatrix approach outperforms the supertree in representing character data, even when a topological constraint is applied.

Chapter 3: Tempo and mode of crocodylomorph body size evolution

Abstract: Climate change is a key factor impacting biodiversity, and Crocodylomorpha is an ideal clade for investigation since their distribution and size may be limited by temperature. The extant diversity of the Crocodylomorpha is surprisingly low for such an ancient clade, but they were much more diverse in the past and showed considerable variation in body size, from cat-sized Sphenosuchia to formidably large *Sarcosuchus.* Body size interacts with many factors, including environment, ecology, physiology and life history, making it an ideal test character for evaluating the tempo and mode of evolution. Phylogenetic comparative methods find that both body size and rates of body size evolution correlate significantly with temperature. An increase in crocodylomorph body size over the past 100 million years may superficially resemble Cope's rule, but is more likely an artefact of decreasing temperatures through the Late Cretaceous and Cenozoic. Rates of crocodylomorph body size evolution have increased, casting doubt over their status as 'living fossils,' or at least some interpretations of such slow-evolving clades. Crocodylomorph body size evolution may follow an Ornstein-Uhlenbeck process, being constrained by external factors to a phenotypic optimum. Crocodylomorph body size evolution is conservative and relatively static, interrupted by environmental change. This is consistent with punctuated equilibrium and the Court Jester hypothesis of macroevolution.

INTRODUCTION

The Crocodylomorpha might be described as something of an evolutionary failure. They are an ancient clade with origins in the Late Triassic (Clark 2002; Sues *et al.* 2003), and the crocodile body plan has existed since at least the Early Jurassic (Tykoski *et al.* 2002). However, their extant diversity isvonly 24 or so species. Other clades of similar antiquity, such as dinosaurs (including birds) and lepidosaurs (Jones *et al.* 2013; Nesbitt *et al.* 2013), have achieved diversities of tens of thousands of species in the same time interval (Jetz *et al.* 2012; Pyron *et al.* 2013). During the Mesozoic, the Crocodylomorpha were represented by a diverse array of species, including derived marine and terrestrial forms. By contrast, extant Crocodylomorpha all share a similar body plan and amphibious mode of life. This loss of diversity has led the extant Crocodylia to be branded 'living fossils' (Meyer 1984), implying they are a relict clade that has atrophied through a failure to adapt.

The term 'living fossil' has multiple definitions. The Crocodylomorpha certainly do not qualify as Lazarus taxa (Wignall *et al.* 1999), as they are well represented throughout their known fossil range. An alternative definition is that of bradytely (Simpson 1944), which describes a decline in rates of evolution. Bradytely as a hypothesis can be tested using phylogenetic comparative methods. Herrera-Flores *et al.* (2017) define a living fossil as a taxon that shows both below-average evolutionary rates and morphological conservatism, variables that can be also tested using phylogenetic comparative methods.

The relative importance of intrinsic ecological interactions and extrinsic environmental changes is a matter of ongoing debate. The Red Queen hypothesis (Van Valen 1979) suggests that evolution is driven by intrinsic factors, such as sexual selection, parasitism and the arms race between predators and prey. The alternative Court Jester hypothesis proposes that evolution is driven by episodic environmental shifts, such as those brought about by climate change, volcanism, bolide impacts and plate tectonics (Barnosky 1999).

Environmental change is of particular relevance to the Crocodylomorpha. Extant representatives are of course subject to anthropogenic climate change. Since the Late Triassic, the Crocodylomorpha have survived multiple dramatic environmental shifts. These include the end-Triassic and end-Cretaceous mass extinctions, the Palaeocene-Eocene Thermal Maximum, the end-Eocene extinction event, and cooling throughout the middle- and upper Cenozoic. The geographic range of the Crocodylia is limited by environmental temperature due to their ectothermic physiology (Markwick 1998). Isotope data has been widely used to measure global temperatures in deep time, and time series of mean temperatures can be compared with evolutionary metrics.

Two recent comparisons between crocodilian diversity and past temperature change found evidence that temperature drove their macroevolution, but there are statistical problems. Martin *et al.* (2014) found a relationship between the diversity of marine crocodylomorphs and sea surface temperature, but this relationship was not sustained in the Thalattosuchia. The phylogenetic correction applied to this analysis used a single topology and node dating scheme, so statistical relationships, or the lack of them, may be artefacts of tree branch lengths and the taxon sample was selective (Mannion *et al.* 2015). In their study, Mannion et al. (2015) used point occurrence data, so there was no consideration of phylogeny in their analyses, and the data may be especially susceptible to preservation bias due to fossil ghost ranges. This study also grouped taxa as marine or terrestrial rather than using phylogenetic grounds, which may conceal evolutionary patterns within separate clades. Using marine and terrestrial groupings may be something of an oversimplification, because amphibious taxa are placed among land-dwelling forms rather than other more comparable aquatic forms. In summary, there is a worthwhile study to be done in which crocodilian diversity through time is tested against temperature change, but appropriate phylogenetic comparative methods should be applied.

Phylogenetic approaches to diversification have identified dynamic evolution in crocodylomorphs (Bronzati *et al.* 2015). Diversification rate shifts occur near the base of the Crocodylomorpha, Crocodyliformes and Neosuchia during the Late Triassic and Lower Jurassic periods. Similar shifts are seen in the Metriorhynchidae and Goniopholididae in the Lower Cretaceous and in the Alligatoridae in the Palaeocene (Bronzati *et al.* 2015). However, the phylogeny of Bronzati *et al.* uses an informal combination of crown and stem phylogenies. The crown topology does not account for the alternative position of *Tomistoma schlegelii* resolved by analysis of molecular data (Oaks 2012).

Improvements in computer processing power, software development and data availability have enabled the rate and mode of phylogenetic hypotheses to be tested in a statistical framework (e.g. Zanno & Makovicky 2012; Sookias *et al.* 2012; Benson *et al.* 2014; Puttick *et al.* 2014). Phylogenetic comparative methods require character data in order to sample evolutionary change. Body size is commonly used as a test character in these analyses (Sookias *et al.* 2012; Benson *et al.* 2014; Puttick *et al.* 2014). Body size interacts with many variables including physiology, population size, resource consumption, geographic range, growth rates, life history, growth rates and reproductive success (Brown & Maurer 1986; LeBarbera 1989; Roy 2008; Cooper & Purvis 2010). Larger animals may be more vulnerable to extinction, requiring more food and taking longer to reach sexual maturity (Hone & Benton 2005). Cope's rule (Cope 1896) postulates that taxa inevitably evolve greater body size over time. However, more recent analyses have raised doubts about this long-standing rule as a possible statistical artefact (Hone & Benton 2005). Nonetheless, body size has advantages over other morphological characters in being applicable to all animals. Body size can be estimated from incomplete remains using proxies, and is therefore less vulnerable to taphonomic bias than taxic diversity.

This study will determine the tempo and mode of crocodylomorph body size evolution through time, using skull width as a proxy. Relative body size data are analysed using time-series and comparative phylogenetic methods to explore how phylogenetic history, Cope's rule and climate change were factors in crocodylomorph evolution.

MATERIALS AND METHODS

Relative body size can be estimated from incomplete fossil remains by using conservative characters as proxies. Commonly used body size proxies in fossil vertebrates are skull length (Therrien & Henderson 2010) and femur length (Benson *et al.* 2012; Sookias *et al.* 2012). These may not be suitable proxies for the Crocodylomorpha, because of the variance in skull and limb morphology of major subclades. Rostral elongation is one of the principal axes of variation among the extant Crocodylia (Pierce *et al.* 2009), as many taxa may have elongated skulls relative to body size. Likewise, derived Thalattosuchia have reduced limbs as an adaptation for swimming, and so femur length is also not representative of body size.

Skull width has been identified as a conservative character relative to body size in extant alligators and caimans (Verdade 1999; Platt et al 2009), and this relationship may be representative of the Crocodylomorpha generally. The validity of skull width as a proxy for relative body size was tested using a linear regression of skull width with body length. The primary literature was searched for images of Crocodylomorpha taken in dorsal view. A total of 16 specimens were identified with sufficient cranial and postcranial elements for skull width and body length to be measured (Supplementary information 2). Skull width was defined as distance between the quadrate bones at their widest point (Fig. 3.1). Body length was defined as the distance from the anterior-most cervical vertebra to the posterior-most sacral vertebra (Fig. 3.1). Skull and tail length were excluded from body length estimates to mitigate the effects of specific adaptations within crocodylomorph subclades. These distances were measured using ImageJ (Schneider *et al.* 2012). Where both skull and postcrania were featured in the same figure, distances were measured in pixels. Where the skull and postcrania were imaged separately, distance was measured in centimetres. The number of centimetres per pixel was used using scale bars in figures with the set scale tool in ImageJ. A simple linear regression of relative skull width to body length (Fig. 3.2) was performed using R (R core team 2014).

A larger dataset of skull widths was assembled using absolute distances. Skull width was measured for as many living and extinct crocodylomorphs as possible, based on images of skulls in dorsal view. Skull width was defined as twice the distance from the midline to the quadrate at its widest point on an axis perpendicular to the midline. The literature was searched for images of crocodylomorph skulls in dorsal view with scale bars (Supplementary information 2). Skull width was recorded using ImageJ (Schneider *et al.* 2012); the scale of pixels in the image was set using the scale bar, and then the width of the skull recorded in centimetres. Skull width was defined as twice the distance

Figure 3.1. Example of body length (left) and skull width (right) estimation from example specimens. Skull width is defined as twice the distance from the midline to the distal most point of the quadrate at its widest point. Image credits: Didier Descouens and Museum of Veterinary Anatomy, São Paulo.

from a complete quadrate bone to the midline of the skull (Fig. 3.1). The final skull width dataset was completed to species level, and contained 162 entries. The available data was limited to those specimens with skulls sufficiently complete for width to be estimated, so the final dataset was not comprehensive. Correcting for ontogeny is extremely difficult, especially in taxa which are represented by very few or single specimens. A further complication is that modern, and hence presumably also fossil, crocodylomorphs continue to grow beyond sexual maturity (Grigg 2015). Where there are multiple specimens of a given taxon, the largest specimen was chosen, since this is the specimen least likely to represent a juvenile. Specimens with apparent neonatal features were excluded from the dataset. All other specimens were assumed to be adults.

A time-series of relative body size was estimated by calculating mean skull width through time. The distribution of each taxon was determined using the tip lengths taken from a distribution of phylogenetic trees (Supplementary information 2). Each of the sampled trees was pruned to exclude tips not represented in the body size dataset. The taxa present in each 1-million-year time interval were determined by finding every branch of the tree corresponding

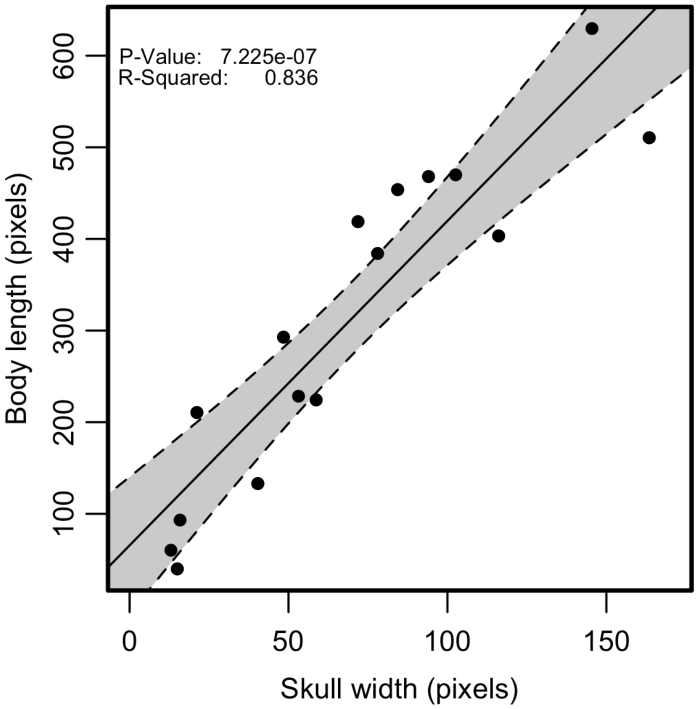

Figure 3.2. Linear regression of body length against skull width. Sixteen taxa were sampled using images sourced from the literature (See Appendix 3). 95% confidence interval shown in grey.

to a single species that had a node date equal to or preceding the interval being measured, and a tip date equal to or succeeding that interval. This novel approach circumvents some problems implicit in determining body size through time simply by the temporal range of fossils. An advantage of this approach is its inference of ghost ranges, time intervals where a taxon is predicted to be present by phylogeny, but in which fossil occurrences are not known. It is conceivable that body size represents a factor in preservation potential, since large skeletal elements might be expected to be more robust to decay and digenesis than smaller elements. Therefore it seems plausible that the representation of crocodylomorph taxa will become skewed towards larger examples in older time intervals. Variations in body size through time estimated using only fossil ranges could therefore be attributed to bias in the fossil record, rather than a true signal. Therefore the inference of ghost ranges through phylogeny may better represent the body size of smaller and older taxa in the dataset.

There are some caveats to using phylogenetic trees to determine the presence of taxa. In a phylogenetic tree, common ancestors can only be hypothetical. If any known fossil species is the true common ancestor of two later taxa, phylogeny will represent it as a sister taxon, potentially inflating ancestral diversity. The approach presented here circumvents this problem by only using tree tips, and not internal branches within the tree. Phylogenetic estimates of diversity are also vulnerable to missing data, and may infer the presence of taxa with long ghost ranges where there may be entire clades. However, this problem is also true of using raw fossil data. Determining the presence of taxa using phylogeny infers the presence of a descendant member of an underrepresented larger clade, and is arguably more representative than omitting it entirely. Another major limitation to phylogenetically-inferred diversity is that it can only infer ghost ranges within or prior to the known fossil range of a taxon. The extinction of a taxon cannot be inferred from its last appearance, and it is extremely likely that many taxa persist through time after their latest fossil representative. Therefore there is a future ghost range that the phylogenetic tree cannot infer. However, this is another caveat that is shared by raw fossil diversity. The approach used here is novel in using phylogeny to infer body size through time. This approach does not factor in anagenesis, in which body size can change within a branch. This is not realistic, since evolutionary change is not instant. However, this is a problem in common with raw fossil data. If a single body size value is extrapolated throughout a fossil range, an assumption is made that the body size value does not change. This is especially true if a taxon is known from only a small number of specimens that are only dated to stage level. Using multiple specimens offers no solution, as variation between individuals is not necessarily a result of anagenesis. It is certainly true that inferring body size through time using a phylogeny, as presented here, has its limitations. However, it is a more conservative approach than using only fossil range data, which is vulnerable to the decay of the fossil record.

For the analysis presented here, trees were taken from the supermatrix analysis performed in chapter 1, with the crown-group topology constrained to that of the molecular analysis by Oaks *et al.* (2012). All trees sampled by this analysis were used. This analysis was selected due to its higher support from the

MK model relative to the supertree analysis, and its more parsimonious topology overall with respect to the original source matrices. The application of the constraint forces the analysis to be congruent with analyses of molecular data.

These trees were each dated using the cal3 method implemented using the PaleoTree package for R (Bapst 2017). The trees were dated to a maximum resolution of 1 million years, as this is a widely used unit of time throughout the literature and the Paleobiology Database (pbdb.org). The cal3 method was selected to estimate branch lengths and node dates as it factors in sampling, diversification and extinction rates. These rates were also estimated using the PaleoTree package. It is arguably more realistic than tree dating methods that limit branch lengths to the first- and last- appearance dates of fossils, especially in cases where taxa are known from very few specimens. It also represents an advantage over the equal method, which increases the age of divergence points in the tree to reapportion time equally across branches. The cal3 method has been shown to give greater precision than the Hedman method (Lloyd *et al.* 2016) and can be applied to large numbers of trees in a practical time frame. The tip date was set to a random point between the first- and last- appearance date. This dating procedure was repeated 10 times for each of the 93 trees in the sample, giving a final set of 930 dated trees. Attributing first- and last-appearance dates to vertebrate taxa is extremely difficult, since many are known from extremely few, or even single, specimens. Crocodylmorph taxa in this study (Supplementary information 2) were dated to stage-level resolution. Stratigraphic stages bearing remains were recovered from the Paleobiology Database (pbdb.org). These stages were then used to find a first- and last- appearance date using the International Chronostratigraphic Chart (Cohen *et al.* 2017).

A time-series distribution of taxa was assembled for each of the 930 trees. Distribution of body size through time was analysed using a linear regression (Table 3.1). Time was represented as a descending scale of positive integers, with values increasing with age. The body-size-through-time curves corresponding to each sampled phylogeny were analysed separately. Model outputs are shown in the supplementary information (Supplementary information 2). Multiple data points were included for each 1-million-year time interval to correspond to body size measurements for each crocodylomorph species present in that interval. This analysis was repeated using an alternative temperature variable (Table 3.1), with mean body size analysed relative to a published $\delta^{18}O$ time series (Prokoph *et al.* 2008). This is a summary palaeotemperature curve including data from planktonic and benthic calcifying marine organisms. It represents the most comprehensive available palaeotemperature curve available, extending throughout the Mesozoic and Cenozoic eras. This study includes multiple $\delta^{18}O$ values for each one million year time bin. In order to reduce the resolution of the curve to the same 1-million-year resolution as the body size curve, a mean $\delta^{18}O$ value was calculated from every value within 1 million year increments. Where there were gaps of more than 1 million years in the temperature curve, the corresponding body size data from the same time interval were omitted from the analysis. As for the time-series analysis, multiple data points were included for each 1-million-year time interval, to correspond to each crocodylomorph species present in that interval. A log-likelihood value was recovered from each model, for comparison using log-likelihood ratio tests. A Shapiro-Wilk test was implemented on the residuals of each linear model to check for a normal distribution. The residuals seem to show a normal distribution. Further, irregularities in the distribution of residuals appear to be driven by outliers not obviously representative of an overall trend. The output statistic of each analysis is tabulated in the supplement (Supplementary Information 2).

The linear analyses were repeated for three key subgroups of the Crocodylomorpha (Table 3.1). These subgroups were identified on ecological grounds, reflecting terrestrial, marine and freshwater modes of life (supplementary information). Since the distribution of taxa through time was defined using phylogeny, monophyly of these groups was a prerequisite so that ghost ranges could be reconstructed as accurately. The terrestrial crocodylomorphs sampled from the tree included all those taxa descending from the common ancestor of *Notosuchus* and *Kaprosuchus.* In the context of the tree used in this analysis, this phylogenetic definition approximates to the Notosuchia and Peirosauridae, including the Mahajangasuchidae. These taxa are mostly assigned a terrestrial mode of life, with the exception of *Trematochampsa*, which may have been partially aquatic (Rogers *et al.* 2007). The marine crocodylomorphs sampled from the tree included all those taxa descending from the common ancestor of *Metriorhynchus* and *Atlantosuchus*. Of the taxa represented in the tree, this corresponds to a monophyletic group comprising the Tethysuchia and Thalattosuchia. The Thalattosuchia are found in exclusively marine sediments (Supplementary Information 2). Most Tethysuchia are found in marine and estuarine sediments, but in the sampled tree there are two exceptions from non-marine sediments, *Sarcosuchus* and *Elosuchus* (Supplementary Information 2). Freshwater members of the Crocodylomorpha were defined as all those taxa descending from the common ancestor of *Calsoyasuchus* and *Crocodylus*. This group corresponds to all members of the Goniopholididae, Paralligatoridae and Eusuchia. The depositional setting of taxa in each group according to the PaleoBiology Database is presented in the Supplementary information.

Each sampled supermatrix phylogeny was tested for goodness of fit of five phylogenetic models using body size as a continuous character (Table 3.2). The models tested were Brownian motion, Ornstein-Uhlenbeck (OU), early burst, directional trend and white noise models, implemented in the geiger package for R (Harmon *et al.* 2016). The Brownian motion model was implemented as a null hypothesis. Brownian motion represents a random walk, with character states free to transition in any direction within morphospace. It does therefore retain an element of phylogenetic signal, making it more realistic than purely random signal. The early burst model may be favoured if the Crocodylomorpha or its subclades underwent an adaptive radiation, as proposed by Brochu (2001), Stubbs *et al.* (2013) and Toljagic & Butler (2013). The trend model may be favoured if Cope's rule has a significant impact, or if evolution has been driven by environmental change over time. The white noise model represents evolutionary stasis, where evolutionary rates remain constant. The stasis model may reflect the relative antiquity and lack of disparity of extant crocodylomorphs. The OU model is similar to the Brownian motion model, but it has an additional parameter that applies force within an axis of morphospace. This force increases with distance from an optimum value, in effect pulling aberrant character states back towards this value over time. This force parameter within the OU model can represent extrinsic variables that limit evolutionary change.

Concerns have been raised about the susceptibility of the OU model to false positive results, it being difficult to distinguish from the Brownian motion model (Thomas *et al.* 2014, Cooper *et al.* 2016). Cooper *et al.* (2016) warn that error propagation increases the likelihood of the OU model being falsely favoured over the BM. These findings were considered in the context of fossil data by Benson *et al.* (2017) in an analysis of body size evolution in dinosaurs. Error propagation was a particular obstacle to Benson *et al.* (2017), since they used regression analysis of a body size proxy to amplify a dataset of body mass estimates. The proxy used was femoral and humeral circumference, which is appropriate for terrestrial dinosaurs with an erect posture. Benson *et al*. (2017) used simulation approaches to calculate the total error propagated through multiple iterations of regression analysis. A problem with the approach in Benson *et al*. (2017) is their assumption that limb dimensions were normally distributed among adults, and does not take into account the possibility of sexual dimorphism. However, Benson *et al.* (2017) did support their findings with the extent of the α-parameter returned by the Ornstein-Uhlenbeck model, which differed markedly from the low value returned by a Brownian Motion model (Benson *et al.* 2017). The analysis presented here avoids the propagation of error to some extent through the use of skull width as a single proxy rather than systematic estimates of mass. Unlike dinosaurs, long bone circumference has not yet been demonstrated to be an effective estimate of crocodylomorph body size. The Crocodylomorpha vary between terrestrial, amphibious and marine ecomorphologies, and also between erect and semi-erect walking posture. Therefore, the biomechanical relationship between body size and the dimensions of limb bones in the group as a whole is not straightforward. This is especially true in marine forms constrained by buoyancy, and in cursorial forms subject to different biomechanical constraints from extant crocodylians. Therefore in this study the most cautious approach is to define skull width as a direct indicator of body size.

The phylogenetic models were fitted to a random sample of 200 trees from the dataset of 930. These models use ancestral state reconstructions to determine the trajectories of character states through time. The analyses were implemented on a sample for pragmatic reasons, in order to complete the analysis in a workable timeframe but represent a diversity of both topology and tree dating schemes. Since the sample of undated trees numbered 93, a sample of 200 trees will include each topology at least twice. Further, since the trees used in the analysis represented a sample of taxa corresponding to those with complete skulls, each of the 93 trees can be expected to show greater overall congruence than the complete supermatrix trees. The analyses were repeated with each of the ecological groups specified for the linear analyses, corresponding to monophyletic groups of terrestrial, marine and freshwater taxa. Models were also fitted to subtrees of each supermatrix tree corresponding to major named groups, specifically the Mesoeucrocodylia, Neosuchia and Eusuchia.

The goodness of fit of each phylogenetic model was examined through the returned a log-likelihood values (Table 3.3). The log-likelihood values of non-random models were each compared to that of the Brownian motion model of the same phylogenetic tree using a log-likelihood ratio test. The extent of support from each model was illustrated by calculating an AIC score from the mean log-likelihood values of each model. These AIC scores were then scaled as AIC weights, which were then plotted as pie-charts to show relative support for each model (Figure 3.6).

In addition to reconstructing character state trajectories, phylogenetic comparative approaches allow the estimation of evolutionary rates. One method of representing evolutionary rates through time is through the calculation of phylogenetically independent contrasts (PICs) according to the methodology of Felsenstein (1985). This approach returns a value of character contrast for each node of a phylogenetic tree. Regression analyses of PICs against time are sometimes referred to as a node height test (Benson *et al.* 2014). A regression analysis of crocodylomorph PICs against time was performed on the assembled body size data using Geiger (Table 3.4). In this analysis time was denoted by node height, or the distance in millions of years between a given node and the tree root. Therefore time is an ascending scale with the time value increasing over time. A potential caveat of this method is that it assumes that morphological diversity has arisen exclusively in a cladogenic manner, which is not realistic since anagenesis must also have played a role.

Table 1. Mean outputs from 930 replicates of linear model analyses of body size in crocodylomorphs and 4 subgroups, tested against time and temperature. Normalcy is represented by the Shapiro-Wilk statistic.

	Mean p-value	Mean r-squared	Mean Slope	Mean Log-likelihood	Mean residual normalcy
Crocodylomorph body size vs. time	0.0000	0.0910	-1.1099	-9008.145	0.9698
Terrestrial body size vs. time	0.0000	0.2737	-0.8362	-765.0619	0.9750
Marine body size vs. time	0.0005	0.1415	-0.8799	-795.4437	0.9206
Freshwater body size vs. time	0.0000	0.0499	-0.4986	-4494.977	0.9288
Crocodylomorph body size vs. temperature	0.0125	0.0091	0.0067	-2465.742	0.9845
Terrestrial body size vs. temperature	0.0045	0.0768	0.0235	-224.2608	0.9346
Marine body size vs. temperature	0.0007	0.1008	0.0299	-269.3592	0.9808
Freshwater body size vs. temperature	0.1230	0.0049	0.0036	-1218.215	0.9822

Table 2. Likelihood and OU parameters returned by fitting of 5 phylogenetic models. Values presented here are an average based on 200 replicates.

	Brownian Motion	Early Burst	Directional Trend	Stasis	Ornstein - Uhlenbeck	OU α	OU optimum
Crocodylomorpha	-804.918	-804.924	-781.314	-676.779	-678.145	2.718	18.51
Mesoeucrocodylia	-733.127	-732.96	-732.827	-640.445	-639.355	1.566	19.394
Neosuchia	-611.676	-610.795	-612.873	-537.512	-536.21	1.235	20.673
Eusuchia	-457.919	-457.921	-427.588	-330.719	-337.804	2.717	20.669
Freshwater	-472.871	-472.873	-458.374	-399.434	-399.529	2.464	19.972
Marine	-128.24	-127.626	-127.534	-125.078	-124.199	0.697	24.228
Terrestrial	-92.319	-92.319	-91.466	-87.958	-87.6	0.601	13.535

Table 3. P-values returned by log-likelihood tests comparing each phylogenetic model with that of the Brownian motion model.

	OU	EB	Trend	Stasis
Crocodylomorpha	0	1	0	0
Mesoeucrocodylia	0	0.563	0.438	0
Neosuchia	0	0.184	1	0
Eusuchia	0	1	0	0
Freshwater	0	1	0	0
Marine	0.004	0.268	0.235	0.012
Terrestrial	0.002	1	0.192	0.003

To circumvent this problem the analysis was applied to a distribution of equally possible topologies and dating schemes. The analysis was performed on all 930 trees in the sample, and repeated for each of the monophyletic groups corresponding to terrestrial, marine and freshwater modes of life specified above. The outputs of each of these linear models are given in Supplementary Information 2. A similar analysis was performed using PICs and relative temperature, substituting the time variable in the previous analysis for $\delta^{18}O$ in corresponding time bins (Table 3.4). Once again this analysis was performed using all the sampled trees, and repeated on the ecological subgroups.

A variable rates analysis of body size evolution was implemented using Bayestraits (Pagel & Meade 2006, www.evolution.rdg.ac.uk). The analysis was implemented on the single tree, derived from the supermatrix tree with the highest MK-model likelihood as demonstrated in Chapter 2. This tree was pruned to include only those tips corresponding to the available skull width data, and dated using the Cal3 method as before. The phylogeny and body size data were tested using models of homogeneous and heterogeneous rates of evolution (Table 3.5). Each model was run for 10,000,000 iterations, sampled at 1,000,000 iteration intervals, with a burn in of 2,500,000. The favoured model was indicated using a log Bayes factor, or twice the difference in log-likelihood between the two models (Gilks *et al.* 1996). The profile of log-likelihood values was checked for a level distribution to indicate convergence. Output from the heterogeneous rates model was submitted to the Bayestraits online postprocessing tool to calculate scalars for evolutionary rate on each edge of the phylogeny. These scalars were mapped onto the tree using the Phytools (Revell 2017) package for R.

Evolutionary rates through time were plotted using the same approach as body size through time. Taxa present in each time bin were determined using each of the 930 trees in the sample, as implemented in the body size through time analysis (Supplementary information). The rate of each of the taxa present was represented by the scalar output from the variable rates analysis. A series of linear regression analyses was implemented to compare the mean evolutionary rate with time in millions of years, with one analysis per time distribution of taxa (Table 3.6).

Table 4. Mean outputs from 930 replicates of linear model analyses of phylogenetically independent contrasts (PIC) in crocodylomorphs and 4 subgroups, tested against time and temperature.

	Mean p-value	Mean r-squared	Mean slope	Mean log-likelihood	Mean residual normalcy
Crocodylomorph PIC vs. time	0.0001	0.0974	2.6003	-909.9252	0.9439
Terrestrial crocodylomorph PIC vs. time	0.1277	0.1015	3.3540	-103.8638	0.9566
Marine crocodylomorph PIC vs. time	0.4744	0.0268	1.7639	-148.5941	0.8179
Freshwater crocodylomorph PIC vs. time	0.0011	0.1188	1.7631	-504.9853	0.8929
Crocodylomorph PIC vs. temperature	0.0002	0.1004	0.0444	-217.7846	0.9721
Terrestrial crocodylomorph PIC vs. temperature	0.1339	0.1524	0.2007	-26.5066	0.8933
Marine crocodylomorph PIC vs. temperature	0.7100	0.0106	-0.0058	-43.8693	0.8998
Freshwater crocodylomorph PIC vs. temperature	0.0006	0.1409	0.0435	-132.5013	0.9599

Table 5. Log-likelihood of Heterogeneous and Homogeneous rate models implemented using Bayesian phylogenetic modelling.

	Log-likelihood
Heterogeneous rate model	-611.655056
Homogeneous rate model	-686.591488

Table 6. Mean outputs from 930 replicates of linear model analyses of evolutionary rates returned by a Bayesian variable rate model of crocodylomorph body size evolution and 4 subgroups, tested against time and temperature.

	Mean p-value	Mean r-squared	Mean slope	Mean log-likelihood	Mean residual normalcy
Crocodylomorph evolutionary rate vs. time	0.000	0.034	0.084	-9059.751	0.954
Terrestrial crocodylomorph evolutionary rate vs. time	0.000	0.090	0.632	-786.935	0.963
Marine crocodylomorph evolutionary rate vs. time	0.003	0.158	0.152	-792.040	0.836
Freshwater crocodylomorph evolutionary rate vs. time	0.003	0.030	0.042	-4504.570	0.909
Crocodylomorph evolutionary rate vs. temperature	0.003	0.012	0.001	-2463.453	0.984
Terrestrial crocodylomorph evolutionary rate vs. temperature	0.038	0.042	0.023	-227.858	0.924
Marine crocodylomorph evolutionary rate vs. temperature	0.000	0.186	0.007	-260.736	0.972
Freshwater crocodylomorph evolutionary rate vs. temperature	0.008	0.013	0.001	-1214.735	0.982

A second series of regression analyses was run comparing mean evolutionary rate through time with temperature (Table 3.6) using a mean $\delta^{18}O$ curve (Prokoph *et al.* 2008). Both time and temperature analyses through time were repeated using subgroups representing terrestrial, marine and freshwater clades (Table 3.3.6).

RESULTS

Linear regression of skull width and body length identified a strong positive correlation, with values of $P = 7.2 \times 10^{-7}$ and $R^2 = 0.83$ (Fig. 3.2). This shows that skull width is conservative with respect to body size, with 83% of skull shape variation being accounted for by body size, which is consistent with analyses of relative skull width in extant Crocodylia (Verdade 1999; Platt et al 2009). It is therefore valid to use skull width as a proxy for relative body size in crocodylomorphs.

The time series plot showing log maximum, minimum and mean body size (Fig. 3.3A, 3.4A, 3.5A, 3.6A) shows considerable variation in any time bin, but a statistically significant long-term rise from the Jurassic to the present day. Regression analysis identified a highly significant relationship between body size and both time and temperature (Table 3.1). All iterations of the analysis found values of $P < 0.05$. This is true for the total-group Crocodylomorpha as well as the terrestrial, marine and freshwater groups analysed separately. Regression of body size with time returned negative values of slope. On a descending time scale, this shows that crocodylomorph body size has increased over time. Regression of body size with temperature found positive values of slope (Fig. 3.7), demonstrating increased body size is associated with more positive $\delta^{18}O$ values, indicating a cooling climate. This relationship between temperature and body size is observed among the Crocodylomorpha and all the tested subclades (Fig. 3.7). The R-squared values returned by regression analyses using temperature are smaller than those returned by analyses where time is the independent variable. This implies that time is a better explanatory variable for body size than temperature. However, the R-squared and P-value summary

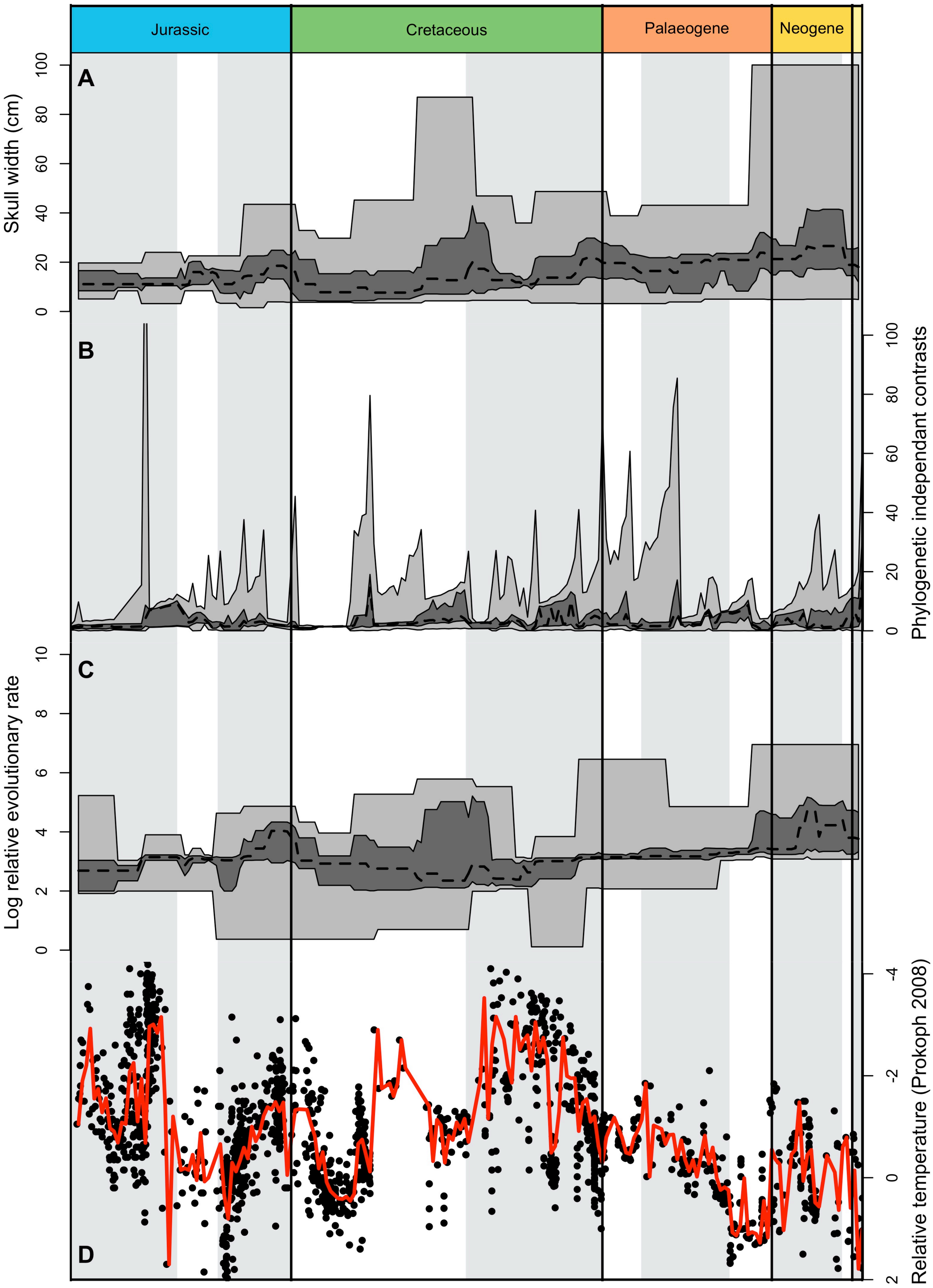

Figure 3.3. Time-series distribution of **A.** Crocodylomorph body size, **B.** Crocodylomorph phylogenetically independent contrasts, **C.** Crocodylomorph relative rate of skull width evolution and **D.** temperature (Prokoph *et al.* 2008). Light grey shows the total data range, dark grey the data variance.

statistics returned by a linear regression are functions of sample size. Since the sample size is dictated by the 1 million year resolution of this analysis, the sample size is therefore arguably self-selected and should be considered with caution. A more conservative approach is to compare the log-likelihood values returned by each model. In contrast to the R-squared and P-value statistics, the log-likelihood values of the models using temperature as a dependent variable were higher than those models using time. Log-likelihood ratio tests returned a p-value of 0 for the higher-scoring models, demonstrating that temperature is a much better explanatory variable for body size than time.

Analyses of phylogenetic independent contrasts with time and temperature returned more variable results. PIC values are shown to increase over time (Fig. 3.3B, 3.4B, 3.5B, 3.6B). A significant relationship between time and PIC value was found among the Crocodylomorpha, and the freshwater forms including the Goniopholididae, Paralligatoridae and Eusuchia (Table 3.5). Terrestrial and marine clades did not return a significant relationship between PIC and time (Table 3.4). On average, analyses of PIC against time universally returned positive slope values, indicating that rates of crocodylomorph evolution are not slowing down. However, some iterations of the analysis of marine crocodylomorph PIC values through time did return negative values of slope, apparently depending upon the dating scheme of the tree. Analyses of PIC values with temperature returned a similar result (Table 3.4), with a significant relationship being identified among the Crocodylomorpha as a whole and the freshwater forms, but not in terrestrial or marine forms (Table 3.4). The r-squared values returned by the analyses using temperature were higher than those returned by the analyses using temperature, with the exception of the marine Tethysuchia and Thalattosuchia. Log-likelihood values returned by the models of PIC against temperature were also higher than those of models of PIC against time for all the groups tested. Log-likelihood ratio tests of these values gave the higher-scoring temperature models a p-value of 0, strongly indicating that temperature is a better predictor of evolutionary rate than time.

Body size trajectories of Crocodylomorpha cannot be explained by a Brownian motion model. Body size evolution shows significantly greater support for the stasis model in the Crocodylomorpha and all the subclades tested (Fig.

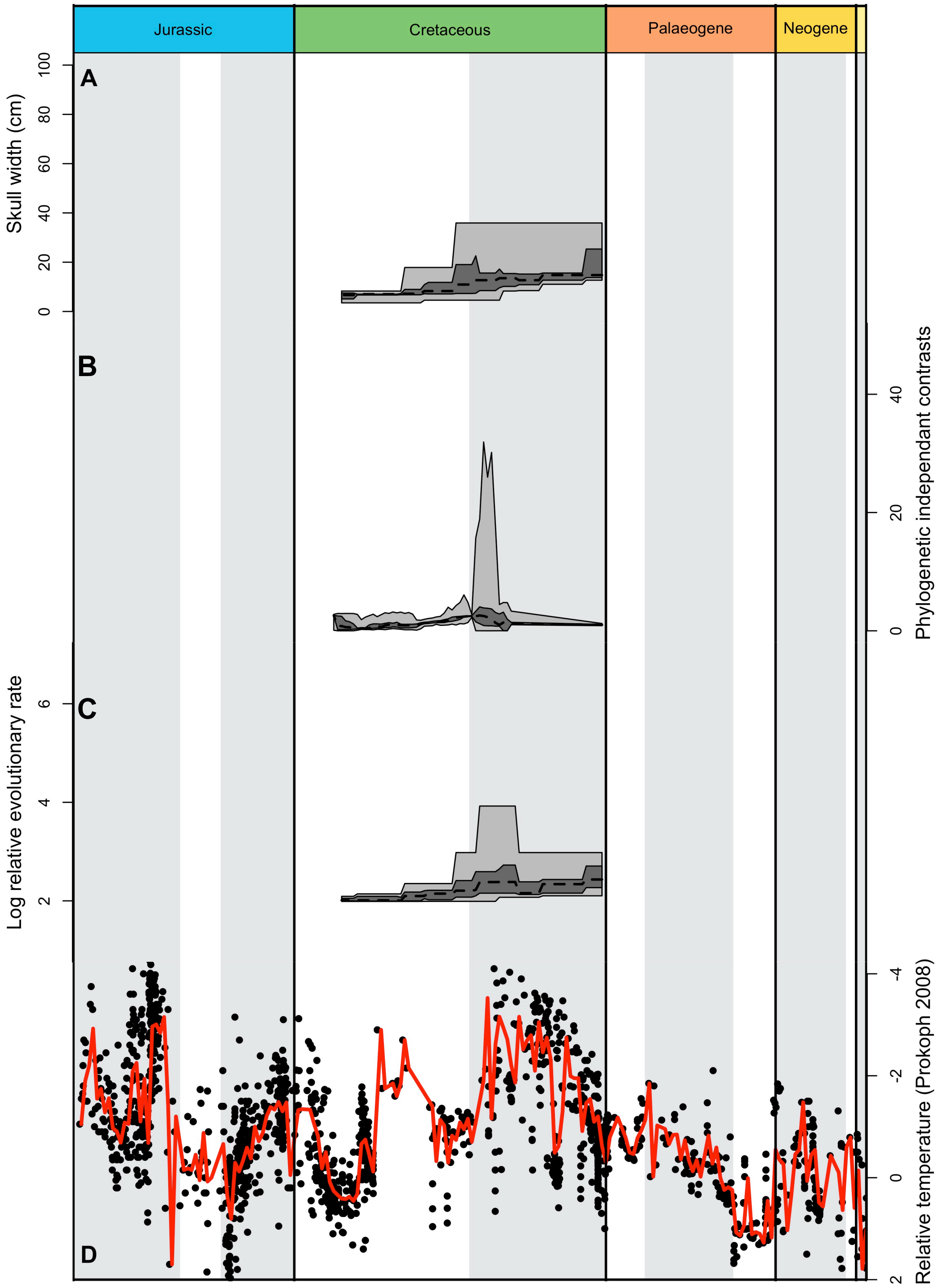

Figure 3.4. Time-series distribution of **A.** Terrestrial crocodylomorph body size, **B.** Terrestrial crocodylomorph phylogenetically independent contrasts, **C.** Terrestrial crocodylomorph relative rate of skull width evolution and **D.** temperature (Prokoph *et al.* 2008). Light grey shows the total data range, dark grey the data variance.

3.9, Table 3). The stasis model had the greatest AIC weight of all the models tested on the Crocodylomorpha, Eusuchia, combined Notosuchia and Peirosauridae, combined Tethysuchia and Thalattosuchia and combined Goniopholididae, Paralligatoridae and Eusuchia. The Ornstein-Uhlenbeck model performed significantly better than Brownian motion in all the clades tested (Table 3.3). The OU model return an alpha parameter of more than 1 when applied to most of the clades tested, with the exception of the combined Tethysuchia and Thalattosuchia, and combined Notosuchia and Peirosauridae (Table 3.2). Groups returning an alpha of more than 1 identified an optimum skull width of between 18.5 cm and 20.7 cm (Table 3.2). The OU model returned the highest AIC weight of all the models tested on the Mesoeucrocodylia and the Neosuchia (Fig. 3.9). The trend model outperformed the Brownian motion model in representing the body size evolution of the Crocodylomorpha, of the combined Goniopholididae, Paralligatoridae and the Eusuchia, and of the Eusuchia. The AIC weight of the trend model was negligible in the clades where it performed significantly better than the Brownian motion model (Fig. 3.9). The early burst model did not perform significantly better than the Brownian motion model in explaining body size evolution in any of the clades tested (Table 3.3).

The output likelihood values of the heterogeneous rates model follow a uniform distribution, indicating that the analysis converged successfully (Fig. 3.10). The heterogeneous rate model returned a higher log-likelihood than the homogeneous rate model (Table 3.5). The difference in log-likelihood returned by homogeneous and heterogeneous rate models was 73. This presents a Bayes factor of 146. This indicates much stronger support for the heterogeneous rate model in the data than the homogeneous rate model. The lowest evolutionary rates are seen in the most basal taxa and in more inclusive branches (Fig. 3.11). Higher evolutionary rates are observed in the Elosuchidae, the common ancestor of the Goniopholididae, and among the crown-group Caimaninae. Very high rates are also observed in large-bodied species of Crocodylidae, specificially *Crocodylus thorbjarnarsoni, Thoracosaurus* and *Eothoracosaurus.*

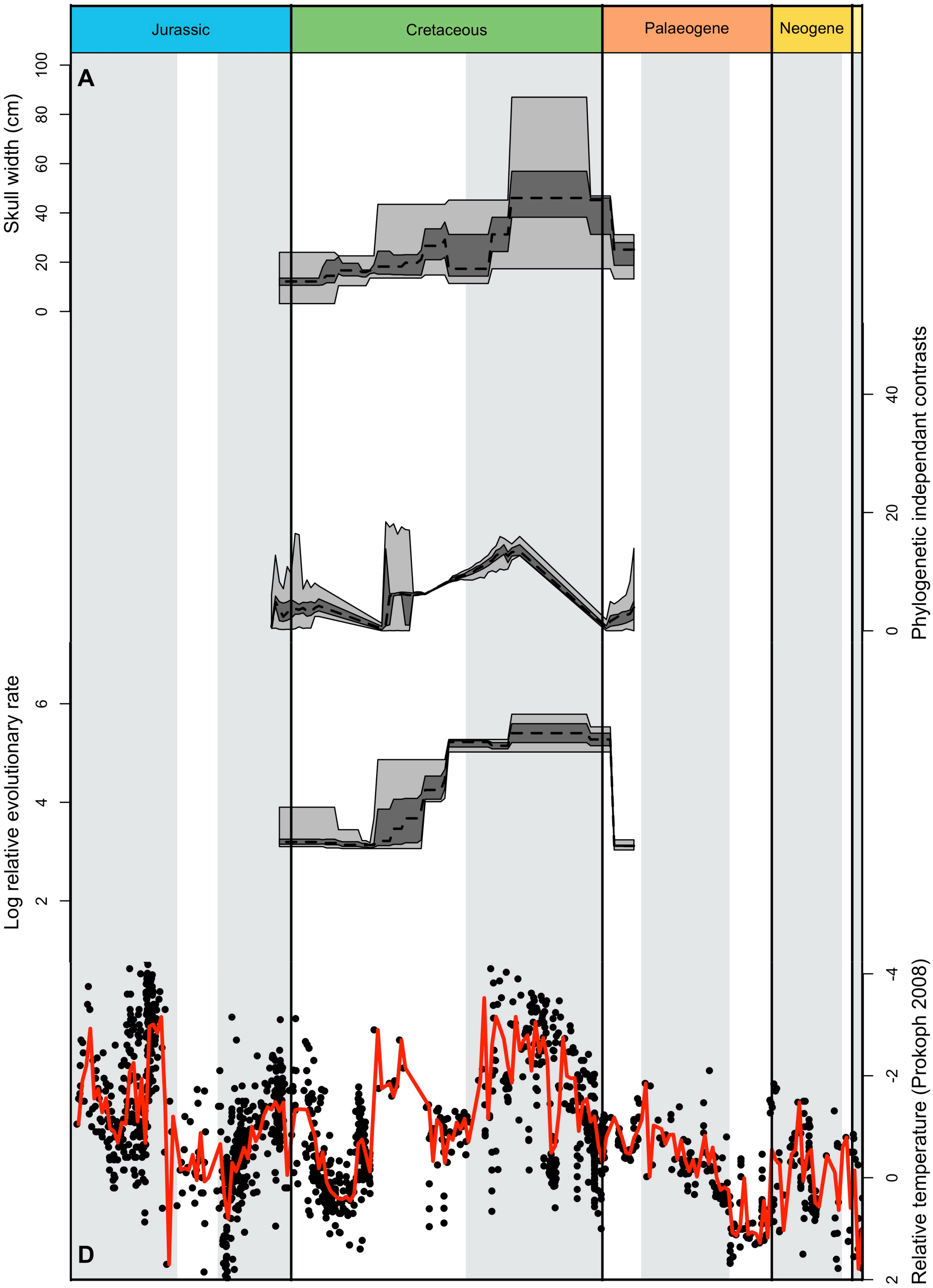

Figure 3.5. Time-series distribution of **A.** Marine crocodylomorph body size, **B.** Marine crocodylomorph phylogenetically independent contrasts, **C.** Marine crocodylomorph relative rate of skull width evolution and **D.** temperature (Prokoph *et al.* 2008).

Rates of skull width evolution returned by the heterogeneous rates model show an increase over time (Fig. 3.3C, 3.4C, 3.5C, 3.6C). Regression of rates of skull width evolution returned by the heterogeneous rates model against time found a significant relationship in all the clades tested (Table 3.6). The slope value returned by these analyses was negative (Table 3.6). On the descending scale used in this analysis, a negative relationship indicates an increase in evolutionary rates over time. Regression analysis of evolutionary rate against temperature also identified significant relationships in all the groups tested (Fig. 3.12). The r-squared values returned by the analyses including temperature were lower than for the analyses where time was the independent variable (Table 3.6). However, the log-likelihood values of analyses with temperature as an independent variable were higher than those where time was used. Log-likelihood ratio tests comparing the two model types consistently found the models including temperature to be more effective, returning a p-value of 0.

DISCUSSION

The Crocodylomorpha and all the subclades tested show a clear increase in body size over time (Fig. 3.3A, 3.4A, 3.5A, 3.6A). This is consistent with qualitative observations of the fossil record. The earliest Crocodylomorpha are small; for example the Sphenosuchia are generally around 1 m in length (Wu & Chatterjee 1993; Sues *et al*. 2003). Very large crocodylomorphs such as *Gryposuchus croizati* (Riff *et al.* 2008)*, Purussaurus brasiliensis* (Aguilera *et al.* 2006)*, Crocodylus thorbjarnarsoni* (Brochu & Storrs 2012) and the extant *Crocodylus porosus* occur more commonly in the later Cenozoic. Very large crocodylomorphs from the Mesozoic such as *Machimosaurus rex* (Fanti *et al.* 2016), *Deinosuchus rugosus* (Colbert *et al.* 1954) and *Sarcosuchus imperator* (Sereno *et al.* 2001) are exceptional and are not representative of the mean body size at the time. A trend towards increased body size could be interpreted as an example of Cope's rule (Cope 1896). However, numerous concerns have been raised about the validity of this supposed rule (Hone & Benton 2005), with some studies finding it to be a statistical artefact (Jablonski 1997) or even a psychological artefact on the part of the researcher (Gould 1997). Further, the increase in size over time observed in

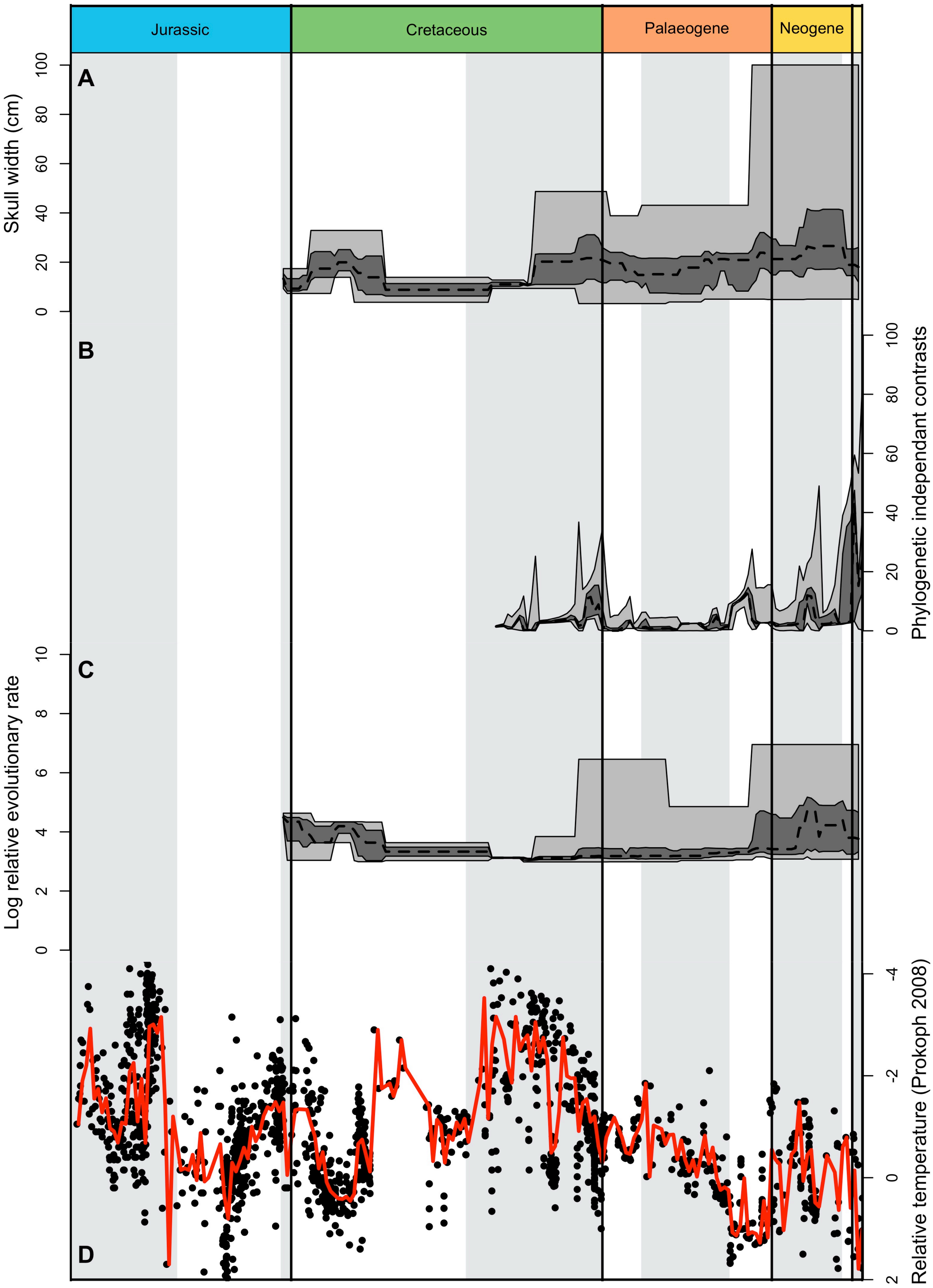

Figure 3.6. Time-series distribution of **A.** Freshwater crocodylomorph body size, **B.** Freshwater crocodylomorph phylogenetically independent contrasts, **C.** Freshwater crocodylomorph relative rate of skull width evolution and **D.** temperature (Prokoph *et al.* 2008).

the Crocodylomorpha is not uniform, with episodic peaks and subsequent declines in body size through time. Cope's rule would imply substantial support for a trend model of body size evolution. The trend model performs significantly better than the Brownian motion model among some crocodylomorph clades, however the relative weight of this model compared to the others tested is negligible (Fig. 3.9). Support for the trend model was not universal to the subclades tested, being significantly better than the Brownian motion model only in the Eusuchia and combined Goniopholididae, Paralligatoridae and Eusuchia. Therefore, the support for the trend model among the total-group Crocodylomorpha may be driven by freshwater taxa rather than representing a group-wide trend. The interactions between body size, rates of evolution and temperature suggest examples of Cope's rule may be driven by external selective pressures rather than a spontaneous trend. This is consistent with the findings of other studies using a comparative phylogenetic approach. Analyses by Sookias *et al.* (2012) suggested an increase in dinosaur body size through time represented a passive shift rather than an active trend.

There is a significant positive correlation between mean body size and $\delta^{18}O$ values. The r-squared value returned by these analyses is stronger than that for time, however as noted previously the r-squared statistic changes with sample size, and in this instance the sample size is self-selected. This relationship is found among the Crocodylomorpha and all the subclades tested. The higher log-likelihood of models using temperature strongly supports temperature as a better predictor of body size than time. A relationship between crocodylomorph evolution and climate has more consistent support in the literature than does Cope's rule (Markwick 1998; Martin *et al.* 2014; Mannion *et al*. 2015). Therefore, the apparent increase in body size is likely to be an indication of decreasing temperatures since the Mesozoic. Increased body size as an adaptation to cooler temperatures, known as Bergman's rule, is well documented (e.g. Brommer *et al.* 2014; Scriven *et al.* 2016; Torres-Romero *et al.* 2016). Increased body size reduces relative surface area, improving the retention of body heat by limiting radiative heat loss. Retention of body heat is critical for ectothermic crocodylomorphs that are unable to generate body heat of their own. The possibility of endothermy among basal crocodylomorphs is a subject of ongoing

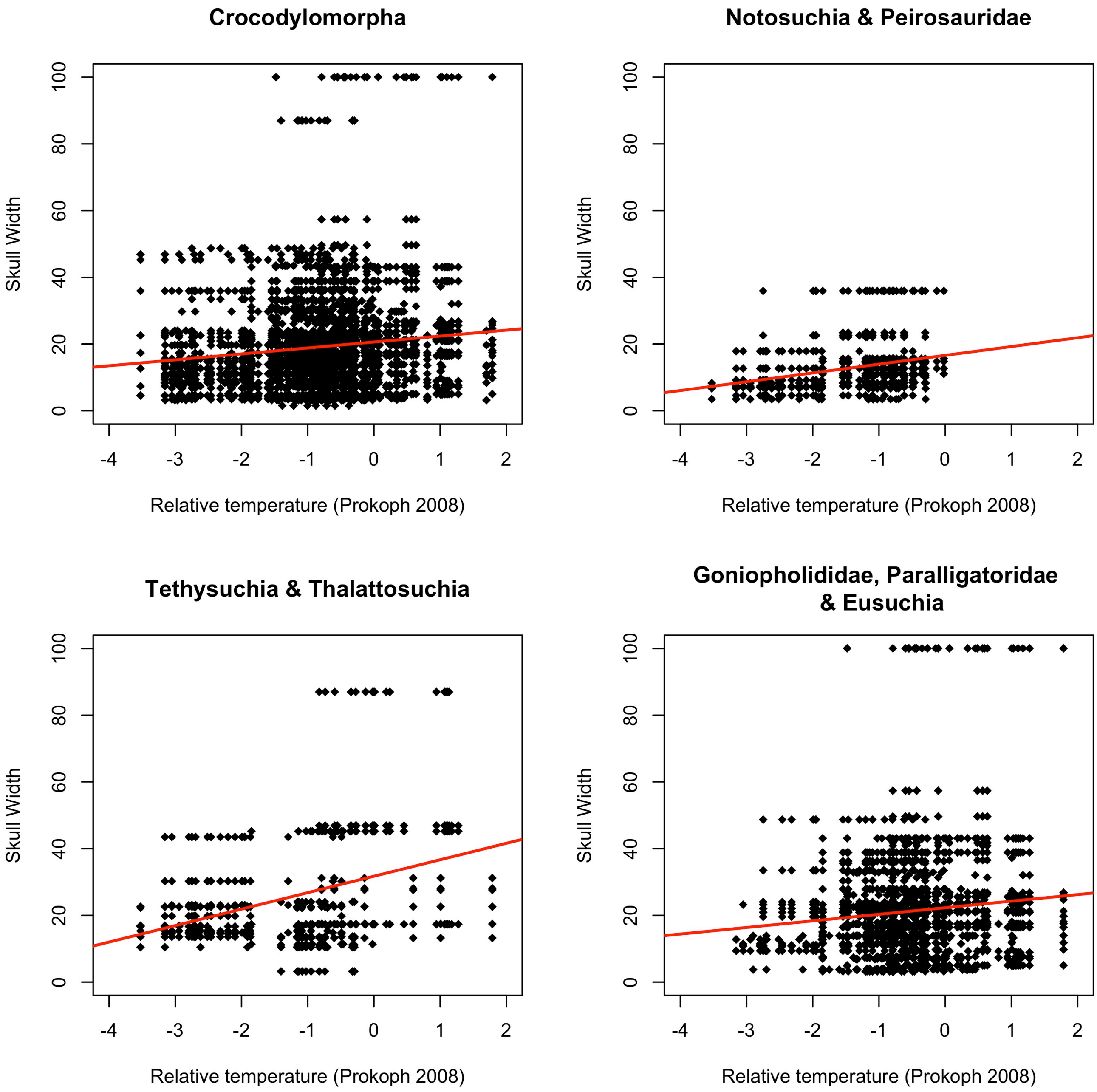

Figure 3.7. Distribution of skull width measures relative to the corresponding temperature for each time-bin in the Crocodylomorpha and three monophyletic subclades.

discussion (Seymour 2004; Martin *et al.* 2014), but this does not preclude a relationship between body size and temperature. Furthermore, there is not sufficient evidence to conclude that temperature is the only driver of crocodylomorph body size evolution.

The stasis model was found to be the best-performing phylogenetic model of body size evolution in all the clades tested, with the exception of the Mesoeucrocodylia and the Neosuchia (Fig. 3.9). Log-likelihood ratio tests confirmed that this improvement in model fit was statistically significant, and the relative AIC weight of these models was greater than the other models tested. Support for the stasis model confirms the versatility of the crocodylomorph body plan, since rapid changes in body size have not been required. In addition, the stasis model offers a possible reason for the low morphological disparity in the crown-group Crocodylia.

Log-likelihood ratio tests find the Orstein-Uhlenbeck model to significantly outperform the Brownian motion model as a predictor of crocodylomorph body size evolution. AIC weights of the models tested showed that the OU model was the best performing model overall in the Mesoeucrocodylia and Neosuchia (Fig. 3.9). Support for an Ornstein-Uhlenbeck model of body size evolution is in line with the regression analyses of body size and temperature. If temperature is a limiting factor in crocodylomorph body size evolution, the probability of given character states may be unequal, in effect pulling character state trajectories towards an optimum. However, as noted previously, concerns have been raised about the OU model and its propensity for false positive results, it being difficult to distinguish from a Brownian motion model (Thomas *et al.* 2014; Cooper *et al.* 2015). Cooper *et al.* (2015) caution against applying the OU model to trees with fewer than 200 tips, a larger sample size than any of the clades tested here. Therefore, a conservative interpretation of these results would be to reject the OU model. However, the Brownian motion model is one of the least-favoured models overall in most of the clades tested. Had the OU model presented a false-positive result, the Brownian motion model might have been expected to perform better compared to the trend, early burst and stasis models. This is with the exception of the combined Tethysuchia and Thalattosuchia and combined

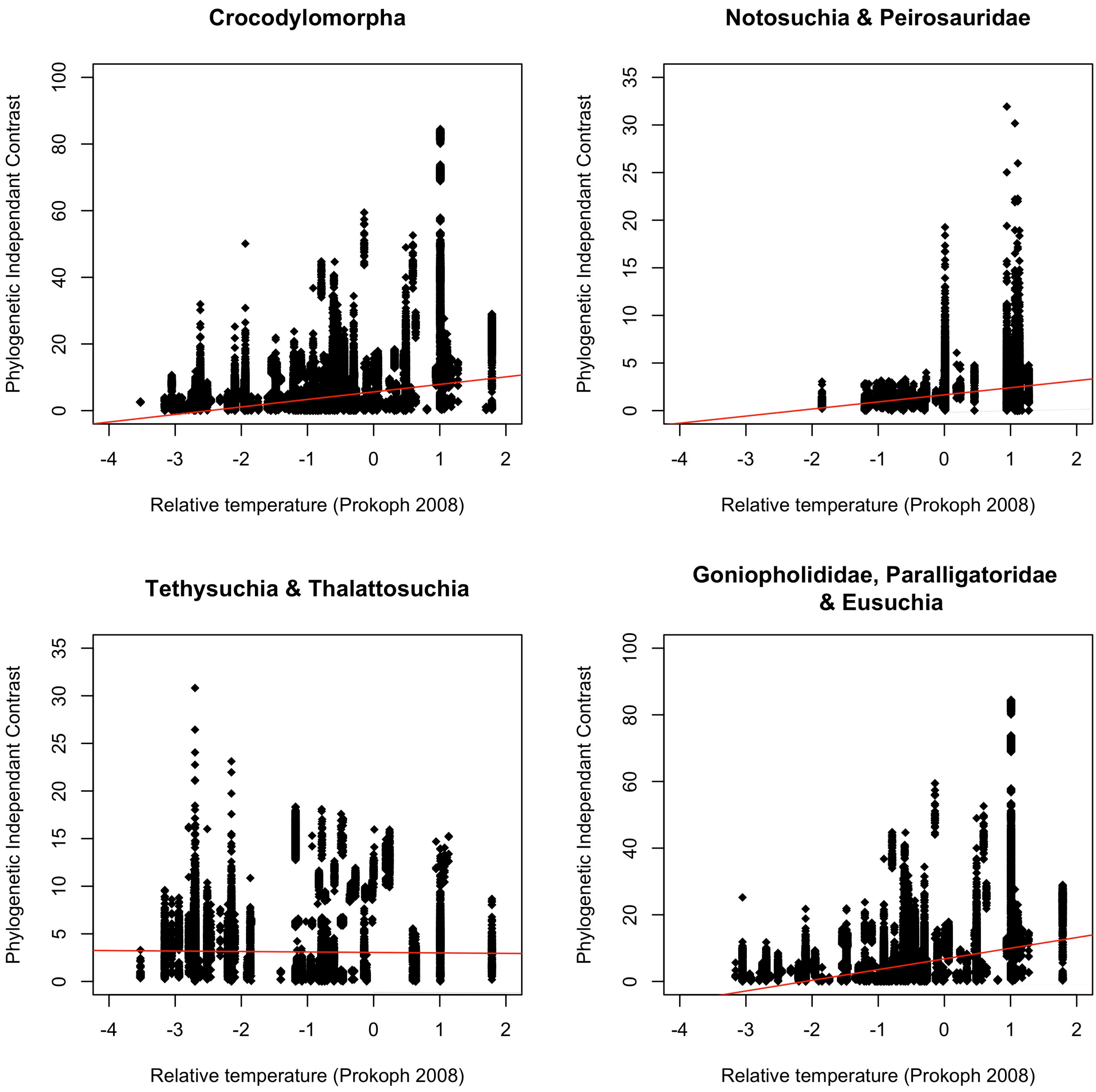

Figure 3.8. Distribution of phylogenetically independent contrasts relative to the corresponding temperature for each time-bin in the Crocodylomorpha and three monophyletic subclades.

Notosuchia and Peirosauridae, where the Brownian motion model achieves a similar log-likelihood and AIC weight as the early burst and trend models. Benson *et al*. (2017) suggest than an α-parameter of "near 0" indicates a false positive result since the α-parameter of the Brownian motion model is fixed at 0 while in the OU model it is free to move. They do not define a threshold to define how far above 0 this parameter should be, so accepting the OU model on these grounds is subjective. The values of the α-parameter returned by this analysis are higher than 0 in all the clades tested. If a threshold of $\alpha = 1$ is defined as an acceptable minimum value for the OU model to be accepted, then the OU model cannot be accepted for all the clades tested. The combined Tethysuchia and Thalattosuchia and combined Notosuchia and Peirosauridae return α-parameter values of less than 1. In the light of this and the relatively high AIC weight of the alternative models in these clades it is safest to consider their support for the OU model to represent a false positive. In both cases, the stasis model achieved a higher log-likelihood and AIC weight and is there for the best model of body size evolution in these marine and terrestrial crocodylomorphs.

The OU model returns an optimum body size of between approximately 18 and 21 cm in all the clades tested where the α-parameter is greater than 1. This range is comparable to average skull width in the extant Crocodylia (Fig. 3.3A), as is to be expected under the terms of the OU model. Average skull width is above the overall optimum through much of the Neogene, a period of relative cooling. Conversely, average skull width is at or below the overall optimum through the Jurassic, Cretaceous, Palaeocene and Eocene, which were relatively warm. This places a transition from less than optimal to greater than optimal size coincident with declining sea-surface temperature in the upper Eocene or Oligocene. However it is perhaps an oversimplification to assume that there is a single optimum value that has not changed through geological time. The analysis shown here is over a relatively long time frame, and it is reasonable to assume that effectors upon an OU model will have changed over time. Further, it has to be considered what role the most recent taxa have in driving the optimum value output by the OU model. Therefore extant Crocodylia have attained an optimum value for current conditions, but this value might be sub-optimal in previous time-bins.

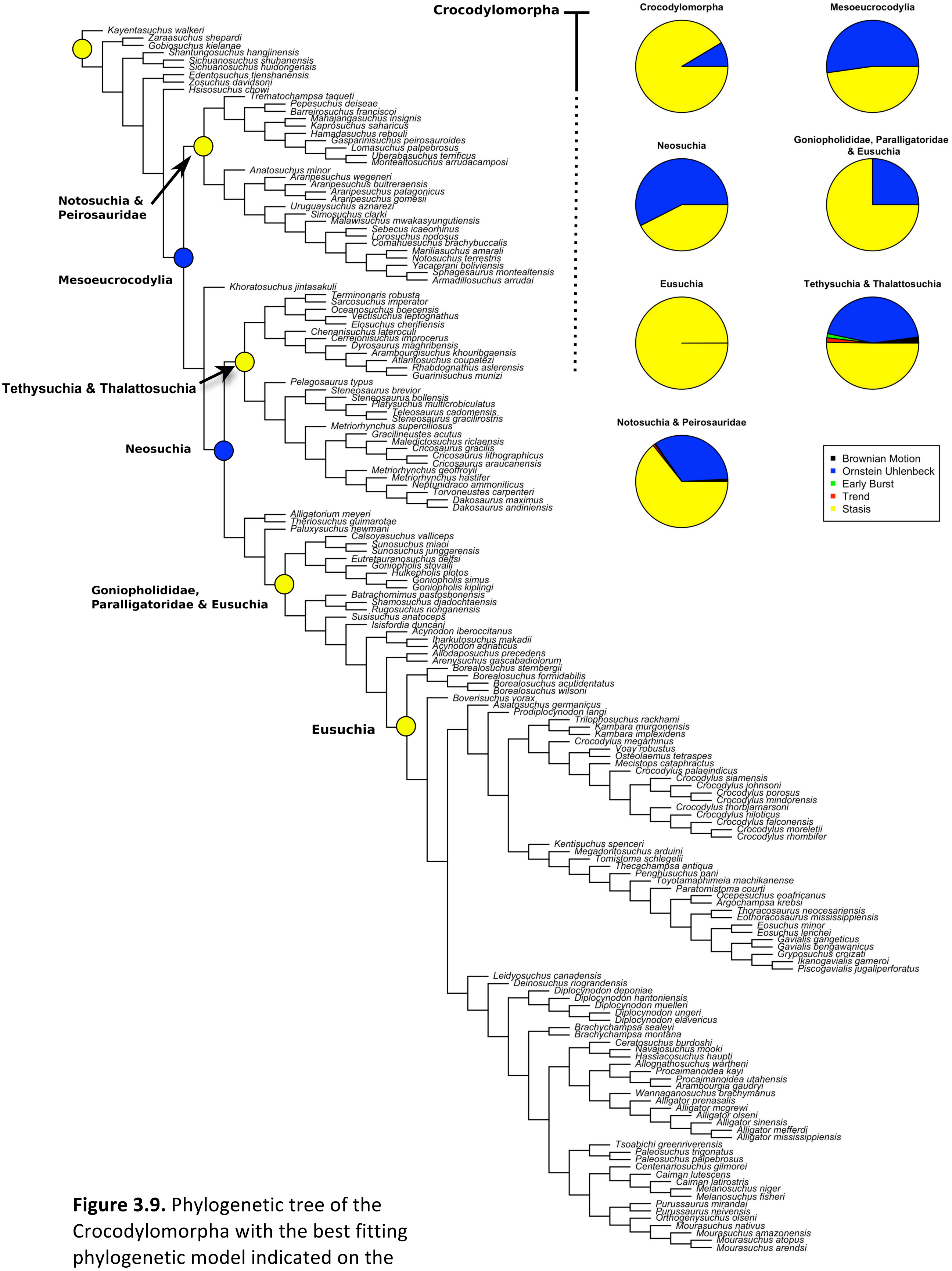

Figure 3.9. Phylogenetic tree of the Crocodylomorpha with the best fitting phylogenetic model indicated on the corresponding node. Relative AIC weights of the models tested are shown in the top right.

Log-likelihood ratio tests comparing the early burst model to the Brownian motion model did not find early burst to be a significantly better model of body size evolution in any of the clades tested. This indicates that rates of body size evolution have not decreased over time, suggesting the current low diversity of crocodylmorphs is not a result of bradytely. However, this finding contrasts with previous work suggesting that crocodylomorph and thalattosuchian diversity arose during adaptive radiations (Toljagic & Butler 2013, Stubbs *et al.* 2013). Unequal preservation potential may offer an explanation for this. For example, the Thalattosuchia mark a transition from a terrestrial to a marine environment, where preservation potential is higher due to the greater sedimentation rate. Therefore an apparent increase in thalattosuchian diversity may be an artefact of an increase in the rate of preservation of thalattosuchian fossils. The trend model significantly outperforms the Brownian Motion model in the total-group Crocodylomorpha, the Eusuchia, and the combined Goniopholididae, Paralligatoridae and Eusuchia. This implies an overall shift in phenotype through time, consistent with the increase in body size suggested by the linear modelling approaches. This model could be in support in Cope's rule, with a trend towards greater body size over time. However, the trend model does not preclude temperature as an alternative driver of body size evolution. Temperatures have decreased over the total time interval of this study, so this model could represent a trend towards adaptation to lower temperatures.

Regression analysis of phylogenetically independent contrasts against time identified a significant correlation in all the clades tested. These analyses consistently returned positive values of average slope. Whether this indicates time as a driver of evolutionary rate is highly debatable, however increasing evolutionary rate is inescapable (Fig. 3.3B, 3.4B, 3.5B, 3.6B). Therefore, the limited diversity of extant Crocodylomorpha is not due to a decay of evolutionary rates, and by this definition they do not qualify as "living fossils". This concurs with the poor fit of the early burst phylogenetic model, which would have implied decreasing evolutionary rates.

Regression of PICs against temperature returned a significant positive relationship in all of the clades tested (Fig. 3.8). Since oxygen isotopes were used

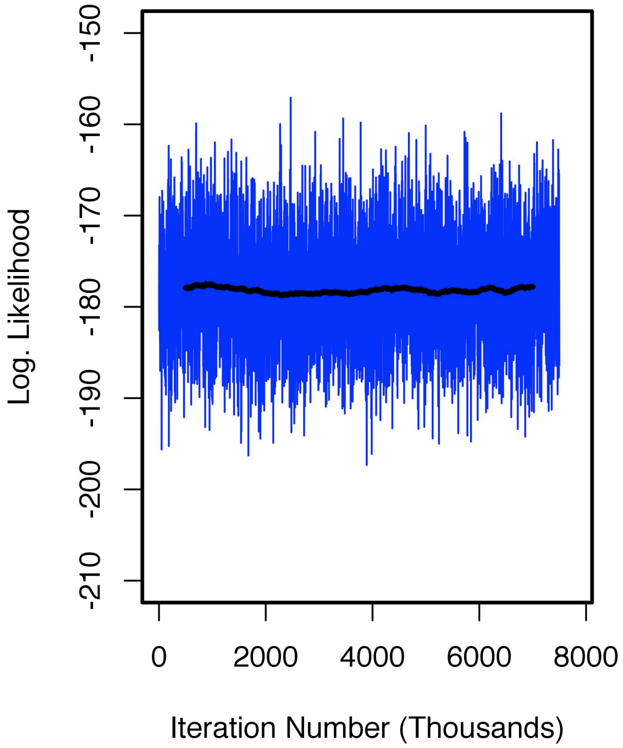

Figure 3.10. Uniform distribution of likelihood values output from a Bayesian variable rates analysis.

as a temperature proxy, the relative temperature scale is inverted; therefore higher δ^{18}O values represent lower temperatures. Therefore, the relationship returned by these analyses indicates that higher PIC values are associated with lower temperatures. These analyses returned higher r-squared statistics than models of PIC where time was the independent variable. These findings are confirmed by log-likelihood ratio tests comparing models using time and temperature, which found temperature to significantly outperform time as a predictor of PIC. These tests consistently returned a p-value of 0.

Bayesian phylogenetic models fitted in Bayestraits identified a much greater signal in support of a heterogeneous rates model than a homogeneous rates model. The variable rate model can be compared to a punctuated equilibrium model of evolution, with relative stasis being interrupted by episodic change. This would be consistent with episodic environmental change, such as

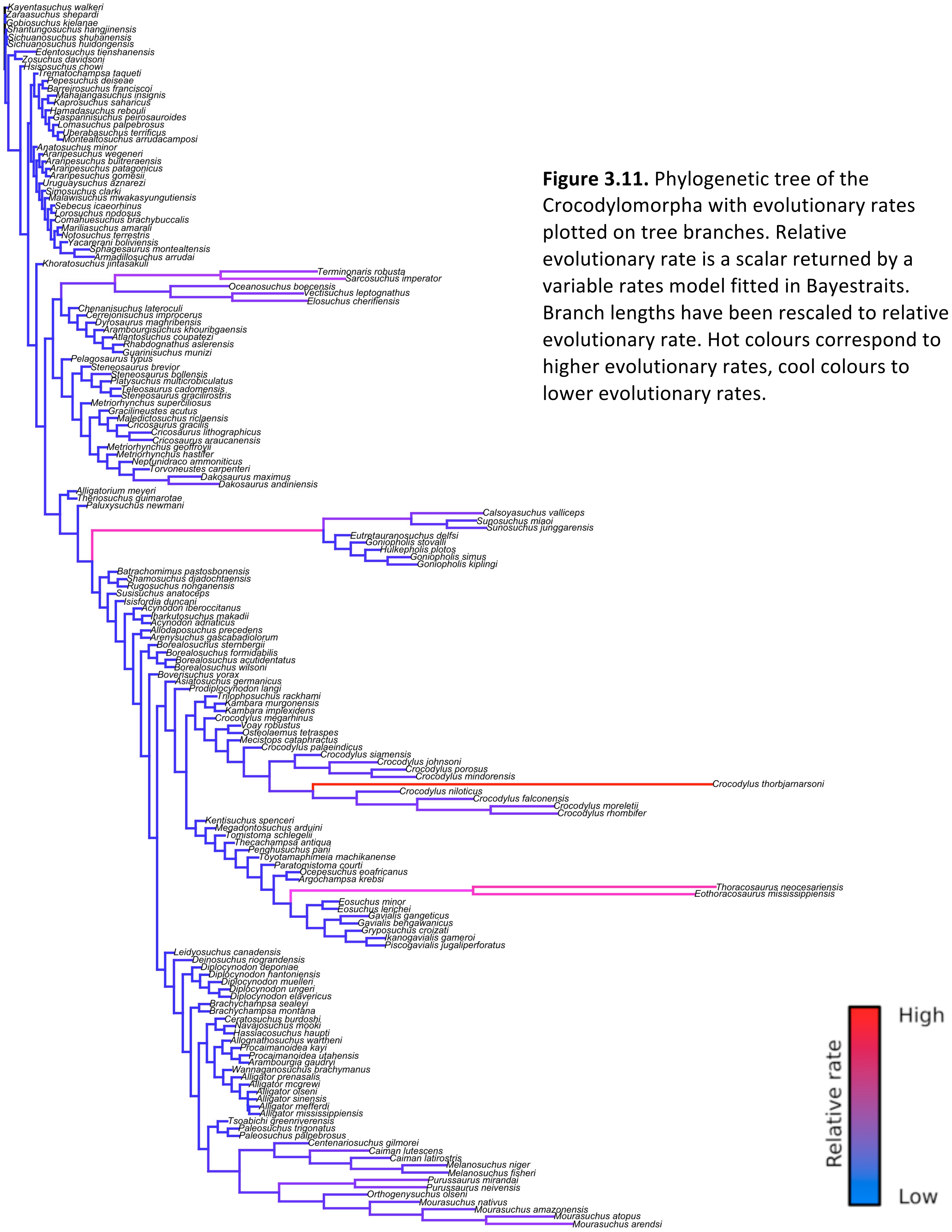

Figure 3.11. Phylogenetic tree of the Crocodylomorpha with evolutionary rates plotted on tree branches. Relative evolutionary rate is a scalar returned by a variable rates model fitted in Bayestraits. Branch lengths have been rescaled to relative evolutionary rate. Hot colours correspond to higher evolutionary rates, cool colours to lower evolutionary rates.

temperature variations, as drivers of body size evolution. Intrinsic biological factors, such as sexual selection, predator-prey arms races and competition, would be expected to result in a homogeneous rate model. The rate of skull width evolution is low in the most inclusive branches, with higher rates being limited to less inclusive branches and tips (Fig. 3.11). This is in contrast to the sister group of the Crocodylomorpha, the birds, which show increased rates of evolution in basal nodes of their phylogeny (Benson *et al*. 2014; Puttick *et al.* 2014). This may be due to differences in metabolic rates, reproductive strategy, body size, ecology or environment. Low rates on more inclusive branches towards the root of the tree concur with the poor support for the early burst model in the analysis above. The evolutionary rates of living crocodylomorph taxa are not especially low when compared to their extinct counterparts.

Regression analysis of evolutionary rates returned by the Bayesian variable rates model found a significant correlation with both time and temperature in all the subclades tested (Fig. 3.3C, 3.4C, 3.5C, 3.6C, 3.12). Slope values of models using time as a variable were positive, indicating an increase in evolutionary rates through time in all the groups tested. This concurs with the low support for the early burst model returned by previous phylogenetic modelling analyses. These findings also agree with regression analyses of PICs through time. Regression of evolutionary rate against temperature found significant negative relationships in all the clades tested. This confirms results from previous analyses, which identify increased rates of skull width evolution being associated with cooler temperatures. However, the r-squared values from these analyses are lower than models where evolutionary rate was compared with time. This is likely to be an artefact of the selected sample size, since the log-likelihood ratio tests comparing models using temperature with those using time consistently find temperature to be the better predictor of evolutionary rate.

Based on the analyses presented here, evolutionary rates of the extant Crocodylomorpha are neither low, nor decreasing. Bradytely does not describe crocodylomorph body size evolution. While evolutionary stasis is supported by phylogenetic modelling approaches, the relatively high evolutionary rate of extant taxa fails to satisfy the criteria for living fossils as set by Herrera *et al.* (2017).

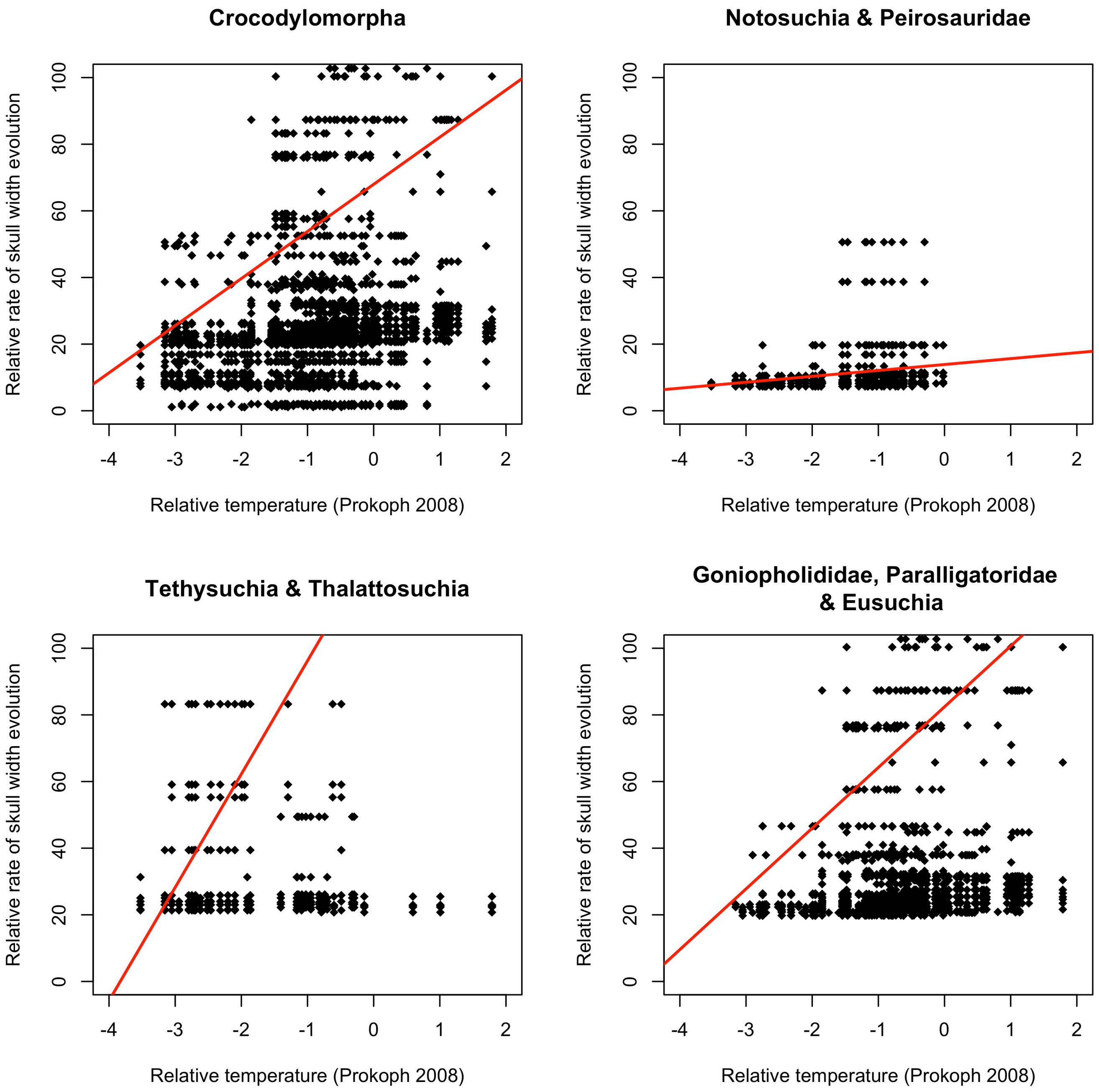

Figure 3.12. Distribution of relative evolutionary rate relative to the corresponding temperature for each time-bin in the Crocodylomorpha and three monophyletic subclades. Relative evolutionary rate is represented by scalar values returned by a variable rate model fitted in Bayestraits.

Since the Crocodylomorpha do not satisfy these definitions, they also do not qualify as Lazarus taxa, and the label of living fossil is likely unjustified.

The analyses presented her consistently favour climate over time as a predictor of body size and rates of body size evolution. Combined with support for the variable rates model, this may be interpreted as support for a Court Jester model (Barnosky 1999) of crocodylomorph macroevolution, driven by environmental change. This is consistent with the findings of previous analyses that have linked diversity with temperature (Markwick *et al* 1998, Martin *et al.* 2014, Mannion *et al.* 2015). However, it must be conceded that there are limitations to the results presented by this analysis. The r-squared values returned by models using temperature are consistently quite weak. The method of testing for relationships with temperature implemented in this study is a simple one. Perhaps using a single time-series to represent global temperatures through time is an oversimplification, since it does not factor in regional geographic variation. Future analyses could utilise general circulation models of palaeoclimate to better achieve more accurate models. This would also open up other possible test variables such as seasonal variations and precipitation. Further, the Court Jester and Red Queen models may not be mutually exclusive. While major changes in body size evolution may be due to environmental variation, intrinsic biotic factors such as sexual selection and competition may still play a role. Testing for the effects of biotic interactions on evolution is a challenging prospect due to the decay of the fossil record, and uncertainty about ecological relationships between extinct taxa. However, perhaps advances in ecological network modelling will offer solutions to these issues.

CONCLUSIONS

There has been a significant increase in crocodylomorph body size through time since the Early Jurassic. However, there are insufficient grounds to cite this as an example of Cope's rule. Temperature consistently outperforms time as a predictor of both body size and rates of body size evolution. Therefore the increase in body size through time may be an artefact of decreasing temperatures rather than an inherent trend.

A relationship between temperature and body size and rates of body size evolution is consistent with previous work linking temperature with diversity.

However, the relationship between temperature and body size and body size evolution is very weak. While temperature may be a more applicable explanatory variable for body size evolution than time, there is not sufficient support to consider it a primary driver. It is likely that other factors, for example sea level, primary productivity and the diversity of other clades also contribute.

Crocodylomorph body size evolution is extremely conservative, with all the clades tested showing substantial support for a stasis model. This may explain the low diversity and disparity in extant forms. Some groups also show support for the Ornstein-Uhlenbeck model, which is consistent with relationships between body size, rate of body size evolution and temperature.

Rates of crocodylomorph body size evolution have not shown significant decline through time. This suggests that there are insufficient grounds to attribute fossil crocodylomorph diversity to adaptive radiations. Therefore peaks in crocodylomorph diversity through time may be a result of preservation or sampling bias. Further, the Crocodylomorpha do not fulfil any published definition of living fossils, and their low extant diversity and disparity cannot be attributed to evolutionary rates.

Chapter 4: Diversity and disparity of the Crocodylomorpha through time

Abstract: The extant Crocodylomorpha show a very limited biodiversity compared with their fossil forebears. They are represented by fewer taxa, and show less ecomorphological variation. How has this morphological and taxic diversity changed through time? Is the diversity of the Crocodylomorpha in the fossil record a real pattern, or is it an artefact of preservation or sampling biases? Are morphological and taxic diversity coupled, or do they change at different rates? To what extent is the diversification of the Crocodylomorpha subject to environmental change, such as climate variations or mass extinctions? This study aims to answer these questions using a combination of time-series data and linear modelling approaches. The analyses demonstrate that the diversity of fossil crocodylomorphs is representative of reality and not an artefact of preservation or sampling. Neosuchian diversity is constrained by temperature, with diversity declining during periods of cooling. Crocodylomorphs commonly exhibit a coupled model of diversity and disparity, with increases and decreases co-occurring at similar rates.

INTRODUCTION

The extant Crocodylomorpha might be described as lacking variety. Their extant diversity of just 24 taxa is meagre compared to clades of similar age such as birds and mammals (Jetz *et al.* 2012; Gómez *et al.* 2016). This might be considered a fall from grace, since the Crocodylomorpha have hundreds of fossil representatives (Bronzati *et al.* 2011; Brochu *et al.* 2013). However, it cannot be assumed that fossil diversity corresponds to true diversity. Fossil forms occur in different time bins, so while overall fossil diversity is higher than extant diversity, variations in diversity occur over time. Extant diversity may represent a long-term decline in crocodylomorph species richness, or merely one of many temporary dips in diversity.

It must be considered that apparent periods of diversification might be an illusion brought about by environmental and diagenetic factors such as sea level, rates of burial and erosion (Smith 2001; Twitchett *et al.* 2001; Dunhill *et al.* 2012). The sum of these factors might bias the fossil record increasingly with geological age, creating a 'pull of the recent' (POR) effect (Raup & Sepkoski 1982). Uneven sampling of crocodylomorph fossils may also influence apparent diversity (Walker *et al.* 2016). The relative extent of sampling bias is extremely difficult to determine, with some studies suggesting that the crocodylomorph fossil record is too incomplete to be informative (Benson *et al.* 2013). However, while preservation bias and 'pull of the recent' may distort or mask patterns in the fossil record, crocodylomorphs may be less vulnerable to these effects than other groups. A significant number of known crocodylomorph taxa have an amphibious or marine mode of life, placing them in environments with higher sedimentation and rates of burial than land-living vertebrates. Further, crocodylomorphs tend to be medium to large in size with robust skulls, limb bones and osteoderms that are relatively resistant to decay, diagenesis and erosion. Therefore, the quality of the crocodylomorph fossil record may relatively good. Since the extant diversity is low compared to fossil diversity, a POR effect is difficult to justify. Further, a study of extant species found most of them to be represented in the Plio-Pleistocene fossil records (Sahney & Benton

2017), suggesting that the impact of the POR was negligible among tetrapods, including crocodylomorphs.

Extant crocodilian morphology is similarly unadventurous, in that they all share a squat, short-limbed body plan with dermal armour and elongated snouts. Likewise, their ecology is limited to the role of amphibious ambush predators, with a spectrum of feeding modes from piscivory to hypercarnivory. This lack of variation is in contrast to the fossil Crocodylomorpha, which includes many novel and unfamiliar morphologies. A long-limbed cursorial gait was present in the most basal Crocodylomorpha (Sues *et al.* 2003, Clark *et al.* 2004), and persisted in some taxa until the Miocene (Paolillo & Linares 2007). The marine Thalattosuchia attained a streamlined, hydrodynamic body plan with reduced limbs and possibly a tail fluke (Young *et al.* 2012). Derived terrestrial Notosuchia included heavily armoured and semi-fossorial forms resembling extant mammals such as armadillos (Marinho & Carvalho 2009) or pigs (Fiorelli & Calvo 2008). Fossil Crocodylomorpha also show a greater diversity of feeding types, including insectivores (Martin & Broin 2016) and possibly herbivores (Buckley *et al*. 2000). Heterodont dentition occurs in multiple crocodylomorph clades, including members of the crown group (Sullivan *et al.* 1986, Pasini *et al.* 2006). This poses the question of how morphological variation has been gained and lost through time. Morphological disparity, the morphological distinctiveness of taxa, presents an alternative metric for quantifying changes in biodiversity through time. The low disparity of extant crocodylomorphs may be part of a long-term decline in morphological variation. Alternatively, morphological variation may have been lost in a stepwise manner through the impact of mass extinctions.

The acquisition of morphological variation relative to taxic diversity is a matter of ongoing debate (Benton 2015). Taxic diversity and morphological disparity may be coupled, co-varying over time, or they may be decoupled, changing over time at different rates. The diversity-first model proposes that disparity emerges after a period of diversification (Benton 2015). The disparity-first model suggests that an increase in morphological variation gives rise to later taxic diversity (Benton 2015).

Controversy surrounds the relative importance of extrinsic environmental change and intrinsic biological factors as drivers of evolution

(Van Valen 1979; Barnosky 1999). The ancestors of the extant Crocodylomorpha have experienced enormous environmental changes. This includes two of the 'big five' mass extinctions, sea level rise in the Mesozoic and prolonged cooling through the Cenozoic. The distribution of extant crocodilians is limited to the tropics, which has been seen as an indicator that their diversity is strongly correlated with temperature (Markwick 1998).

Analysis of taxic diversity identified a limited relationship between diversity and temperature through time, but this was conditional on the exclusion of the Metriorhychidae (Martin *et al*. 2014). However, Martin *et al.* did not account for preservation or infer ghost ranges. Therefore, the findings of this study could be real or could be attributed to preservation bias. A later study of crocodylomorph fossil occurrences (Mannion *et al.* 2015) confirmed a relationship between temperature and crocodylomorph diversity. However, Mannion *et al.* took no account of Lazarus taxa or fossil ghost ranges. They attempted to correct for sampling bias using shareholder quorum sampling (SQS; Alroy 2010; Alroy 2014). SQS reduces the statistical power of diversity time-series data since it deletes significant amounts of data. Further, the accuracy of SQS has also been found to be adversely affected by unequal relative abundance of sampled taxa (Hannisdal *et al.* 2017). Hannisdal *et al*. concluded that SQS diversity was a function of raw richness and species evenness. Mannion *et al.* and Tennant *et al.* (2016) also binned taxa as marine or terrestrial, rather than using a monophyletic definition. Fluvial and lacustrine taxa were grouped together with land-dwelling forms, and separated from other aquatic forms in the marine realm. This is something of an oversimplification, since diversity and temperature may interact differently between land-living and amphibious taxa.

This study aims to characterise the acquisition and loss of crocodylomorph diversity and morphological variation through time, and consider the relative rates of change in diversity and disparity through time. We take an alternative approach to the methods of Martin *et al.* and Mannion *et al.* by using phylogenetic lineages through time as a measure of diversity. This approach counters some of the effects of preservation bias and unequal sampling by inferring missing data through the reconstruction of fossil ghost ranges. Crocodylomorph taxa are grouped according to a phylogenetic definition rather than by geological setting. A high-resolution disparity curve is estimated from a large supermatrix of morphological character data. Diversity and disparity time-series data are then tested for relationships with environmental variables using linear modelling approaches.

MATERIALS AND METHODS

Diversity through time

Time series of crocodylomorph diversity through time were assembled by counting the number of lineages through time. This approach includes both ghost ranges and hypothetical common ancestors in the estimated diversity, reducing the susceptibility of diversity estimates to preservation bias. This method does present a caveat in that it assumes no known fossil taxon represents the common ancestor of any other taxon. In theory this could inflate the diversity estimate, but the likelihood of a common ancestor being preserved is unknown and may be extremely small. The lineages through time approach can also only infer ghost ranges previous to the known fossil range and cannot infer missing data more recent than the fossil range. However, this caveat is shared by other methods of reconstructing diversity. The constrained supermatrix analysis presented in chapter 2 was used as an input phylogeny to determine the distribution of taxa through time. The entire sample of trees generated by the analysis was used. Each tree was dated using the Cal3 method implemented in the PaleoTree Package (Bapst 2016). Each tip was dated to stage level using the Palaeobiology Database (paleodb.org). These stage-level dates were then converted into numerical first- and last- appearance data using the international stratigraphic chart. The Cal3 method was implemented using a random observation date treatment, where the tip date is taken to be a random point between the estimated first- and last- appearance date. Each tree was dated 10 times with this random date treatment. This approach mitigates the effect of low-resolution of stage-level tip dating by repeating analyses using a distribution of equally likely dating schemes. Diversification, extinction and sampling rates used by the Cal3 algorithm were also estimated using PaleoTree.

To estimate the number of taxa in each time interval, each dated tree was time-sliced at 1 million year intervals. Taxa extinct at the time of each slice were discarded. The remaining tree tips were counted and used to resolve the range, variance and mean number of taxa per 1 million year time interval (Fig. 4.1A). This approach inferred ghost ranges for each taxon, and included common ancestors. The time interval of each time series was constrained between the first- and last appearance dates for the entire clade, therefore excluding ghost ranges preceding the fossil record. This process was then repeated for three major crocodylomorph subclades. These subclades were defined monophyletic groups, corresponding approximately to ecomorphological grades. These are the same groups that were implemented in Chapter 3. A clade of terrestrial Crocodylomorpha was defined as all descendants from the common ancestor of *Notosuchus* and *Kaprosuchus* (Fig. 4.2A). According to the tree, these taxa represent a combined clade including all Notosuchia, Peirosauridae and Mahajangasuchidae. A second clade corresponding approximately to marine crocodylomorphs was defined as all descendants of the common ancestor of *Metriorhynchus* and *Atlantosuchus* (Fig. 4.3A). This clade represents the combined Tethysuchia and Thalattosuchia. Finally, a third clade of amphibious terrestrial crocodylomorphs was identified, including the entire crown-group (Fig. 4.4A). This group was defined as all descendants of the common ancestor of *Crocodylus* and *Calsoyasuchus*. This corresponds to the Goniopholididae, Paralligatoridae and Eusuchia.

Disparity through time

Disparity was quantified using generalised Euclidean distances (GED) and eigenvectors of character data, using the supermatrix assembled in Chapter 2. GED was selected as the most appropriate distance measure since it has a relatively high fidelity when applied to incomplete data (Lloyd 2016). Euclidean distance is calculated using Pythagorean geometry, representing the hypotenuse of a hyper-dimensional right-angled triangle (Wills 1998). The lengths of the opposite and adjacent sides of the triangle are represented by the difference in

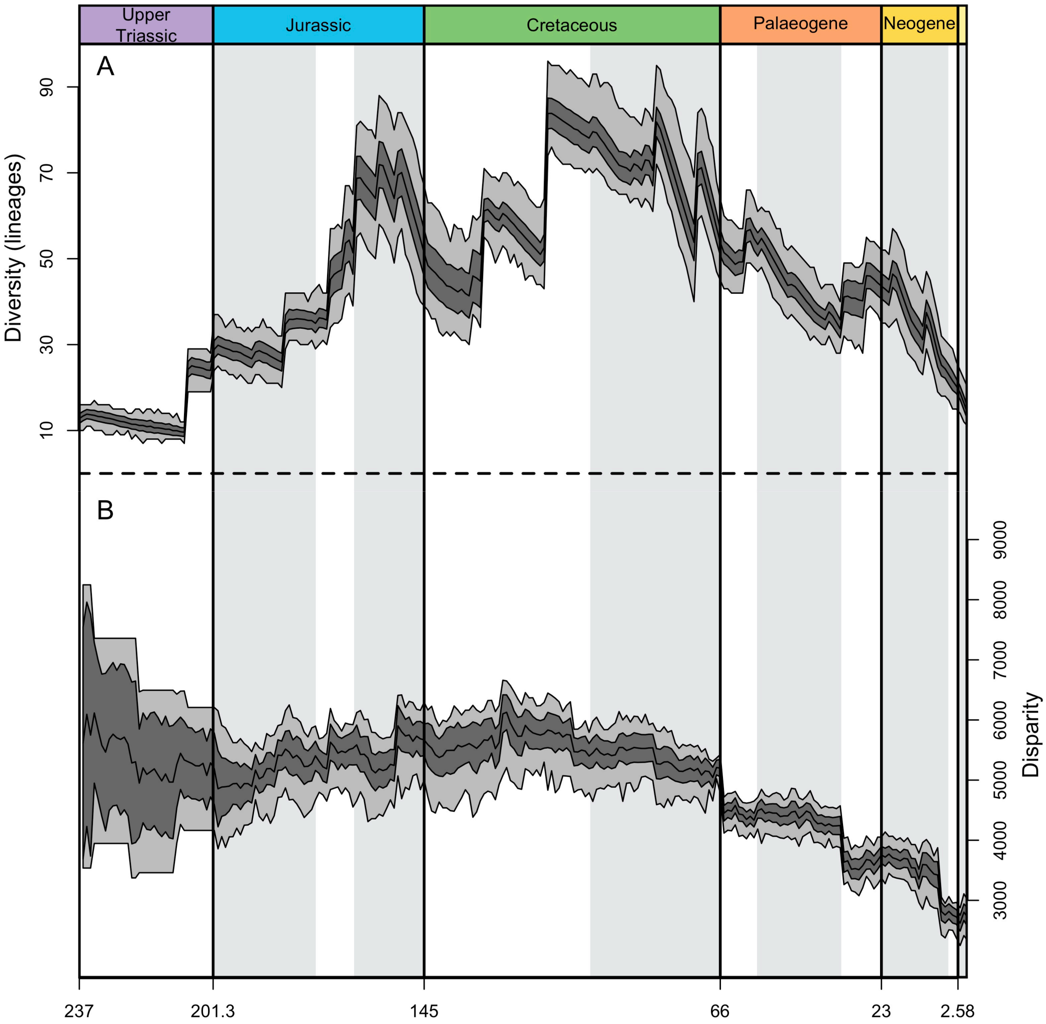

Figure 4.1 Time-series distribution of total-group diversity and disparity through time. A) Diversity estimated using lineages through time from a sample of phylogenetic trees. B) Disparity estimated using sum of ranges, calculated using scores from a PCO analysis of a matrix of character data. The presence or absence of each taxon indicated by the phylogenetic tree with the highest MK-model likelihood. Disparity errors are estimated using bootstraps. Light grey shows the total data range, dark grey the data variance.

trait value between two taxa, with each additional trait being represented by an additional dimension. Generalised Euclidean distance infers missing data using a weighted average, which is an essential attribute for calculating disparity from fossil data (Wills 1998). However, this may have the effect of artificially smoothing disparity curves where the quantity of missing data is high.

To lessen the impact of smoothing due to missing data, characters that were represented by less than 10% of taxa were removed from the supermatrix. Principal component analysis of the GED matrix was implemented using PAST (Hammer *et al.* 2001). A post-ordination approach to disparity was chosen to help mitigate effects of redundant characters. Since two redundant characters will have a perfect correlation, they contribute equally to any given principal coordinate axes. Redundant characters may be expected to adversely affect the accuracy of axis weights, but these weights are not used in calculating disparity. PAST was selected for its ability to calculate GED and PCOA data on such a large matrix. However, PAST has a limitation in that it cannot calculate Euclidean distances from unordered multistate characters. An unordered character has equal distance in morphospace between states, with the number of that state representing only a label. To mitigate this problem, all unordered characters with more than two states were also removed from the matrix.

The first three axes returned by the PCO analysis were plotted as bivariate morphospaces (Fig. 4.5). Three major subgroups were isolated from the data to visualise differences in ecology. These groups correspond to the same subgroups used in Chapter 2. Terrestrial Crocodylomorpha were represented by the combined Notosuchia and Peirosauridae, including the Mahajangasuchidae. Marine Crocodylomorpha were represented by the combined Tethysuchia and Thalattosuchia. Crocodylomorpha living in a freshwater environment were denoted by the combined Goniopholididae, Paralligatoridae and Eusuchia. Differences in morphospace occupancy between these subgroups was analysed using a non-parametric multivariate analysis of variance (NPMANOVA) test. The NPMANOVA test was implemented on the first 195 axes, which collectively account for 56% of the total variation in the data set. Axes 196 onwards accounted for such a small fraction of morphological diversity that PAST was

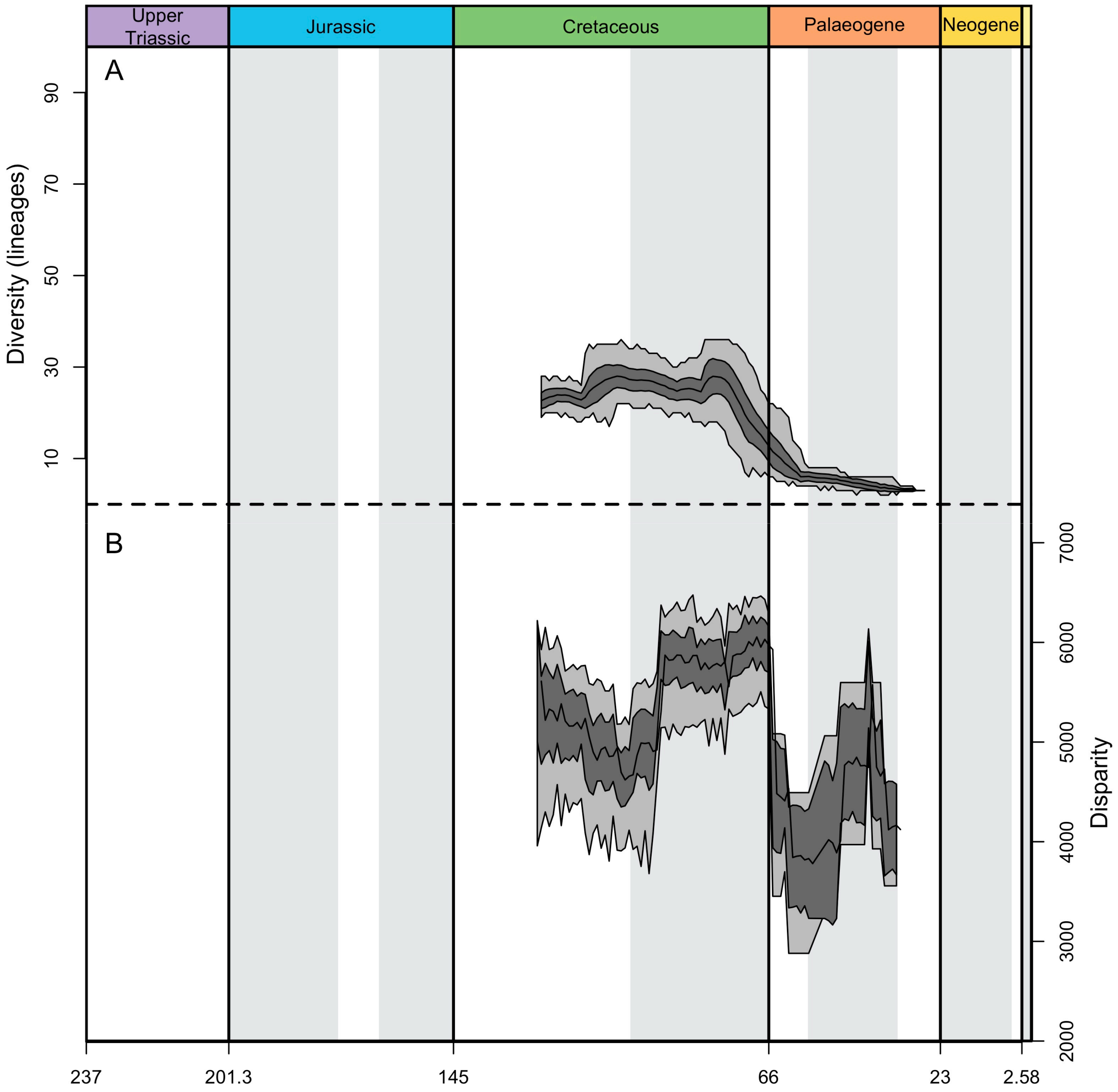

Figure 4.2 Time-series distribution of terrestrial crocodylomorph diversity and disparity through time. A) Diversity estimated using lineages through time from a sample of phylogenetic trees. B) Disparity estimated using sum of ranges, calculated using scores from a PCO analysis of a matrix of character data, with the presence or absence of each taxon indicated by the phylogenetic tree with the highest MK-model likelihood. Disparity errors are estimated using bootstraps. Light grey shows the total data range, dark grey the data variance.

unable to return the necessary number of decimal places, giving a PCO score of 0 for all taxa.

Disparity through time curves were assembled by subsetting the PCOA matrix to represent taxa present at 1 million year intervals through time (Fig. 4.1B, 4.2B, 4.3B, 4.4B). The taxa present in each time bin were determined using the tip dates and branch lengths of a phylogenetic tree from the sample returned by the constrained supermatrix analysis implemented in chapter 2. The tree selected from the sample was that with the highest Lewis-MK likelihood, as determined by the evaluations in chapter 2. This tree was dated using the Cal3 method, with the tip date treatment set to stage resolution. The tree was dated using the same data used in the diversity curve (Supplementary information 3). This dating scheme is a liberal estimate, the fidelity of which will be tested post-hoc through bootstrapping of the disparity data. The time interval of the analysis was broken up in to 1-million year time bins. The species present in each time bin were determined by finding all species with a tip date later than each respective bin, and of those all species with an ancestral node date earlier than each respective bin (Supplementary information). This approach presents an advantage over other methods by including ghost range taxa. Determining the distribution of taxa through the stratigraphy of fossils would have omitted this, and would be more susceptible to preservation bias. Furthermore, this approach allows disparity to be calculated to a much greater resolution than other methods, which can limit curves to a far smaller number of time-bins due to the availability of fossils. A limitation of this approach is that it assumes that character states remain the same within a species temporal range, and so an entirely punctuated model of character evolution, which is unlikely due to anagenesis. However this is a limitation that is shared by stratigraphy-based methods. Using a tree to estimate taxa in a disparity curve is not novel, having been employed by Wilberg (2017). Wilberg incorporated gradualism into versions of their disparity curves, but this did not result in much change the curve topology (Wilberg 2017).

To calculate a disparity value for each time bin, the taxa represented in that bin were used to subsample the matrix of eigenvectors returned by the

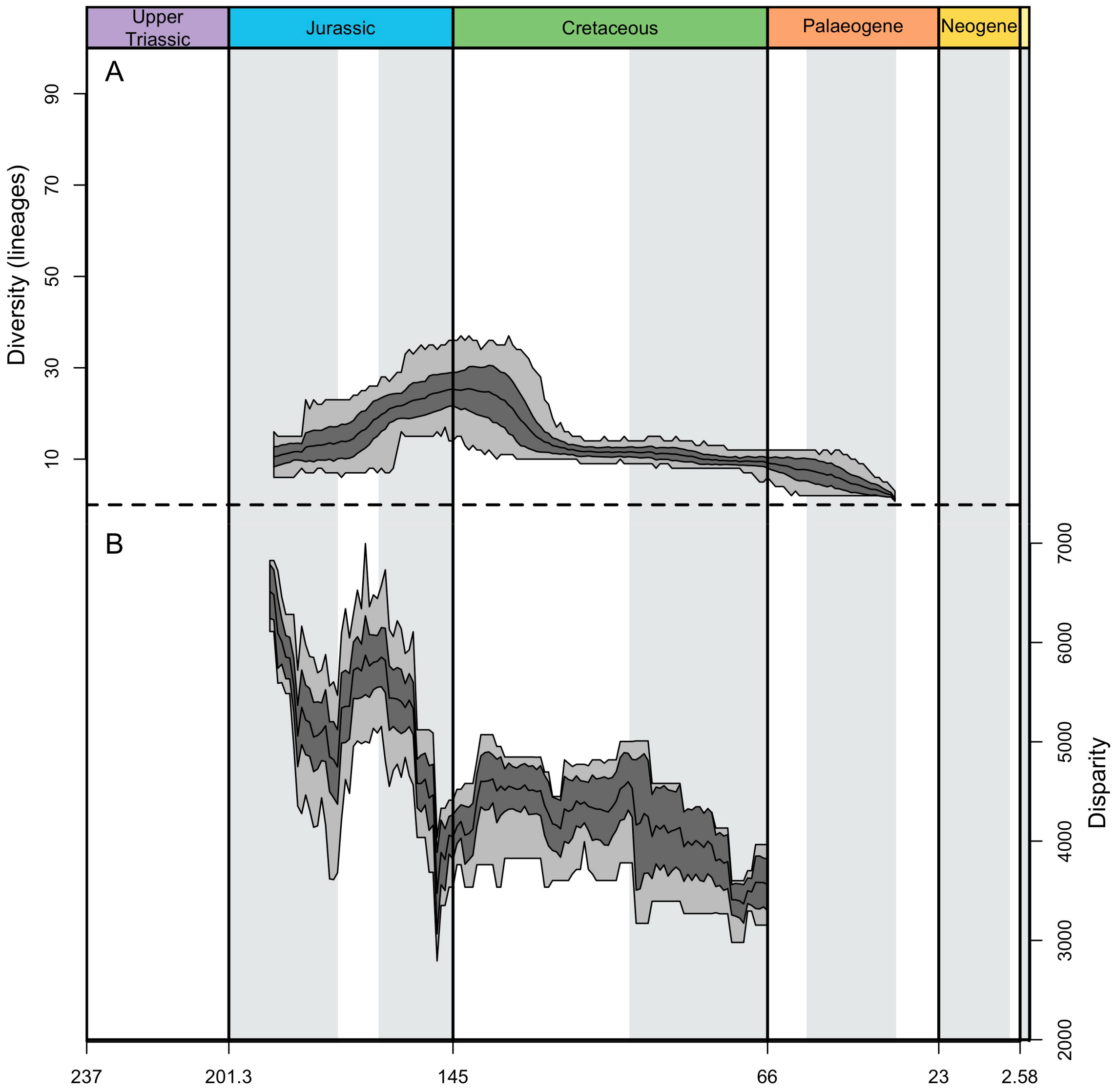

Figure 4.3 Time-series distribution of marine crocodylomorph diversity and disparity through time. A) Diversity estimated using lineages through time from a sample of phylogenetic trees. B) Disparity estimated using sum of ranges, calculated using scores from a PCO analysis of a matrix of character data, with the presence or absence of each taxon indicated by the phylogenetic tree with the highest MK-model likelihood. Disparity errors are estimated using bootstraps. Light grey shows the total data range, dark grey the data variance.

PCOA analysis. The sum of variances calculated from these subset matrices as a disparity metric. Sum of variance was selected as the disparity metric because it can easily be applied to the continuous post-ordination eigenvectors. Sum of variance is appropriate for these data as PCOA axes are by definition orthogonal to each other, and therefore they do not covary. In addition, the sum of variance may be expected to be robust to the effects of a heterogeneous distribution of points. Other disparity metrics, such as the sum of ranges or morphospace area, would be vulnerable to the effect of outlying points. The disparity time-series was bootstrapped by repeating the sum of variance calculations with 25% of the taxa in each bin removed at random, rounded up to the nearest whole number. The analysis was bootstrapped for 100 replicates. The disparity time-series and bootstrapping was repeated for each of the subgroups shown in the morphospace analysis, including predominantly terrestrial (Fig. 4.2B), marine (Fig. 4.3B) and freshwater (Fig. 4.4B) groups. Bootstrapping does present a drawback because sums of variance cannot be calculated from datasets of fewer than two entries. Since bootstrapping removes 25% of taxa from a sampled time-bin, disparity can only be calculated for time bins with four or more taxa. Therefore the disparity time-series do not equal diversity time-series in length.

Linear models of time-series data

Univariate linear models were used to test interactions of variables representing environmental factors and preservation biases with diversity and median generalised Euclidean distances through time. Independent variables for each model were selected to represent environmental factors, the diversity of contemporary clades, and sampling effects. Multivariate linear modelling approaches required the implementation of stepwise deletion of variables, and using multiple time-series would have permitted a wide spectrum of model complexity that would be very difficult to compare empirically.

An initial univariate linear model was fitted to each diversity time-series using disparity as an independent variable (Fig. 4.6, 4.7, 4.8, 4.9). This serves as a null hypothesis, that diversity and disparity are coupled. The log-likelihood of this model would be

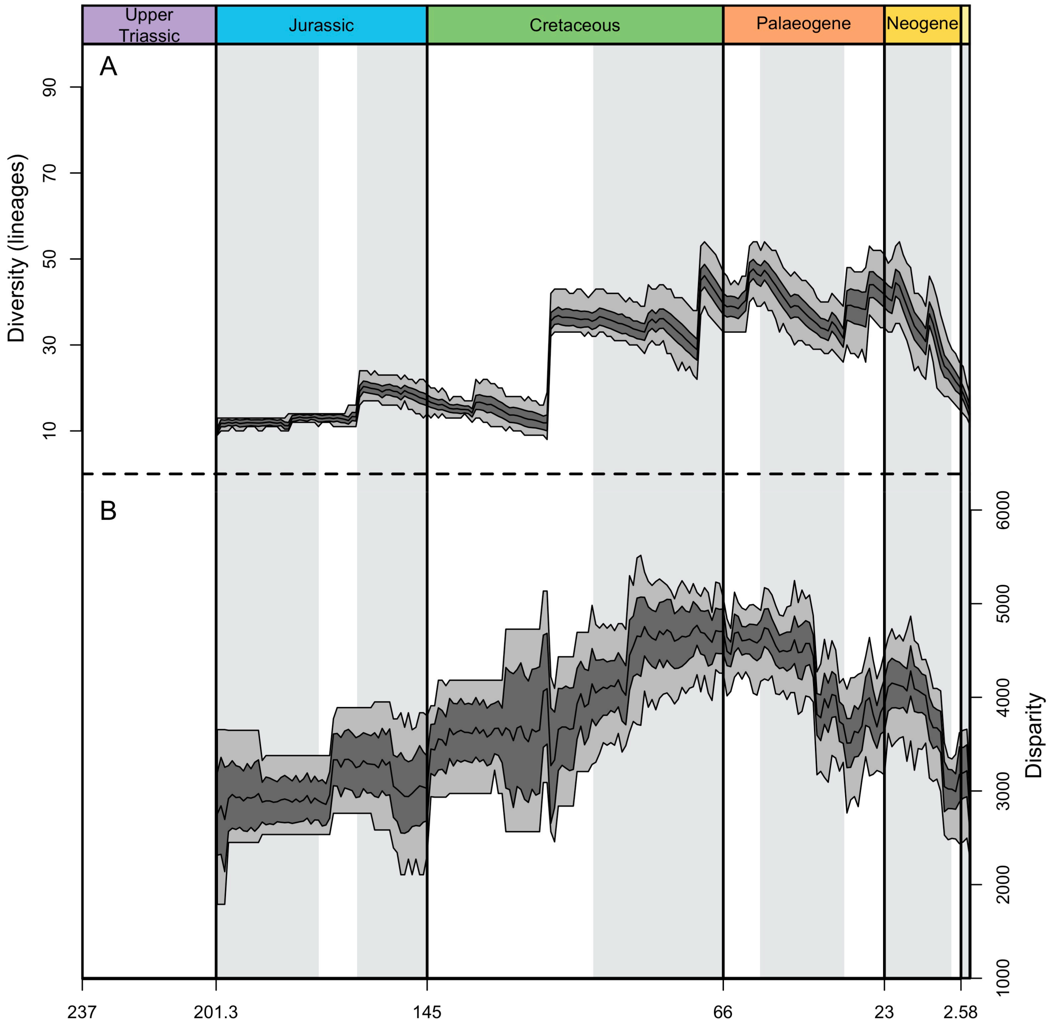

Figure 4.4 Time-series distribution of freshwater crocodylomorph diversity and disparity through time. A) Diversity estimated using lineages through time from a sample of phylogenetic trees. B) Disparity estimated using sum of ranges, calculated using scores from a PCO analysis of a matrix of character data, with the presence or absence of each taxon indicated by the phylogenetic tree with the highest MK-model likelihood. Disparity errors are estimated using bootstraps. Light grey shows the total data range, dark grey the data variance.

used as comparison for the likelihood of all other subsequent models. In addition the p-value and r-squared value of each model was recovered, and the residuals of each model were checked for normalcy using a Shapiro-Wilk test (Supplementary in formation 3).

Environmental variables were represented by time-series data recovered from the literature (Fig. 4.6, 4.7, 4.8, 4.9). The deep-time temperature curve was taken from Prokoph *et al.* (2008), based on the $\delta^{18}O$ isotope proxy. Prokoph's curve was favoured due to its comprehensive time-interval from the Upper Triassic to the uppermost Quaternary. A proxy curve of primary productivity was also taken from Prokoph *et al.* (2008), estimated using the $\delta^{13}C$ isotope (Fig. 4.6, 4.7, 4.8, 4.9). These are both summary curves incorporating isotope data from a range of sources. It was important to consider global temperature as this has been posited as a key determinant of crocodilian distribution. The sea level curve was taken from Miller *et al.* (2005) (Fig. 4.6, 4.7, 4.8, 4.9). This curve was selected because of its comprehensive coverage of sea level throughout the Mesozoic and Cenozoic eras in a single time-series. Sea level could have one of two effects on the crocodilian fossil record, either as an environmental driver, changing the distribution of suitable habitats, or as a bias to preservation potential.

The diversity through time of contemporary reptilian groups was estimated using lineages through time estimations derived from phylogenetic trees, in a comparable manner to the crocodylomorph diversity data estimated above. Diversity through time curves were assembled from phylogenetic trees of three major sauropsid clades contemporaneous with fossil crocodylomorphs. Dinosaurs and sauropterygians may exhibit an overlap in ecospace with crocodylomorph clades, such as the terrestrial non-neosuchians and thalattosuchians respectively. Correlations between crocodylomorph diversity and the diversity of contemporary sauropsid clades may indicate common factors driving diversity, or common preservation biases in their fossil records (Fig. 4.6, 4.8). A dinosaur curve was estimated using the strict consensus topology estimated in Lloyd *et al.* (2016). A diversity curve of the Sauropterygia was estimated from the strict consensus of Benson *et al.* (2012). Each of these trees was tip-dated

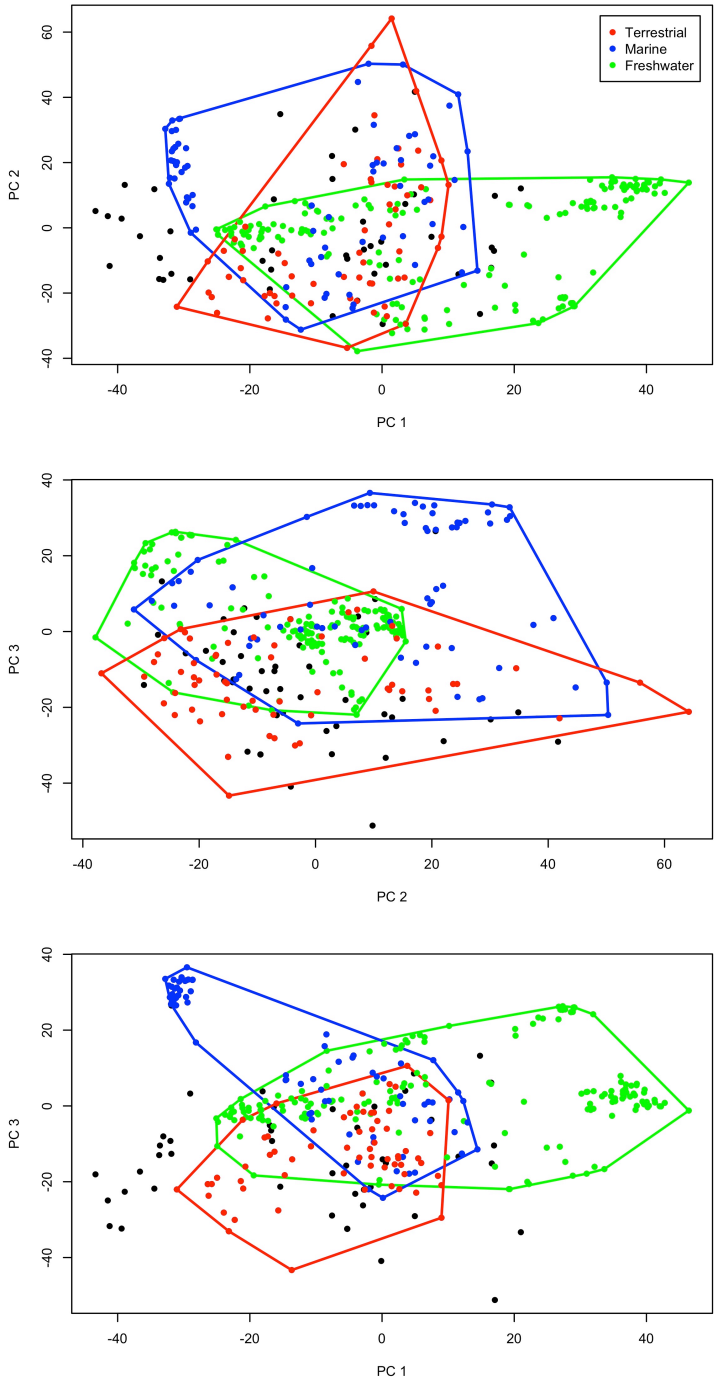

Figure 4.5. Morphospace occupancy of the Crocodylomorpha, using axes from PCO analysis. Freshwater taxa (green) include the combined Goniopholididae, Paralligatoridae and Eusuchia. Marine forms (blue) include the combined Tethysuchia and Thalattosuchia. Terrestrial forms (red) include the combined Notosuchia and Peirosauridae.

randomly 100 times using the equal method implemented in PaleoTree. First- and last-appearance dates were recovered from the Paleobiology Database. Tips on each tree that were not represented in the Paleobiology database were omitted. Both trees were then time-sliced at one million year intervals, and the tips counted. The mean diversity value across all trees was calculated to give a single time-series for each clade. The time interval of each time series was constrained between the first- and last appearance dates for the entire clade, therefore excluding ghost ranges preceding the fossil record.

The fossil record has undergone continuous decay through time. Therefore, representations of diversity through time are subject to variations in preservation bias, such as depositional environment, sea level and body size. Likewise, diversity estimates are limited by the sampling of fossil specimens, which may vary according to geography, climate, rates of erosion, and human factors such as interest, political geography and social mobility (Dunhill *et al.* 2012). Approaches to correct for these effects are controversial. For time-series data from phylogenetic data a common practice has been to plot residuals from a linear model of diversity against the number of taxa-bearing formations through time (Smith & McGowan 2007). This has received criticism, because the two variables must inevitably correlate for sparsely occurring taxa such as dinosaurs and crocodylomorphs (Benton 2015), and therefore this approach represents circular reasoning. Simulation studies have given considerable weight to these concerns (Brocklehurst 2015; Sakamoto *et al.* 2016) making positive correlations between diversity and the number of formations meaningless. However, a negative correlation between diversity and number of formations effectively demonstrates that sampling does not drive the diversity of fossils.

The number of crocodylomorph fossil-bearing formations was included as a proxy for sampling bias (Fig. 4.6, 4.7, 4.8, 4.9), as used by Smith and McGowan (2007). Formation data was assembled from the Paleobiology database (paleodb.org, supplementary information 3). This approach may be applied in a time-series framework, but its effectiveness is doubtful (Benton 2015), with concerns that relations to diversity represent redundancy. In addition, the diversity of contemporary clades can also serve as an indicator of preservation effects, especially among groups that are unlikely to have shared ecological

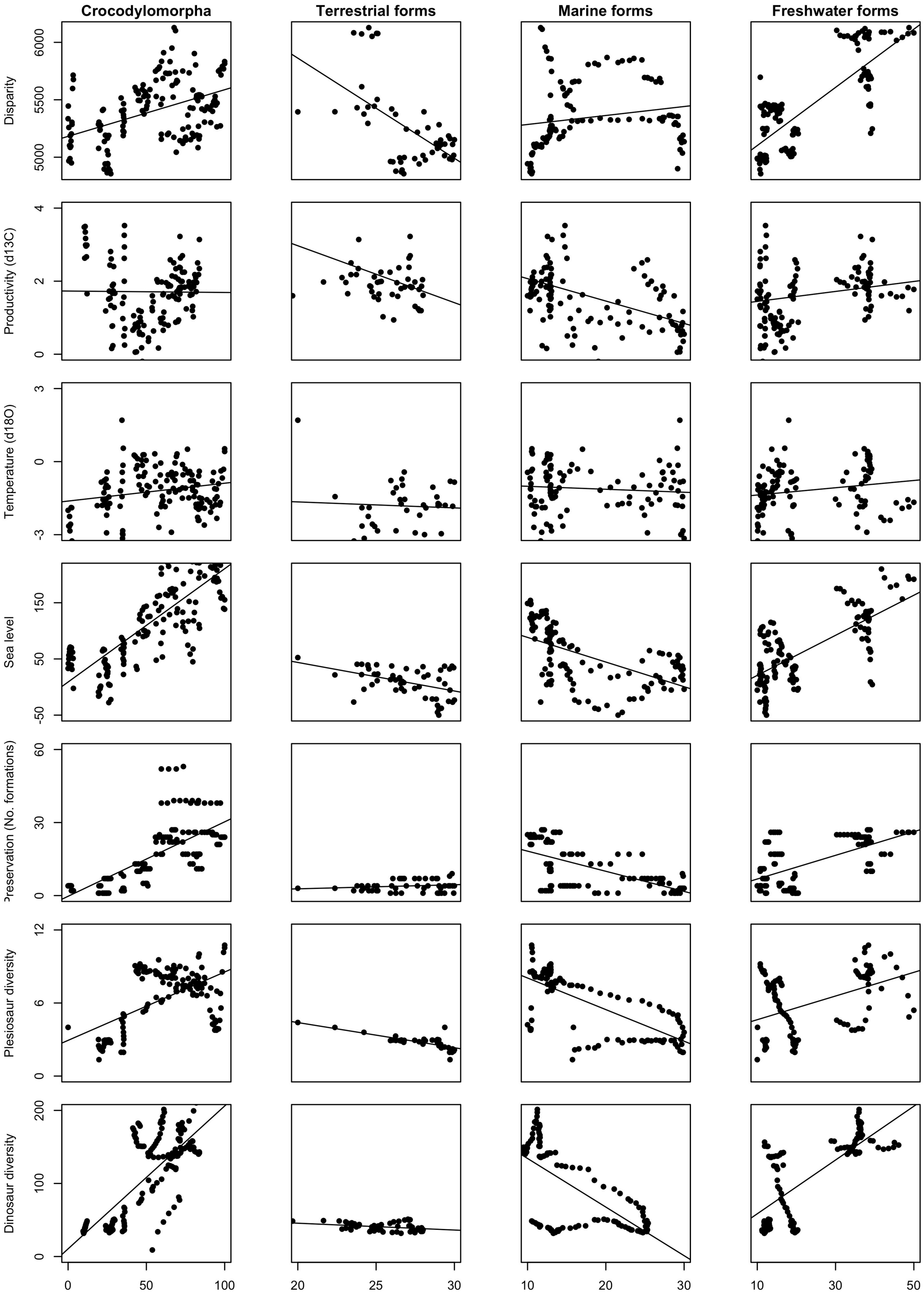

Figure 4.6. Diversity of Mesozoic Crocodylomorpha and three subgroups compared to disparity and other environmental and biotic variables. Each point denotes a single 1-million-year time-bin during the tenure of each group.

interactions. Furthermore, while sea level may impact diversity directly through changes to the distribution of ecospace, relationships between diversity and sea level may arise for other reasons. Sea level may share a common cause (= driver) with diversity, for example through factors such as climate change. Alternatively sea level may functions as a proxy for preservation bias, with increased sedimentation promoting fossilisation.

The ecological and climate regimes of the Mesozoic and Cenozoic differ dramatically, so drivers of crocodylomorph diversity cannot be assumed to be constant. To mitigate this complication, time-series data curves were separated to represent Mesozoic and Cenozoic time intervals. Modelling approaches were then applied to the same subgroups as the morphospace analyses and diversity curves. The combined Tethysuchia and Thalattosuchia were omitted from the analyses of the Cenozoic, since the diversity of these groups yielded quantities of disparity data too low for meaningful statistical power.

Diversity and disparity time-series data were further analysed using multivariate linear approaches. For Mesozoic and Cenozoic diversity and disparity time series, a multivariate linear model was assembled including both temperature proxies, number of formations and relative sea level. Models of Mesozoic diversity and disparity included these environmental variables and the diversity curves of contemporaneous reptile groups. Cenozoic models of crocodylomorph diversity and disparity omitted diversity data from contemporaneous clades because there is no clade of comparable ecology to the mostly amphibious Cenozoic Crocodylomorpha. This process was repeated for crocodylomorph diversity and disparity curves corresponding to each of the sampled groups. Each multivariate model was refined through a process of stepwise deletion. This process removes variables with non-significant effects until the most efficient possible model is found. The relative contribution of the remaining variables to the multivariate model was estimated using AIC scores recovered from the final model, computed as relative AIC weights (Fig. 4.10, 4.11). Like the univariate models, overall relative likelihood of each model was estimated using a log-likelihood value. Summary values from each model and residual normalcy were recovered as before.

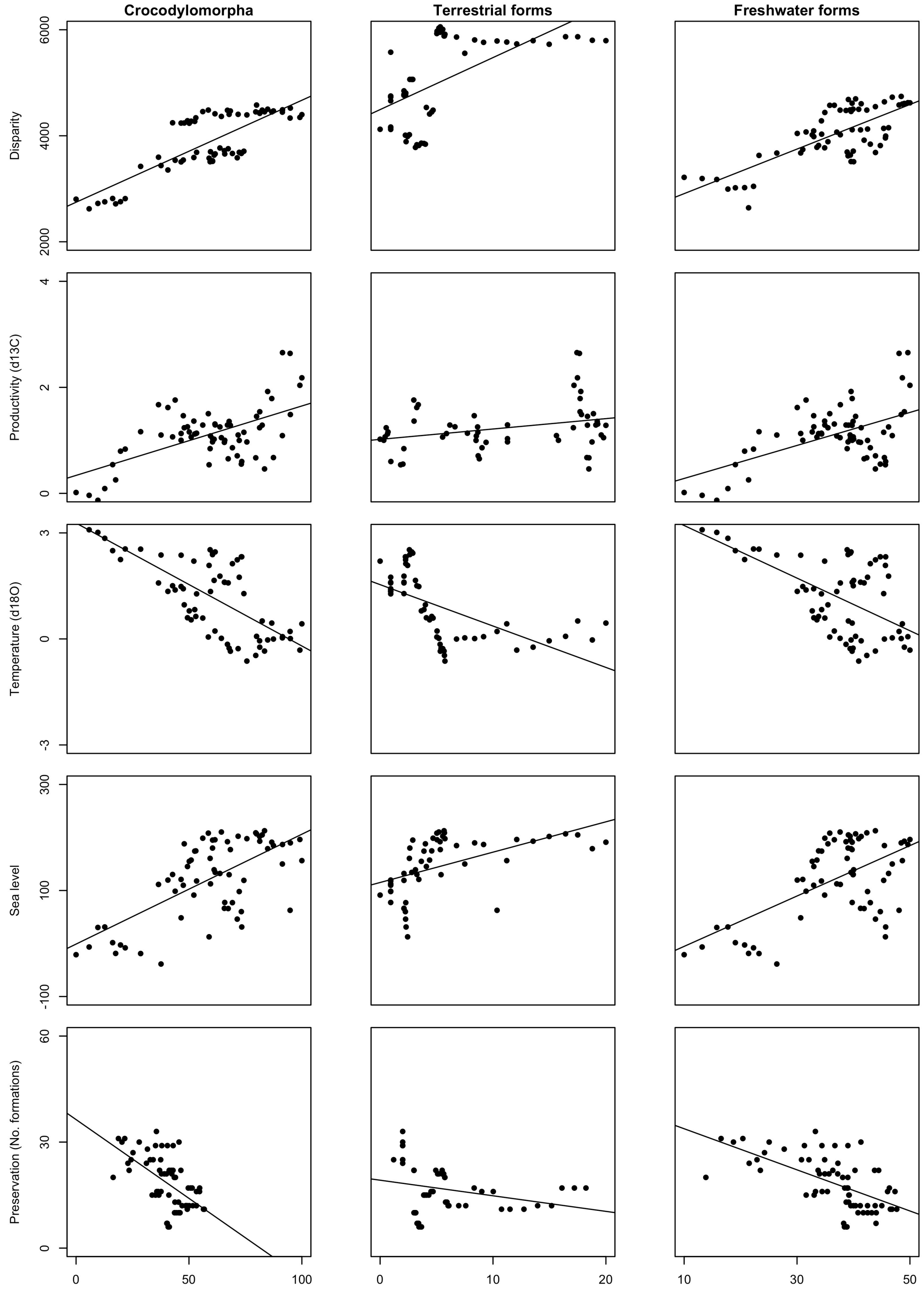

Figure 4.7. Diversity of Cenozoic Crocodylomorpha and two subgroups compared to disparity and other environmental variables. Each point denotes a single 1-million-year time-bin during the tenure of each group.

RESULTS

Morphospace occupancy of the Crocodylomorpha

The subgroups of the Crocodylomorpha analysed occupy different regions of morphospace (Fig. 4.5). The terrestrial Crocodylomorpha, including the Notosuchia and Peirosauridae, return scores intermediate to low in value on principal component 1 and 3. These taxa achieve a representative spectrum of low to high scores on principal component 2. Such terrestrial Crocodylomorpha are the highest-scoring taxa on principal component 2 and lowest-scoring on principal component 3. Marine crocodylomorphs, the combined Tethysuchia and Thalattosuchia, show intermediate to low scores on principal component one. Members of this group show a representative distribution of scores on principal component 2, and intermediate to high scores on principal component 3. The marine Crocodylomorpha are the highest-scoring group on principal component 3, and the lowest-scoring group on principal component 1 of the subgroups tested. Freshwater crocodylomorphs, including the Goniopholididae, Paralligatoridae and Eusuchia, occupy a region of morphospace where the scores on principal components 1 and 3 are intermediate to high, but scores on principal component 2 are intermediate to relatively low. These taxa are the highest-scoring on principal component 1 and lowest-scoring on principal component 2. The crocodylomorph taxa outside these sub groups, including all non-mesoeucrocodylian Crocodylomorpha such as the Protosuchia, score intermediate values on principal components 2 and 3. These taxa score intermediate to low values on principal component 1, and include the lowest-scoring of all the taxa analysed. These areas of morphospace to show a considerable overlap, with a large fraction of each being shared by the other two sub groups. However, non-parametric analysis of variance using all the principal components suggests that the morphospace occupancy differs significantly between each of the subgroups tested.

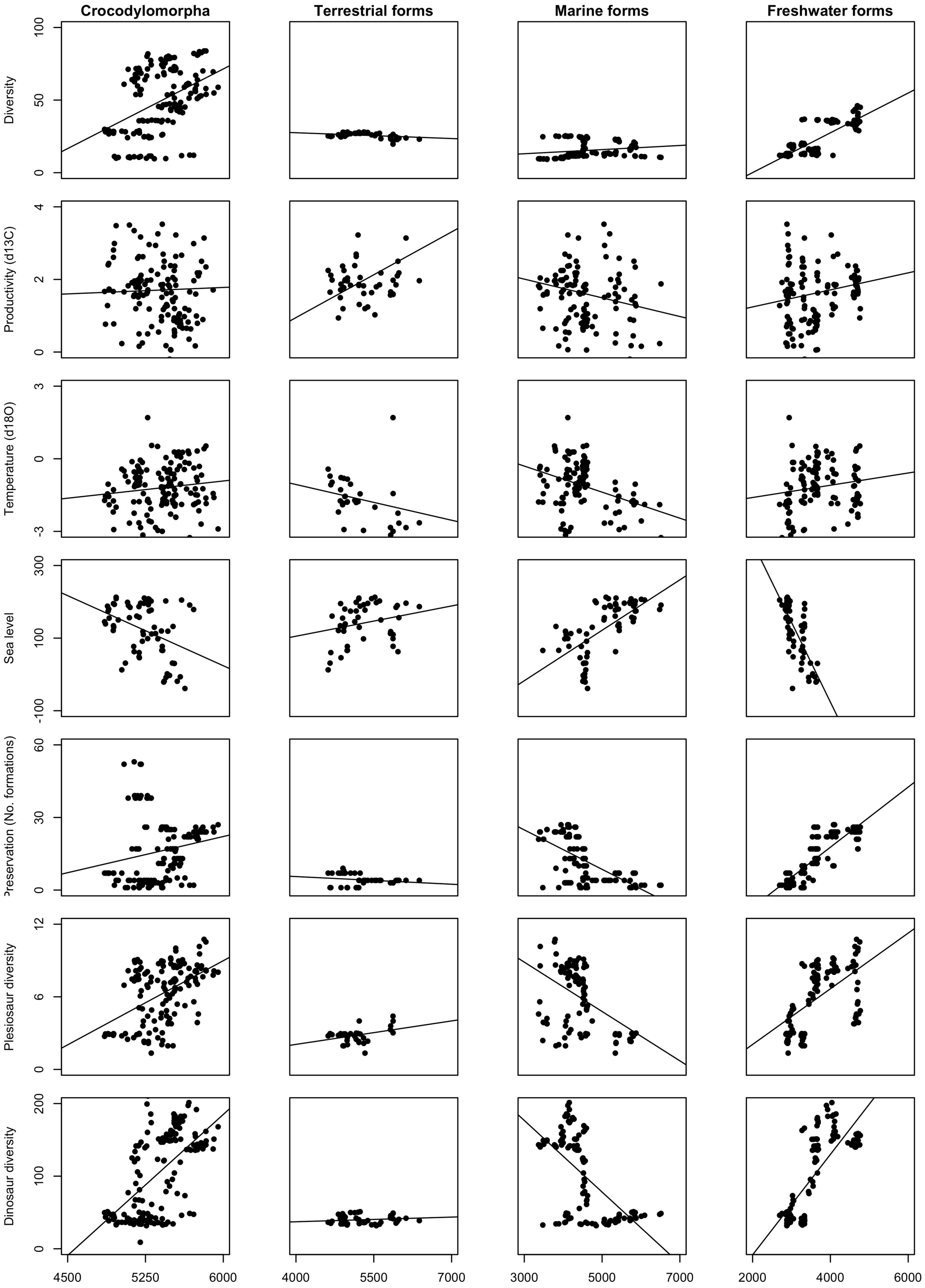

Figure 4.8. Disparity of Mesozoic Crocodylomorpha and three subgroups compared to diversity and other environmental and biotic variables. Each point denotes a single 1-million-year time-bin during the tenure of each group.

Diversity & Disparity through time

The diversity of the Crocodylomorpha shows a number of key stages through the Mesozoic and Cenozoic (Fig. 4.1). Diversity shows an overall increase in diversity from the Late Triassic until the latest Early Cretaceous. Diversity then declines through the Late Cretaceous until the present day (Fig. 4.1A). However, changes in diversity through time are irregular, with episodic peaks and troughs (Fig. 4.1A). Diversity increases in a stepwise manner, peaking in the Late Jurassic, before a period of decline across the Jurassic-Cretaceous boundary into the Early Cretaceous. Increase in diversity then resumes in the same stepwise manner until diversity peaks again. In the Late Cretaceous the decline in diversity is interrupted by two sharp increases in diversity, followed by a steep decline (Fig. 4.1A). Loss of diversity through the Cenozoic is less steep, and pauses through the Oligocene and into the early Miocene before resuming a steep decline to the present day (Fig. 4.1A).

The morphological disparity through time of the Crocodylomorpha is less variable than diversity, but still shows a number of distinct variations (Fig. 4.1B). Disparity appears to decline through the Late Triassic, but the variance of disparity estimates is very wide at this point. Disparity climbs gradually through the Jurassic until a peak in the Early Cretaceous (Fig. 4.1B). Disparity then begins a gradual decline through the Late Cretaceous. The Cretaceous-Palaeogene boundary is marked by a sharp drop in disparity. Disparity remains stable through the Palaeocene and Eocene, followed by a second sharp drop at the Eocene-Oligocene boundary (Fig. 4.1B). Disparity stabilises once again in the Oligocene and much of the Miocene, with a final sharp drop to modern levels of disparity in the late Miocene (Fig. 4.1B).

The diversity of the combined terrestrial crocodylomorph clades Notosuchia and Peirosauridae is relatively stable through the Early and Late Cretaceous, with a modest and localised peak in the Late Cretaceous (Fig. 4.2A). Diversity declines steeply from the Late Cretaceous to the end of the Palaeocene. Diversity through the Eocene and early Oligocene remains low, declining gradually until their extinction (Fig. 4.2A). Morphological disparity in these terrestrial crocodylomorphs seems fairly stable through the Early Cretaceous,

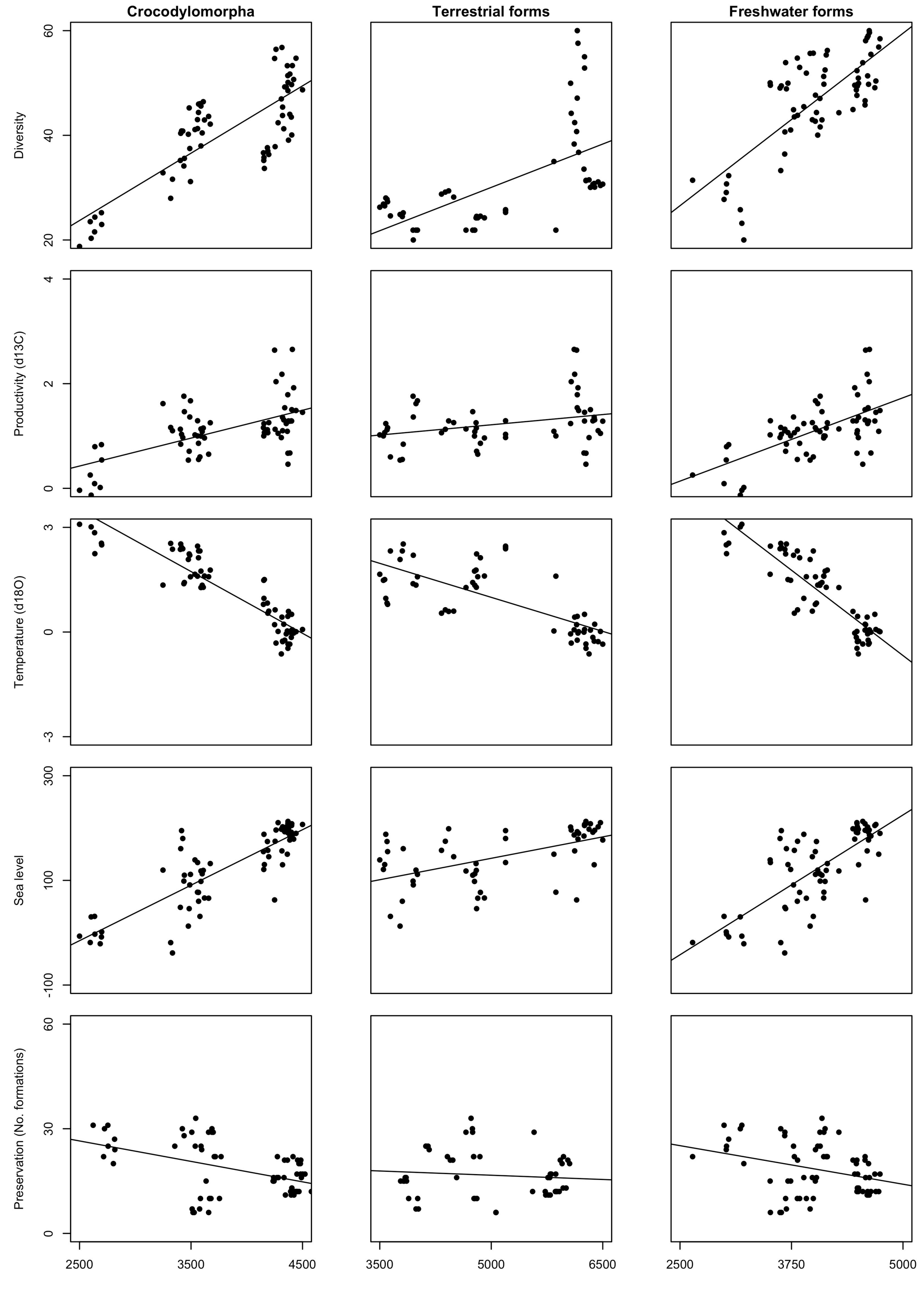

Figure 4.9. Disparity of Cenozoic Crocodylomorpha and two subgroups compared to diversity and other environmental variables. Each point denotes a single 1-million-year time-bin during the tenure of each group.

but the variance of the disparity estimates is wide. There is a sharp increase in disparity during the early Late Cretaceous, followed by a period of stability that persists until the end of the Cretaceous (Fig. 4.2B). Disparity then decreases sharply across the Cretaceous-Palaeogene boundary. Disparity increases rapidly during the early Eocene, remaining stable for a time before declining sharply at the end of the Eocene (Fig. 4.2B).

Diversity of the combined marine crocodylomorph clades Tethysuchia and Thalattosuchia shows a gradual increase from the Early to Middle Jurassic, the rate of increase then climbing from the Middle Jurassic until the Early Cretaceous (Fig. 4.3A). Diversity in the Early Cretaceous then declines sharply, stabilising in the latest Early Cretaceous and throughout the Late Cretaceous. Following the Cretaceous-Paleogene boundary, diversity declines steadily, with the last members of the group going extinct no later than the Eocene (Fig. 4.3A). Disparity of these marine crocodylomorphs decreases steeply through the Early Jurassic (Fig. 4.3B). Disparity recovers quickly, peaking in the Middle Jurassic, before a second period of steep decline through the Late Jurassic. Disparity increases across the Jurassic-Cretaceous boundary, achieving some stability through the Early Cretaceous. Marine crocodylomorph disparity declines steadily through the Late Cretaceous (Fig. 4.3B).

The combined freshwater Crocodylomorph clades, including the Goniopholididae, Paralligatoridae and Eusuchia, show a stepwise increase in diversity through the Mesozoic (Fig. 4.4A). Diversity shows a small but sharp increase across the Middle-Late Jurassic boundary. This increase in diversity is gradually lost through the Late Jurassic and into the Early Cretaceous, but this decline is interrupted by a sharp increase in the later half of the Early Cretaceous (Fig. 4.4A). Diversity remains stable through the remainder of the Early Cretaceous and through most of the Late Cretaceous, before a brief peak in diversity shortly before the Cretaceous-Paleogene boundary. This peak in diversity is followed by a short dip during the Palaeocene (Fig. 4.4A). Diversity peaks again at the Palaeocene-Eocene boundary, followed by a gradual decline throughout the Eocene. Diversity recovers in the Oligocene and into the early Miocene, but then resumes its decline through the upper Miocene to the present day (Fig. 4.4A). These freshwater crocodylomorphs undergo a stepwise increase

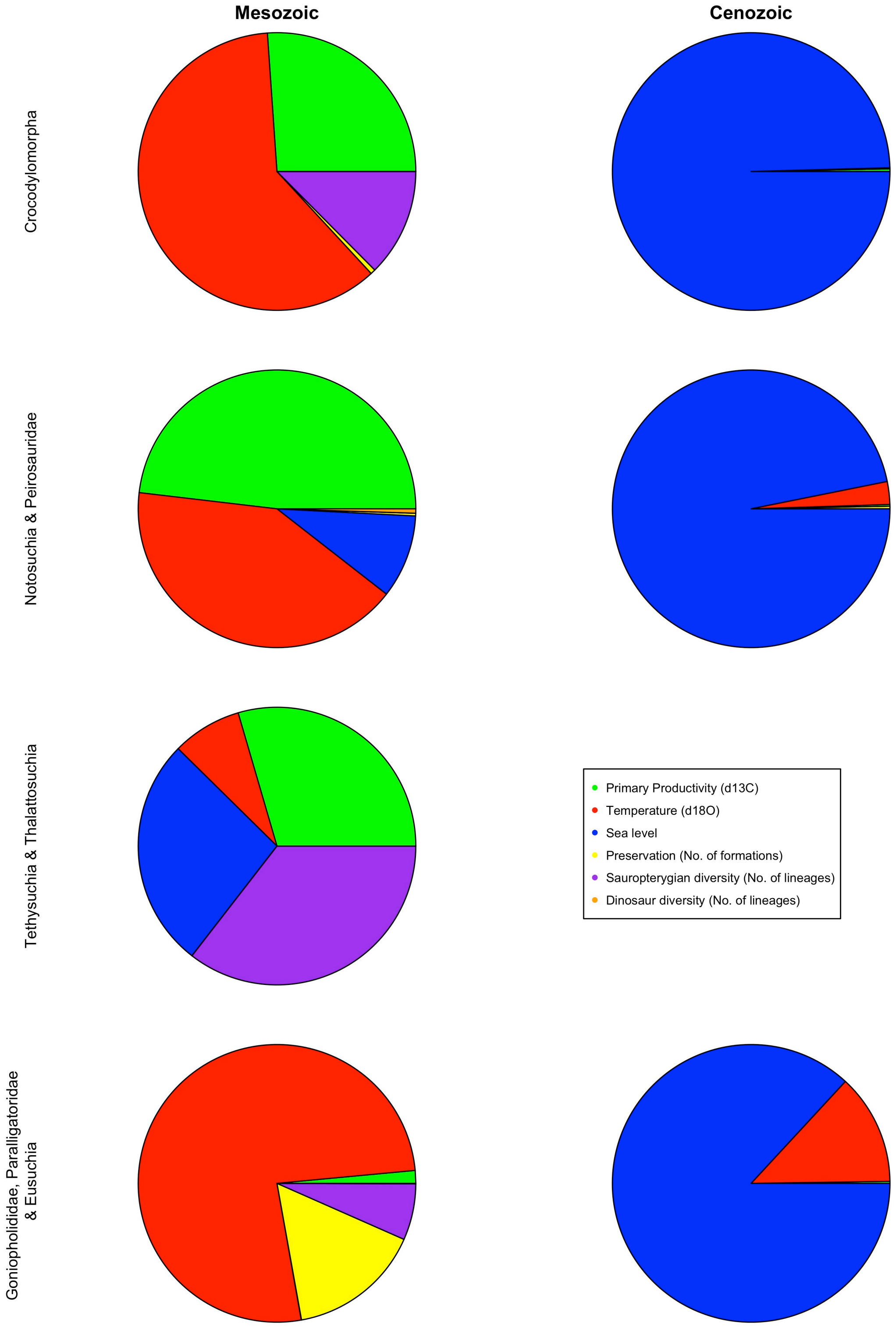

Figure 4.10. Relative weights of remaining variables in multivariate models of diversity following stepwise deletion.

in disparity through the Jurassic and Lower Cretaceous (Fig. 4.4B). Longer periods of relative stability are interrupted by sharp increases in disparity in the Middle Jurassic and across the Jurassic-Cretaceous boundary. Disparity continues to increase across the Early-Late Cretaceous boundary, but at a more gradual rate. Disparity stabilises early in the Late Cretaceous and remains constant throughout the Palaeocene and through the first half of the Eocene (Fig. 4.4B). In the middle Eocene, disparity drops sharply, followed by a period of more gradual decline until the Eocene-Oligocene boundary (Fig. 4.4B). Disparity recovers somewhat during the Oligocene, remaining fairly stable for much of the Miocene. In the late Miocene disparity undergoes another sharp drop to levels similar to that of extant forms (Fig. 4.4B).

Modelling of time-series data

Linear models of time-series data against the diversity of crocodylomorph clades find highly variable relationships (Fig. 4.6, 4.7, 4.8, 4.9). Univariate models of diversity using disparity as an independent variable were the best performing model across all the clades tested in both the Mesozoic and Cenozoic eras. One possible exception is a linear model of diversity and disparity among marine crocodylomorphs from the Mesozoic, which has an extremely weak r-squared value. Most diversity-disparity models have positive lines of slope, however the Mesozoic terrestrial forms show a negative line of slope.

Some linear models did not return normalcy in their residuals, and so do not satisfy the assumptions of a linear model (Table 4.1). Temperature and sea level did not show residual normalcy among most Mesozoic clades. Likewise the number of formations through time did not find normally distributed residuals when compared with Cenozoic diversity. Two exceptions are the terrestrial Mesozoic crocodylomorphs, which show residual normalcy when analysed with temperature, and marine Mesozoic crocodylomorphs, which show residual normalcy when compared with sea level. However, a linear model of terrestrial crocodylomorph diversity with temperature only recovered a p-value of 0.74, and an R-squared value of 0.003, both indicating that this model performs very poorly despite the normal residuals (Table 4.1). Linear models of

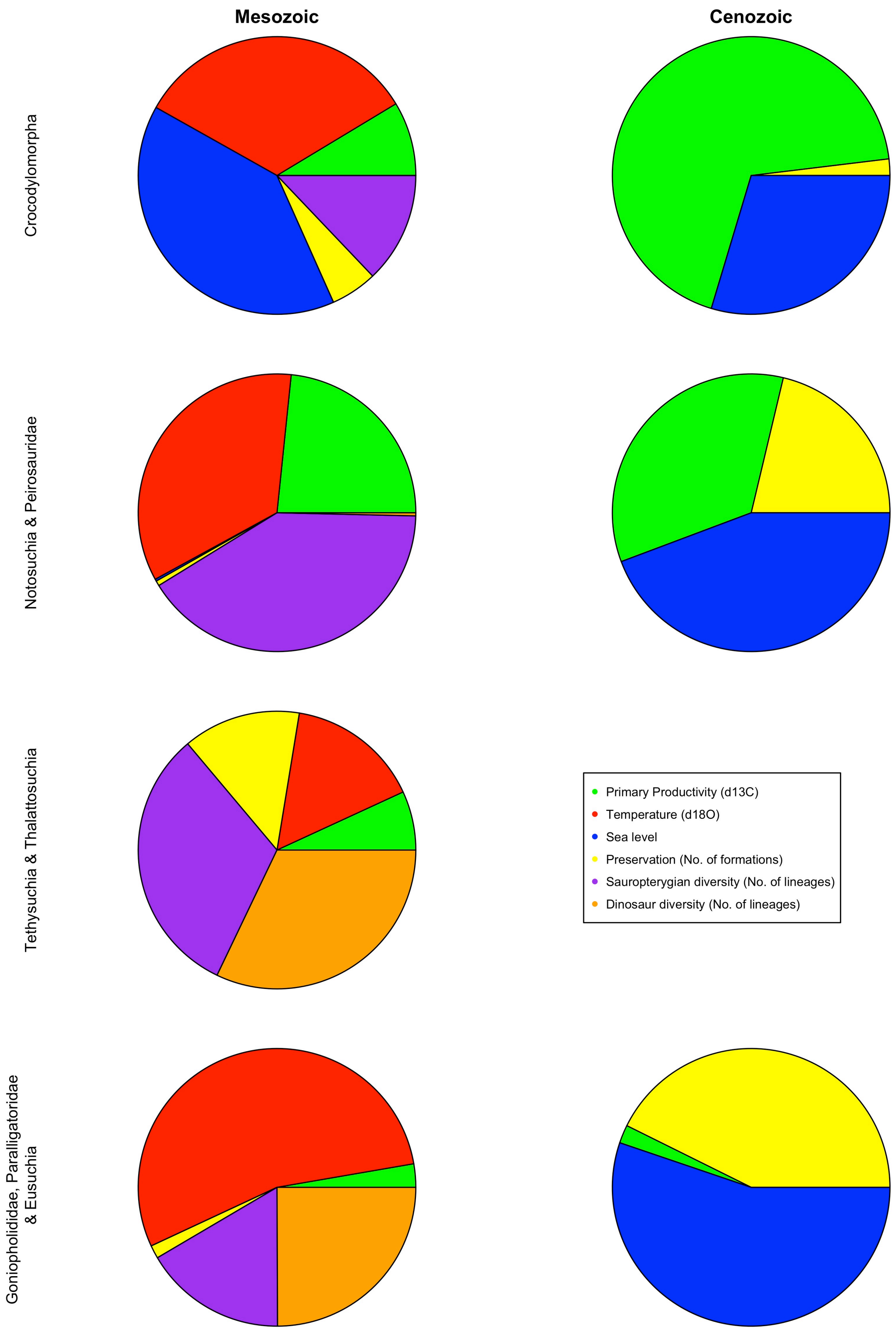

Figure 4.11. Relative AIC weights of remaining variables in multivariate models of disparity following stepwise deletion.

Mesozoic marine crocodylomorph diversity with sea level performs better, returning a value of $p<0.001$, an r-squared value of 0.29 and a negative line of slope. Models of diversity and sea-level during the Cenozoic return normally-distributed residuals, positive lines of slope, significant p-values and r-squared values of more than 0.25 across all the clades tested. Linear models of diversity and primary productivity in the Cenozoic do not find residual normalcy except among terrestrial crocodylomorphs, however the r-squared value of these terrestrial forms is extremely weak. Productivity does find residual normalcy in the Mesozoic, however the analyses only return significant p-values among terrestrial and marine forms. In the Cenozoic only the terrestrial crocodylomorphs show residual normalcy, and this example has an extremely low R-squared value and a relatively high log-likelihood value (Table 4.2). The diversity of other sauropsid clades consistently perform relatively well as predictors of diversity in all the Mesozoic clades tested. Linear models all return residual normalcy, with p-values of less than 0.001, and r-squared values above 0.1 and sometimes as high as 0.59. Models of total-group and freshwater crocodylomorphs show a positive relationship with plesiosaur and dinosaur diversity, while terrestrial and marine groups show a negative relationship (Table 4.1).

When relative model likelihood is estimated using log-likelihood values, multivariate models outperform all univariate models in predicting disparity through time in all the clades tasted (Table 4.2). However, many of these models do not satisfy the requirements of a linear model, having a non-normal distribution of residuals. The exceptions to this are the total-group Crocodylomorpha in both the Mesozoic and Cenozoic, and freshwater forms in the Cenozoic. In addition, multivariate models of crocodylmorph diversity in the Mesozoic return a non-significant p-value. The next best performing model among Mesozoic clades is dinosaur diversity. These models find normally distributed residuals and return significant p-values (Table 4.1). Lines of slope are positive, with the exception of marine forms. R-squared values are relatively high, over 0.3, but with the exception of terrestrial crocodylomorphs which return an r-squared of less than 0.1. The best-performing model of Cenozoic terrestrial crocodylomorphs that has normally-distributed residuals is sea-level.

		Mesozoic			
		croc	terrestrial	marine	freshwater
Residual normalcy	Disparity	3.10E-02	2.48E-03	9.20E-06	3.53E-04
	Productivity	4.06E-06	3.11E-06	8.16E-09	6.08E-09
	Temperature	1.89E-01	2.46E-02	2.38E-01	1.54E-01
	Sea level	5.55E-02	6.92E-01	2.39E-04	1.60E-01
	Preservation	1.83E-09	3.56E-03	9.20E-05	4.06E-04
	Plesiosaur diversity	1.99E-02	1.20E-04	2.07E-07	3.40E-05
	Dinosaur diversity	1.41E-04	1.93E-02	3.19E-08	3.51E-05
	Multivariate	3.23E-03	5.47E-01	2.19E-02	1.13E-01
p. Value	Disparity	2.72E-09	1.07E-05	3.99E-02	3.42E-32
	Productivity	9.35E-01	1.74E-02	6.64E-05	9.51E-02
	Temperature	7.94E-03	7.34E-01	3.64E-01	3.80E-02
	Sea level	1.03E-14	8.18E-01	2.52E-06	1.64E-08
	Preservation	9.84E-28	2.33E-01	7.58E-15	1.14E-17
	Plesiosaur diversity	2.18E-14	1.00E-07	7.69E-18	9.69E-08
	Dinosaur diversity	1.32E-32	1.94E-02	9.17E-17	1.78E-22
	Multivariate	2.37E-02	2.10E-02	3.67E-02	6.50E-03
R-squared	Disparity	2.00E-01	3.24E-01	3.39E-02	6.48E-01
	Productivity	4.73E-05	1.12E-01	1.26E-01	2.13E-02
	Temperature	4.86E-02	3.23E-03	7.78E-03	3.63E-02
	Sea level	6.10E-01	1.07E-03	2.94E-01	3.95E-01
	Preservation	5.28E-01	2.83E-02	3.89E-01	4.22E-01
	Plesiosaur diversity	3.38E-01	5.82E-01	5.04E-01	2.17E-01
	Dinosaur diversity	5.90E-01	1.04E-01	4.31E-01	5.10E-01
	Multivariate	7.47E-01	9.45E-01	8.98E-01	5.41E-01
Log-likelihood	Disparity	-1.11E+03	-4.12E+02	-9.95E+02	-9.98E+02
	Productivity	-2.24E+02	-6.19E+01	-1.84E+02	-2.04E+02
	Temperature	-1.90E+02	-5.27E+01	-1.52E+02	-1.64E+02
	Sea level	-3.46E+02	-2.81E+02	-3.66E+02	-3.61E+02
	Preservation	-5.74E+02	-1.16E+02	-4.20E+02	-4.57E+02
	Plesiosaur diversity	-3.02E+02	-1.61E+01	-2.18E+02	-2.66E+02
	Dinosaur diversity	-8.05E+02	-1.60E+02	-6.44E+02	-6.90E+02
	Multivariate	-4.80E+02	-1.63E+01	-1.99E+02	-3.66E+02

Table 4.1. Outputs of univariate and multivariate linear models of Mesozoic crocodylomorph diversity. Residual normalcy is summarised by a p-value from a Shapiro-Wilk test. Variables included in the multivariate models are shown in figure 4.10.

Sea level models give normally-distributed residuals in all clades except Cenozoic freshwater crocodylomorphs. These models show positive lines of slope among all clades tested except among marine and terrestrial crocodylomorphs from the Mesozoic. Of these models, all return significant p-values and relatively high r-squared values from 0.15 up to 0.7. Together productivity and temperature are generally the worst performing variables in explaining disparity, having the highest log-likelihood values, with the exception of terrestrial crocodylomorphs in the Mesozoic (Table 4.2). Several of these models do not satisfy the assumption of residual normalcy, or return significant p-values. The worst performing variable among Mesozoic terrestrial crocodylomorphs is plesiosaur diversity. However, plesiosaur diversity satisfies residual normalcy, returning significant p-values in all the clades tested and r-squared values of between 0.1 and 0.3. Models of disparity with number of formations through time satisfy residual normalcy in all clades except freshwater crocodylomorphs from the Cenozoic. Of these models, all Mesozoic clades returned significant p-values, along with Cenozoic total-group Crocodylomorpha. These models have positive values of slope, with the exception of terrestrial and marine forms from the Mesozoic. However, the total-group Crocodylomorpha in the Mesozoic show a very weak correlation, with an r-squared of less than 0.05 (Table 4.2).

DISCUSSION

Morphospace occupancy of the Crocodylomorpha

The large overlap in morphospace between each of the subgroups tested (Fig. 4.5) complements the phylogenetic modelling analyses performed in Chapter 3, which found considerable support for a stasis model. Therefore overall the Crocodylomorpha show relatively limited morphological variation within morphospace, irrespective of phylogenetic history or ecological modes. However, the subgroups tested do occupy significantly different regions of morphospace. As discussed previously, the subgroups have a phylogenetic

		Cenozoic		
		croc	terrestrial	freshwater
Residual normalcy	Disparity	1.06E-03	1.07E-02	5.19E-02
	Productivity	5.72E-01	1.95E-02	4.48E-01
	Temperature	5.37E-02	1.95E-01	1.86E-02
	Sea level	2.94E-02	2.19E-02	1.31E-02
	Preservation	2.42E-01	1.99E-01	3.56E-01
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	9.57E-01	8.29E-07	7.54E-02
p. Value	Disparity	2.50E-15	1.42E-06	7.92E-13
	Productivity	3.78E-07	2.62E-02	3.83E-06
	Temperature	8.03E-12	1.20E-06	9.70E-08
	Sea level	1.65E-09	4.09E-05	2.05E-07
	Preservation	4.74E-07	4.40E-02	5.50E-08
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	2.04E-08	6.76E-05	4.17E-08
R-squared	Disparity	6.27E-01	3.58E-01	5.54E-01
	Productivity	3.34E-01	8.98E-02	2.85E-01
	Temperature	5.21E-01	3.62E-01	3.61E-01
	Sea level	4.36E-01	2.74E-01	3.46E-01
	Preservation	3.29E-01	7.44E-02	3.72E-01
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	8.28E-01	6.07E-01	7.32E-01
Log-likelihood	Disparity	-4.80E+02	-4.33E+02	-4.79E+02
	Productivity	-3.85E+01	-3.23E+01	-4.08E+01
	Temperature	-7.74E+01	-6.24E+01	-8.69E+01
	Sea level	-3.58E+02	-2.87E+02	-3.63E+02
	Preservation	-2.12E+02	-1.80E+02	-2.10E+02
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	-1.84E+02	-1.30E+02	-1.85E+02

Table 4.2. Outputs of univariate and multivariate linear models of Cenozoic crocodylomorph diversity. Residual normalcy is summarised by a p-value from a Shapiro-Wilk test. Variables included in the multivariate models are shown in figure 4.10.

definition that reflects a general, but not absolute, ecomorphological mode. The separation in morphospace between each of these subgroups could be attributed to functional variation, with biomechanical constraints of locomotion and feeding in different settings driving morphospace occupancy. However, such ecological separation might be expected to result in less overlap between the morphospace of each group. Analysis of disparity in mandible morphology by Stubbs *et al.* (2013) used geometric morphometrics to demonstrate a distribution of crocodylomorph taxa through morphospace comparable with those found in this analysis. Stubbs *et al*. (2013) found that Tethysuchia and Thalattosuchia occupy a different region of principal component 1 from the Notosuchia and Peirosauridae, with the Eusuchia and other Neosuchia forming an intermediate group. However the separation between the taxa included in the subgroups in this analysis is much wider in Stubbs *et al.*, possibly because of their use of functional morphology rather than cladistics data. Therefore in the case of the morphospaces synthesized in this example, perhaps it is more conservative to attribute the differences in morphospace occupancy to shared phylogenetic history than function.

Effect of sampling and preservation on diversity estimates

Models of Mesozoic crocodylomorph diversity with number of formations are relatively well supported, with significant p-values and relatively high r-squared values in most subgroups, with the exception of the terrestrial Crocodylomorpha (Table 4.1). When analysed in this manner, preservation outperforms other variables in most of the linear models of Mesozoic diversity according to log-likelihood values. Most multivariate models following stepwise deletion do not include preservation (Fig. 4.10, 4.11), with the exception of freshwater crocodylomorphs in the Mesozoic. Superficially this may appear to indicate that diversity is driven by the number of crocodylomorph fossil-bearing formations. However, of the groups tested, the only subgroup where the relationship was both significant and positive was the freshwater forms (Fig. 4.6), and therefore it is likely they that are driving this relationship among the total-group Crocodylomorpha. Further, this relationship is to be expected, since the number

		Mesozoic			
		croc	terrestrial	marine	freshwater
Residual normalcy	Diversity	1.24E-04	2.78E-03	5.12E-11	5.46E-02
	Productivity	5.37E-06	3.34E-01	2.40E-07	4.59E-08
	Temperature	3.91E-01	1.94E-04	2.11E-01	2.53E-01
	Sea level	2.96E-06	3.03E-02	7.75E-02	2.36E-03
	Preservation	1.64E-09	1.46E-03	7.50E-03	5.82E-05
	Plesiosaur diversity	2.84E-02	7.00E-02	6.69E-05	9.78E-05
	Dinosaur diversity	2.92E-02	1.79E-02	2.68E-02	6.90E-06
	multivar	1.49E-02	4.59E-01	2.53E-01	3.87E-01
p. Value	Diversity	2.72E-09	1.07E-05	3.99E-02	3.42E-32
	Productivity	7.49E-01	3.36E-07	8.61E-02	1.38E-01
	Temperature	1.05E-01	4.89E-03	5.65E-05	8.41E-02
	Sea level	1.23E-03	1.86E-03	5.54E-09	8.43E-13
	Preservation	6.16E-03	5.99E-03	4.34E-16	2.43E-39
	Plesiosaur diversity	6.43E-11	2.26E-02	6.99E-08	1.48E-10
	Dinosaur diversity	1.25E-18	2.26E-02	3.68E-15	4.89E-30
	multivar	1.04E-01	8.94E-02	3.67E-02	1.06E-01
R-squared	Diversity	2.00E-01	3.24E-01	3.39E-02	6.48E-01
	Productivity	7.29E-04	4.22E-01	2.46E-02	1.69E-02
	Temperature	1.84E-02	2.00E-01	1.42E-01	2.53E-02
	Sea level	1.52E-01	1.78E-01	4.14E-01	5.53E-01
	Preservation	4.62E-02	1.41E-01	4.17E-01	7.25E-01
	Plesiosaur diversity	2.60E-01	1.48E-01	2.41E-01	2.97E-01
	Dinosaur diversity	3.87E-01	9.97E-02	3.96E-01	6.21E-01
	multivar	4.13E-01	7.87E-01	5.88E-01	8.28E-01
Log-likelihood	Diversity	-7.08E+02	-9.69E+01	-3.88E+02	-4.44E+02
	Productivity	-2.24E+02	-5.12E+01	-1.90E+02	-2.04E+02
	Temperature	-1.92E+02	-4.85E+01	-1.44E+02	-1.64E+02
	Sea level	-3.72E+02	-2.76E+02	-3.60E+02	-3.51E+02
	Preservation	-6.31E+02	-1.13E+02	-4.17E+02	-4.07E+02
	Plesiosaur diversity	-3.10E+02	-2.85E+01	-2.41E+02	-2.59E+02
	Dinosaur diversity	-8.37E+02	-1.60E+02	-6.48E+02	-6.72E+02
	multivar	-8.94E+02	-1.85E+02	-7.12E+02	-7.46E+02

Table 4.3. Outputs of univariate and multivariate linear models of Mesozoic crocodylomorph disparity. Residual normalcy is summarised by a p-value from a Shapiro-Wilk test. Variables included in the multivariate models are shown in figure 4.11.

of taxa is directly dependent on the number of places where their fossils can be found. This relationship has been suggested as a proxy for sampling (Smith & McGowan 2007), but this relationship probably represents correlation when applied to raw taxic diversity (Benton 2015; Sakamoto *et al*. 2016). Diversity as lineages through time may be less vulnerable to this systematic flaw to a limited extent, since taxa may be inferred in the absence of specimens or formation exposure. In addition, the number of rock formations through time can be expected to be a function of time, with more ancient formations being lost more readily. As such the number of formations through time may function simply as a proxy for time. Therefore instead of representing preservation as a driver of apparent diversity, this model may be confirming an increase in diversity over time.

A linear model of Mesozoic marine crocodylomorph diversity with the number of formations did return a significant p-value and an r-squared value of 0.38 (Table 4.1). It was also one of the higher-likelihood models according to log-likelihood scores. However, the line of slope of this model is negative (Fig. 4.6), so the number of taxa is highest when the number of crocodylomorph-bearing formations is low. Therefore the diversity of Mesozoic marine crocodylomorphs cannot be attributed to the availability of rock formations. This raises the question of what is driving support for this linear model. Similar to models showing a positive correlation, in this model the number of formations may be functioning simply as a proxy for time, rather than preservation. Ostensibly this model is identifying a significant decline in diversity over time in Mesozoic crocodylomorphs, which is visible in the diversity time-series.

Without normally distributed residuals (Table 4.2), models of Cenozoic diversity with number of formations do not satisfy the assumptions of a linear model. Further, the regression lines of these models have a negative line of slope. This strongly suggests that diversity of crocodylomorphs in the Cenozoic is not an artefact of preservation or sampling bias. The number of formations increases over time, since less time has elapsed for erosion and diagenesis to destroy the more recent examples, and with more preservation of rock the more recent formations may be shorter in temporal duration. However, diversity shows an

		Cenozoic		
		croc	terrestrial	freshwater
Residual normalcy	Diversity	4.38E-02	7.83E-05	2.65E-01
	Productivity	3.21E-02	1.95E-02	5.88E-01
	Temperature	6.20E-01	4.29E-02	7.98E-02
	Sea level	1.31E-02	1.49E-02	6.32E-01
	Preservation	3.59E-02	7.21E-02	3.29E-01
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	1.04E-03	3.60E-01	1.93E-05
p. Value	Diversity	2.50E-15	1.42E-06	7.92E-13
	Productivity	2.61E-07	2.62E-02	3.36E-08
	Temperature	1.62E-26	4.72E-10	1.04E-23
	Sea level	1.63E-18	2.01E-05	5.58E-13
	Preservation	1.28E-04	4.83E-01	1.14E-02
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	7.83E-04	4.41E-02	1.78E-07
R-squared	Diversity	6.27E-01	3.58E-01	5.54E-01
	Productivity	3.41E-01	8.98E-02	3.81E-01
	Temperature	8.32E-01	5.22E-01	7.95E-01
	Sea level	7.03E-01	2.93E-01	5.59E-01
	Preservation	2.06E-01	9.34E-03	9.60E-02
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	8.19E-01	6.70E-01	1.00E+00
Log-likelihood	Diversity	-2.09E+02	-1.44E+02	-2.02E+02
	Productivity	-3.81E+01	-3.23E+01	-3.61E+01
	Temperature	-4.27E+01	-5.44E+01	-4.94E+01
	Sea level	-3.37E+02	-2.87E+02	-3.50E+02
	Preservation	-2.18E+02	-1.82E+02	-2.22E+02
	Plesiosaur diversity	N/A	N/A	N/A
	Dinosaur diversity	N/A	N/A	N/A
	multivar	-4.56E+02	-4.15E+02	-1.97E+03

Table 4.4. Outputs of univariate and multivariate linear models of Cenozoic crocodylomorph disparity. Residual normalcy is summarised by a p-value from a Shapiro-Wilk test. Variables included in the multivariate models are shown in figure 4.11.

overall decline through the Cenozoic, despite the increasing availability of rocks to preserve crocodylomorph remains. Therefore the apparent decline in crocodylomorph diversity through the Cenozoic (Fig. 4.1A) can conclusively be interpreted as real.

While linear models of diversity with number of formations may not be able to provide a convincing indication of the effects of preservation, the effects of preservation and sampling bias may be evident elsewhere. For all the Mesozoic crocodylomorph groups tested, diversity shows a significant correlation with the diversity of dinosaurs and plesiosaurs. It is tempting to attribute this to ecological interaction between these groups, but this premise is implausible. Terrestrial crocodylomorphs show a significant correlation with the marine plesiosaurs, and the marine crocodylomorphs show a significant correlation with the terrestrial dinosaurs. Similarities in diversity through time between these isolated groups must be attributed to global processes. Preservation bias may represent such a global process, with the apparent diversity of all three clades being transformed by taphonomy, diagenesis and erosion over a comparable time interval. This is difficult to test empirically, and there may be other global factors that could drive a similar autocorrelation in diversity curves, for example global temperature, primary productivity or sea level.

Models showing relationships between diversity and sea level may also be indicators of interaction between diversity and preservation. Higher sea level can be expected to lead to an increase in submarine environments that may promote preservation through increased burial. Therefore preservation of any given specimen may increase with sea level. Diversity shows significant correlations with sea level in all the clades tested in both Mesozoic and Cenozoic eras, and log-likelihoods indicate these models have relatively high likelihood compared to others. Sea level is also retained as a variable in most of the multivariate models. However, sea level may interact with diversity in other ways besides preservation, through the redistribution of ecospace. This is especially relevant in the example of the Crocodylomorpha, since many species were amphibious and would have inhabited oceans, river systems, estuaries and marine habitats subject to sea level change.

In sum, preservation potential may effect the perception of crocodylomorph diversity through time. However, this is very difficult to test empirically, and it is clear that some apparent patterns of crocodylomorph diversity through time are real. There are several variables that may show effects of preservation on Crocodylomorph fossil diversity, but all of these variables may be attributable to other processes. These findings demonstrate the necessity of using lineages through time from phylogeny, thereby including common ancestors and ghost ranges, rather than raw species richness as an indicator of diversity through time.

Diversity and disparity through time

There are some similarities in the topography of diversity and disparity curves in total-group Crocodylomorpha, although the relative range of disparity values is much more muted than diversity (Fig. 4.1). Both curves share a decline through the Triassic, followed by an overall increase peaking in the Early Cretaceous. Both curves also agree on a subsequent decline, which is interrupted by the Cretaceous-Palaeocene and Eocene-Oligocene boundaries. A loss of both disparity and diversity is observed in the late Miocene (Fig. 4.1). The disparity curve of the total-group disparity curve also shows similarities with published disparity curves estimated using geometric morphometric data collected from skulls (Wilberg 2017). Wilberg (2017) used an assortment of disparity metrics, however all of them agreed upon details observed in the disparity curve presented here. All four of the disparity curves presented by Wilberg agree that there is an overall increase in disparity through the Mesozoic, peaking in the Late Cretaceous, and then declining throughout the Cenozoic, similar to the disparity curve in this analysis. All four disparity curves agree on a steep decline in disparity in the late Cretaceous, which is interrupted by the Cretaceous-Palaeogene boundary (Wilberg 2017). There are further specific similarities shared by the disparity curve presented here with a sum of variances curve presented by Wilberg. Both curves show a steep decline in disparity in the upper Jurassic, a period of stability through the Oligocene and Miocene, and a steep decline in the late Miocene (Wilberg 2017). Perhaps the similarities between

Wilberg 2017 and the analysis shown here is due to conservative morphology. The skull morphometric data used by Wilberg may be showing the same disparity variation as the phylogenetic character data used here.

Covariation between diversity and disparity is also evident in the tested subgroups. The terrestrial Crocodylomorpha show a period of relative stability in the Cretaceous, with a peak in the Late Cretaceous (Fig. 4.2). Both diversity and disparity decline steeply across the Cretaceous-Palaeogene boundary. However, while diversity remains low during the Eocene disparity does recover somewhat (Fig. 4.2). The marine Crocodylomorpha shows much higher diversity and disparity in the Jurassic than most of the cretaceous, but disparity decreases much more quickly than diversity (Fig. 4.3). Freshwater crocodylmorphs show a similar stepwise increase in diversity and disparity through the Jurassic and Cretaceous periods, both peaking in the late Cretaceous, and then showing a similar decline through the Cenozoic (Fig. 4.4). The decline in both diversity and disparity is interrupted by a period of recovery and stability across the Palaeogene-Neogene boundary (Fig. 4.4).

Disparity was the highest likelihood variable in predicting diversity in all the clades tested in both the Cenozoic and Mesozoic, with the exception of freshwater crocodylomorphs in the Cenozoic, which fail to return normally-distributed residuals (Table 4.3, 4.4). Collectively, both these models and the time-series curves indicate a coupling of diversity and disparity. There is not sufficient cause to attribute these data to either a disparity-first or diversity-model. These are models where diversity and disparity are decoupled and increase at different rates. Such patterns are something of an over-simplification, with disparity patterns having been attributed to the magnitude of morphological change, diversification rates, extinction rates and selection. However, disparity-first models are anticipated in situations where extinction rates decrease over time, and in clades that diversify exponentially (Foote 1996). Disparity curves at species-level resolution have previously been found to peak faster than their equivalent disparity curve in several invertebrate clades, including gastropods (Wagner 1995), crinoids (Foote 1994, 1995) and marine arthropods (Briggs *et al.* 1992, Foote & Gould 1992, Wills *et al.* 1994). This is generally less true of higher-rank taxonomic groups, which tend to show a greater coupling of diversity with disparity (Foote 1996). This contrasts strongly with the coupled diversity-disparity profile in the data presented here. Perhaps this is in agreement with support for a stasis model of body size evolution demonstrated in Chapter 3, indicating that rates of morphological change, extinction and diversification are very stable among crocodylomorphs. Decoupling of diversity can occur during periods of decline as well as diversification. Rate of decline in diversity was found to be slower that the rate of decline in disparity in trilobites (Foote 1993). The authors suggest that morphology was not a determining factor in the extinction of trilobites. This bears comparison with the loss of crocodylomorph diversity and disparity through the Cenozoic, since disparity remains stable for long periods while diversity is undergoing continuous decline.

There are some limitations to these analyses that must be acknowledged as caveats a conclusion that diversity and disparity are coupled. First, the variance in disparity estimates can be extremely wide at the beginning of a sample time-interval, and when the sample size is small. This greater variance is most likely due to small sample size and increasing uncertainty of node dates in the phylogenetic tree. This creates a much wider relative variation in the presence or absence of taxa in each 1-million-year time interval. Secondly estimating the presence or absence of taxa using a phylogenetic tree can only infer ghost-ranges previous to the fossil range. Absences from the fossil record following the fossil range of a taxon cannot be inferred. This may result in a backward ‘smearing’ effect, deforming the apparent rates of change in diversity and disparity. A phylogenetic curve may exaggerate older diversity or disparity and disguise the impact of mass extinctions as long-term decline (Lane *et al.* 2005; Brocklehurst *et al.* 2013). However, a range-top ghost range will by definition be younger than the ghost range previous to fossil occurrences. Therefore, subsequent diagenesis and erosion will have less time to act on specimens. Perhaps a range-top ghost range will be shorter than its older phylogenetically inferred counterpart. However, both diversity and disparity curves in this analysis have been determined using phylogenetic trees, therefore any distortion is likely to be equal between both curves.

Rapid changes in diversity and disparity are associated with mass extinctions (Fig. 4.1, 4.2, 4.3, 4.4). Among the total-group Crocodylomorpha, there is an increase in diversity coincident with the end-Triassic and end-Eocene events (Fig. 4.1A). These events are also coincident with decreases in disparity. There is a decrease in diversity across the Cretaceous-Palaeogene boundary (Fig. 4.1A), which may have been a more profound event due to the possible backward 'smearing' effect of phylogenetic diversity curves. The Cretaceous-Palaeogene boundary also sees a sharp drop in disparity in the total-group Crocodylomorpha (Fig. 4.1B). Previous studies of diversity across the Jurassic-Cretaceous boundary have suggested that a mass extinction may have taken place (Benson *et al.* 2009), while others have found the loss of diversity in this period to be more gradual (Tennant *et al.* 2016). There is a decrease in diversity across the Jurassic-Cretaceous boundary, although disparity dips only slightly. The terrestrial Crocodylomorpha show a dramatic decrease in diversity across the Cretaceous-Palaeogene boundary (Fig. 4.2A). Again, this decrease may have been muted by the limitations of estimating diversity from phylogenetic trees. There is also a sharp drop in disparity coincident with the Cretaceous-Palaeogene boundary (Fig. 4.2B). The diversity of the marine Crocodylomorpha seems relatively unaffected by the Jurassic-Cretaceous boundary, continuing to increase into the Cretaceous (Fig. 4.3A). Disparity increases rapidly for a short time across the boundary before stabilising in the Early Cretaceous (Fig. 4.3B). The diversity of freshwater Crocodylomorpha does not change coincident with the Jurassic-Cretaceous boundary, but disparity does see a sharp increase (Fig. 4.4). There is a sharp and substantial increase in diversity coincident with the mid-Aptian extinction event (Fig. 4.4A), but disparity remains stable (Fig. 4.4B). Diversity drops across the Cretaceous-Palaeogene boundary, but disparity does not show a very noticeable change (Fig. 4.4B). Both diversity and disparity show a sharp increase following the end-Eocene extinction event (Fig. 4.4). Diversity and disparity both show a steep decline coincident with the mid-Miocene extinction event (Fig. 4.4). These changes in diversity and disparity support extinction events as significant factors in the evolution and diversification of crocodylomorphs. The disparity through time of all the clades tested frequently show long periods of stability between extinction events, further emphasizing their significance (Fig. 4.4B).

Among Mesozoic crocodylomorphs, primary productivity only shows a significant correlation with diversity in the terrestrial and marine subgroups (Table 4.1). These models return only modest r-squared values of 0.11 and 0.12 respectively, and according to their log-likelihood values these models have relatively low likelihood. Therefore it is difficult to link primary productivity to diversity of crocodylomorphs in the Mesozoic. This is generally also true of Cenozoic diversity, but the diversity of freshwater Crocodylomorpha do not satisfy the assumption of normally-distributed residuals, and the total-group Crocodylomorpha achieve a somewhat higher r-squared value.

Multivariate Mesozoic disparity models either do not return significant relationships or do not find normally-distributed residuals (Table 4.2). Cenozoic disparity curves return normally distributed residuals for the total-group Crocodylomorpha and terrestrial forms, and both the clades return significant p-values. However, the r-squared value for the terrestrial forms is extremely low, 0.08, and the log-likelihood of both models is the poorest of all the disparity models tested on their respective clades. The only multivariate models of disparity that found both normally-distributed residuals and significant p-values were the Cenozoic total-group and freshwater Crocodylomorpha . These models do retain primary productivity as a variable. However, the support for primary productivity as a variable in freshwater crocodylomorph disparity is far outweighed by sea level and the number of crocodylomorph fossil-bearing formations. The greater support for primary productivity as a variable in a model of total-group crocodylomorph disparity is likely driven by the terrestrial Crocodylomorpha, which show an extremely small sample size during the Cenozoic. From these observations, primary productivity cannot justifiably be identified as a principal driver of Crocodylomorph disparity, however it may have had some small influence in the Cenozoic. Alternatively disparity and primary productivity may have had a common driver.

Sea level performs poorly in the Mesozoic diversity across most of the clades tested, either failing to return normally-distributed residuals or not achieving a significant p-value (Table 4.1). The exception is a linear model of sea level compared with diversity of Mesozoic marine crocodylomorphs, which satisfies residual normalcy and returns a significant p-value. The r-squared value is the second lowest among the models tested for Mesozoic marine crocodylomorphs, but the log-likelihood indicates that it is one of the better performing models. This finding contradicts previous work by Pierce *et al.* (2009), who found the diversity of thalattosuchians to increase with sea level. A similar result was found by Martin *et al.* (2014), with increases in taxic diversity being associated with higher sea level. Sea level performs rather better among diversity models in the Cenozoic, satisfying residual normalcy, with significant p-values and relatively high r-squared values. Log-likelihood indicates sea level is among the second best-performing dependant variable among Cenozoic models, and there is considerable support for sea level as a variable in multivariate models. As noted previously this may be an indicator of increased preservation potential with higher sea levels. This seems likely for the terrestrial Cenozoic crocodylomorphs. Alternatively, higher sea levels may redistribute ecospace such that it encourages greater diversity of crocodylomorphs.

Sea level performs well as an explanatory variable in models of disparity. Most models run satisfy residual normalcy, with the exception of Cenozoic freshwater crocodylomorphs. These models return significant p-values and relatively high r-squared values. Log-likelihood values also indicate that these models perform well (Table 4.1). This cannot be attributed to preservation bias, since disparity represents morphological variability and is less susceptible to taphonomy and diagenesis. Coupling of diversity and disparity also fails to present a satisfactory explanation, since a relationship between sea level and diversity has not been observed. Therefore perhaps the relationship between sea level and disparity is an ecological one. Speculatively, higher sea levels could create greater areas of marine shelf habitat for marine crocodylomorphs, and promote swampy or lacustrine habitats further inland. Alternatively, high sea levels may increase the isolation of landmasses, since bodies of deep water will widen. Such isolation may lead to an increased distinction between regional crocodylomorph faunas, increasing disparity. Analysing relationships between crocodylomorph disparity and palaeogeography is a potential avenue for further study. These results concur with those of Pierce *et al.* (2009), which found the diversity of the Thalattosuchia to correlate strongly with sea level.

Temperature performed poorly as an explanatory variable in models of diversity in most of the subgroups tested. Only terrestrial crocodylomorphs satisfied residual normalcy in the Mesozoic, and only freshwater crocodylomorphs satisfied residual normalcy in the Cenozoic (Table 4.2). Of these models only the freshwater crocodylomorphs returned a significant p-value and high r-squared value. The log-likelihood values showed that these models performed relatively poorly compared to other variables, even when the p-values were significant (Table 4.2). Models of disparity with temperature only satisfied residual normalcy in terrestrial and freshwater marine crocodylomorphs. These returned significant p-values. The r-squared value returned by Mesozoic terrestrial forms was modest, around 0.2, but the Cenozoic subgroups both found high r-squared values of more than 0.5 (Table 4.3, 4.4). However, log-likelihood values suggest that these models have relatively lower likelihood compared to other variables. These findings show notable comparison with those of Mannion *et al.* (2015), who identified a relationship between temperature and diversity in terrestrial crocodylomorphs. However, the findings of Mannion *et al.* included amphibious forms in the sample of terrestrial crocodylomorphs. Perhaps the findings presented here show that those of Mannion *et al.* were driven by land-living terrestrial forms. The analyses presented here contradict the findings of Martin *et al.* (2014), who only found a relationship between temperature and diversity in the Thalattosuchia by excluding Metriorhynchidae. Since Martin *et al.* did not apply a phylogenetic correction, Lazarus taxa will be under-represented in their data. Therefore preservation or sampling effects may bias the apparent diversity of the metriorhynchid fossil record. If metriorhynchid fossil diversity is driven by preservation or sampling, a relationship between true diversity and temperature may be obscured. These results also contrast with those of Mannion *et al.*, which identified a relationship between temperature and the diversity of marine Crocodylomorpha. The approach of Mannion *et al.* was similar to that presented here in that marine Tethysuchia were included in the sample of marine

Crocodylomorpha. However there was a significant methodological difference in their application of subsampling to correct for preservation and sampling.

The clade showing the greatest interaction with temperature in this analysis is freshwater crocodylomorphs in the Cenozoic. This is a large group and accounts for the majority of Cenozoic crocodylomorphs, and also includes the entire crown-group. Since the Cenozoic also sees dramatic changes in climate, it seems highly plausible that climate change is a major factor in the decline of crocodylomorph diversity since the Cretaceous. As well as support from linear modelling approaches, features within the diversity and disparity curves are coincident with climate events. As noted previously, diversity and disparity changes are associated with the Eocene and Miocene extinction events, which have been attributed to climate change (Shevenell *et al.* 2004, Molina *et al.* 2006). In addition, the diversity and disparity of the Cenozoic freshwater forms shows a period of recovery and stability coincident with the Miocene climate optimum (Böhme 2003).

The affinity of diversity and disparity in the Cenozoic with temperature raises the question of why such relationships were not greater in the Mesozoic. Perhaps the coolest Mesozoic temperatures were warm enough not to place constraints on crocodylomorph physiology. Alternatively, perhaps the physiology of stem-group Crocodylomorpha was fundamentally different from that of the crown-group. Endothermy is ubiquitous in the crocodylomorph sister group, the birds. This invites the question of when endothermy was acquired in the Archosauria. The occurrence of feathers in non-avian theropod dinosaurs (e.g. Ji 1998; Xu *et al.* 2000; Xu *et al*. 2004) strongly suggests endothermy is not an autapomorphy of crown-group birds. A filamentous integumentary covering would be advantageous in slowing radiative heat loss from an endothermic physiology. Likewise, such a covering would be detrimental to an ectotherm since it would insulate the body from environmental heat sources. This hypothesis is supported by observations of the naked mole rat, which shows a secondary loss of endothermy and a corresponding loss of body hair (Daly *et al.* 1997). Feather-like coverings similar to theropod protofeathers are now also known in the Ornithischia (Zheng *et al.* 2009; Godefroit *et al.* 2014) and the Pterosauria (Kellner *et al.* 2009). If these filamentous structures are homologous it is conceivable that endothermy arose in the Archosauria no later than the Late Triassic. If these filaments are homoplastic then the point of origin for avemetatarsalian endothermy is harder to determine (Barrett *et al.* 2013), but this does not preclude endothermy in basal Pseudosuchia. Non-neosuchian Crocodylomorpha commonly exhibit a cursorial anatomy and erect limb posture (Sues *et al.* 2003; Paolillo & Linares 2007; Pol *et al.* 2012). Bipedal posture is known in the Sphenosuchia (Sues *et al.* 2003, Clark *et al.* 2004) and among more basal Pseudosuchia (Nesbitt 2007). It has been suggested that such anatomy is an indicator of an active metabolism (Pontzer *et al.* 2009). While the extant Crocodylomorpha are exclusively ectothermic, this may be a secondary adaptation and not representative of basal Crocodylomorpha (Seymour *et al.* 2004). Extant crocodylomorphs do retain some characters that might be associated with endothermy, such as a four-chambered heart (Webb 1979, Seymour *et al.* 2004), high anaerobic capacity and a system of air sacs in the lungs (Seymour *et al.* 2004). The benefits of endothermy are more limited in warm, stable climates, while ectothermy presents advantages through lowering energy requirements (Seymour *et al.* 2004). Therefore, perhaps the independence of stem-group crocodylomorph diversity from temperature is a reflection of a higher metabolic rate.

The analyses presented here generally favour a Court Jester-like model of crocodylomorph macroevolution over a Red Queen-like model. The disparity curves have indicated long periods of stasis punctuated by discrete events. Mass extinctions appear to have been an influential factor for both diversity and disparity. Sea level and temperature have both been interpreted as potentially influential factors in crocodylomorph evolution, especially in the Cenozoic. While relationships with diversity in other reptile clades have been identified, these fail to provide convincing evidence of macroevolution through biotic interactions. As noted previously, the ecology of marine crocodylomorphs and terrestrial dinosaurs are too far removed for interactions to be plausible. Therefore, common patterns between the diversity of different clades may be attributed to preservation bias, or alternatively extrinsic global factors which affect the diversity of marine and terrestrial reptiles alike. However, the red-queen and court-jester hypotheses are not necessarily mutually exclusive, and there may be other biotic interactions determining crocodylomorph macroevolution. This presents avenues for further study, perhaps incorporating recent advances in ecological nice modelling or trophic web modelling.

CONCLUSIONS

Long-term patterns in crocodylomorph diversity may be influenced by preservation and sampling. However, increase in diversity over time with decay of the fossil record makes this something of an intractable issue. This highlights the importance of applying phylogenetic correction to estimates of diversity. The decrease in crocodylmorph diversity through the Cenozoic cannot be attributed to the number of crocodylomorph fossil-bearing formations, giving reassurance that this pattern is real. Diversity shows a strong relationship with disparity, which is less susceptible to preservation and sampling effects, therefore suggesting that large-scale patterns in the Mesozoic are real and not preservation or sampling artefacts.

Crocodylomorph diversity and disparity through time are coupled. This concurs with an extremely conservative morphology, indicated by results in Chapter 3. These findings contrast with other studies of vertebrates and invertebrates, which have generally favoured a disparity-first model. The morphospace occupancy of crocodylomorph subclades shows considerable overlap, however phylogenetic groups with generally distinct ecomorphological grades do occupy significantly different morphospace from one another.

Diversity and disparity through time follow a pattern that is supportive of a punctuated model of evolution, with periods of stability interrupted by periods of change. Extinction events have had considerable influence in both the diversification of the Crocodylomorpha through the Mesozoic and their decline in the Cenozoic. There are short periods of decoupling between diversity and disparity during the Cenozoic, with disparity being retained during a period of diversity loss, indicating that morphology was not a factor in their loss of diversity.

This punctuated mode of evolution conforms to a court-jester like model of evolution, where evolutionary change is driven by environmental change. Sea level shows a close interaction with diversity and disparity. This may be a preservation effect, with greater potential for fossil preservation during times of high sea level. It may also be a biogeographic variable, changing the relative distribution and isolation of taxa. Alternatively it may be a combination of both factors. Temperature does not appear to be a principal driver of diversity or disparity in the Mesozoic, but it is a clear significant driver in the Cenozoic. Cooling appears to be of greater significance than warming, with diversity and disparity recovering during periods of stability.

Chapter 5: Conclusions

Research outcomes detailed over Chapters 2-4 present tentative answers to the questions laid out in Chapter 1.

What do previous analyses conclude about the phylogenetic relationships of crocodylomorph taxa?

The matrix representation parsimony method is certainly capable of estimating accurate supertrees. However, it is also prone to producing highly inaccurate trees within a tree sample. Therefore, it is adviseable that samples of MRP supertrees be evaluated using source-tree or character data. Supermatrix approaches remain a major undertaking that may be impractical for individual researchers. Due to the accumulation of inapplicable characters and and loss of information through taphonomy and diagenesis, the volume of missing data in supermatrices is likely to be very high. Source matrices are seldom comprehensive in their coverage of fossil morphology, with specimens being encoded to different character schemes. As a result, morphological data observable in fossils may not be recorded in the literature. Assembling a supermatrix to a high standard is more achievable through review of fossil specimens than scraping data from the literature. However, tiling source matrices to estimate crude supermatrices can perform surprisingly well when analysed using parsimony. Due to the volume of redundant characters, the accuracy of trees returned by such analyses is likely to be lower than a supermatrix assembled from observations of fossils. In spite of this, simple source matrix-based supermatrices overall outperform the MRP method in summarising source tree topology.

Supertree and supermatrix approaches identify a broad consensus on the topology of crocodylomorph phylogeny. The Sphenosuchia lie outside the Crocodyliformes. The Crocodyliformes are monophyletic, including a paraphyletic grade of protosuchians and a monophyletic Mesoeucrocodylia. The analyses disagree on the position of the Peirosauridae, with the supertree placing them close to the Neosuchia, but the supermatrix tree affiliating them with the Notosuchia. The Neosuchia includes a monophyletic clade including the Tethysuchia and Thalattosuchia, and a monophyletic clade including the Goniopholididae and

Eusuchia. Neither supertree nor supermatrix analyses recover the crown-group topology predicted by phylogenetic analyses of molecular data. Due to the many advantages of molecular data, it is likely that this is due to poor morphological character choice. It is therefore advisable for future phylogenetic analyses of crown-group morphology to be constrained to topology from molecular analyses.

Are innovations in probabilistic approaches to phylogeny applicable to very large datasets?

It is likely that Bayesian methods represent an improvement on more traditional parsimony-based phylogenetic and supertree methods. However, in real-world situations, there are practical limitations to these methods. Baysian supertree approaches are known to perform well with large datasets, however in the example presented here convergence was not achieved in a practical time-scale. A high degree of source tree incongruence is a possible contributing factor. Similarly, Bayesian implementation of the Lewis MK model could not reach convergence when analysing the supermatrix, even with the inclusion of a start tree parameter. Both the size of the supermatrix and the volume of missing data are likely contributing factors.

Do living examples of the Crocodylomorpha qualify as 'living fossils'?

Rates of crocodylomorph body size evolution increased over time, therefore they do not satisfy the definition of bradytely. The crocodylomorph fossil record is relatively good, with examples known throughout the Mesozoic and Cenozoic eras, so they do not qualify as Lazarus taxa. They follow an extremely conservative model of body size evolution, with many clades showing evolutionary stasis. However, rates of evolution among extant examples is not uncommonly low, meaning they do not satisfy the definition of living fossils according to Herrera *et al.* (2016). Therefore, there are not sufficient grounds to consider extant crocodylomorphs as living fossils. The perception of crocodylomorphs as living fossils is likely a reflection of their low diversity, phylogenetic uniqueness and the antiquity of the stem-group Neosuchia.

Is crocodylomorph evolution driven by long-term environmental change, or by biological interactions such as predation and competition?

There is not sufficient evidence from the analyses presented here to evaluate the extent of biotic interactions in the evolution of the Crocodylomorpha. There are strong relationships between the diversity and disparity of the Crocodylomorpha with the diversity of other reptile groups in the Mesozoic, but these relationships could be attributed to a common cause, preservation or sampling. Biotic interactions, such as predator-prey arms races, sexual selection and competition, may have driven crocodylomorph evolution to a degree, but the extent of this is not clear.

There are multiple lines of evidence that support environmental change as a driver of Crocodylomorph evolution. Temperature variation outperforms time as a predictor of body size evolutionary rates. Therefore, increase in crocodylomorph body size through time is better attributed to temperature than as an example of Cope's rule. Phylogenetic models of crocodylomorph body size evolution show some support for an Ornstein-Uhlenbeck model, indicating the presence of external factors. Temperature and sea level both interact with diversity and disparity through time. Temperature decline appears to have been a key factor in the loss of crocodylomorph diversity in the Cenozoic, with diversity being lost in periods of cooling and recovering in periods of stability. In addition, major shifts in diversity and disparity occur coincident with extinction events. Further, rates of character evolution are heterogeneous, with generally low rates being periodically interrupted by increased rates. Therefore, crocodylomorph macroevolution does conform with a court-jester like model of evolution, at least to some extent.

Are evolutionary rates stable or subject variation?

Phylogenetic models of body size evolution suggest that crocodylomorph diversification is highly conservative, commonly adhering to a stasis model. Analysis of within-branch evolutionary rates favour a heterogenous rates model, with the average rate increasing over time. When evolutionary rate is measured using phylogenetically independent contrasts, temperature serves as a better predictor than time. It is clear that evolutionary rates are variable and have increased over time.

How has the taxic and morphological diversity of crocodylomorphs changed through time?

The diversity and morphological disparity of the Crocodylomorpha and its subclades are coupled. This contrasts with analyses of other clades that commonly find disparity to increase ahead of diversity. This may be a reflection of the extremely conservative evolution of crocodylomorph morphology, with morphological change remaining relatively constant, accumulating over time with increased diversity. There may be short periods of decoupling during the decline of the Crocodylomorpha through the Cenozoic, with disparity remaining stable while diversity declines. This suggests that morphology was not a factor in the decline of Crocodylomorph diversity.

Implications for the Crocodylomorpha in the 21st century

Anthropogenic climate change remains a major threat to current biodiversity. From the fossil record it is apparent that the survival of crocodylomorph taxa is governed by rates of cooling, with greater diversity being associated with periods of warming. This might imply that the crocodilians may be relatively unaffected by increased temperatures due to the greenhouse effect, however this interpretation would be a complacent oversimplification. Anthropogeneic climate change is advancing at a far greater rate than any climate changes the crocodylomorphs have endured in the past. The sensitivity of crocodylomorph diversity to environmental change is of greater significance than specific interactions between diversity and temperature, since interactions between crocodylomorph diversity and climate may be more complex.

A negative relationship between crocodylomorph body size and temperature suggests anthropogenic climate change may result in a decrease in crocodilian body size. Body size is a key factor in prey selection among living crocodiles (Cott 1961). Therefore, climate change may cause an ecosystem-wide shift in predation pressure, potentially causing long-term damage to entire food webs and threatening biodiversity.

If the diversity of the Crocodylomorpha is defined by temperature, anthropogenic climate change may enable extant examples to become invasive species. They may outcompete native predators, or exhaust the supply of prey in some areas, further threatening biodiversity. Changes in the geography of crocodylomorph populations may bring them in to conflict with humans. Extant crocodylomorphs are dangerous and responsible for hundreds of attacks on humans and livestock (CrocBITE). Conflict with humans will also adversely affect crocodylomorphs. For example, the Indian gharial is listed as critically endangered by the International Union for Conservation of Nature (IUCN) Red List (icunredlist.org). The gharial is threatened by human activities such as sand mining, livestock, civil engineering projects and fishing practices (Gharial Conservation Alliance).

The conservation of extant crocodylomorphs is of particular concern. The low diversity and ancient origins of the extant crocodylomorphs lend them great phylogenetic uniqueness compared to most vertebrates. Therefore, they represent a greater extant diversity per taxon than other groups. The total biodiversity of life following an anthropogeneic mass extinction will be severely diminished if crocodylomorphs are not among the survivors.

Future directions

Meta-analytical approaches to phylogeny using morphological data are in need of improvement. Taxon incompleteness and inapplicable characters are an inescapable reality of working with large fossil data sets. Principal coordinates analysis may offer a means to improve the completeness and data independence of character matrices. However, the availability of methods to formulate phylogenetic hypotheses from continuous eigenvalues is limited.

Since supermatrix completeness presents an obstacle to Bayesian implementation of the Lewis MK model, supertree approaches may be an effective means of incorporating Bayesian approaches into large-scale phylogenetic analyses. If Bayesian analyses are more accurate than parsimony approaches, source trees re-analysed using Bayesian methods may be expected to be more congruent than those analysed using parsimony. In turn this greater congruence may make implementation of the Bayesian supetree approach more feasible.

Diagnosing discrete morphological characters can be subjective, and finding sufficient morphology to distinguish two species can be difficult. Estimating continuous shape metrics using geometric morphometrics may present a means to improving the consistency and completeness of morphological data, while also eliminating subjectivity. Molecular analyses of living taxa may offer a way to vet the suitability of morphological characters through testing for phylogenetic signal. A set of guidelines could then be applied to character matrices of extinct taxa, potentially increasing the resolution of consensus trees.

The relationship between crocodylomorph diversification and evolution with temperature merits better understanding. Temperature may affect crocodylomorphs directly, but also indirectly through other variables such as precipitation and seasonal fluctuations. The utility of time-series data may be limited in resolving a model of what is likely a complicated network of interactions. Geographic information systems (GIS) and spatial statistical approaches such as ecological niche modelling (ENM) may present a more comprehensive solution to understanding the impact of climate change on crocodylomorph diversity.

The analyses presented here find strong support for a court jester-like model of crocodylomorph evolution, where both diversification and evolutionary rate are driven by environmental change. While this may be the dominant driving factor, biological interactions such as competition, parasitism and predation pressure will probably have some effect. Advances in ecosystem and food web modelling (Aydin *et al.* 2007, Legagneux *et al.* 2012) may offer a means to test the suitability of the red queen hypothesis as a model of crocodylomorph evolution.

The independence of non-neosuchian diversity from temperature raises questions about the physiology of basal crocodylomorphs, and the possibility of secondary ectothermy in neosuchians. Reconstructing the evolution of metabolic rates presents itself as a worthy topic for further investigation. Bone histology and comparative anatomical approaches could be employed to generate a dataset of characters correlated with physiology. The acquisition of these characters could be estimated using an ancestral state reconstruction. This approach may reveal what factors initiated the evolution and secondary loss of endothermy, and how many times endothermy has emerged among amniote taxa. Further, it may resolve whether the evolution of endothermy was a discrete event, or a gradual shift.

The rapid increase in rates of body size evolution among the basal Alligatoridae is an anomaly. Similarly there is a very rapid increase in eusuchian diversity after global temperatures stabilised in the Miocene. Comparative phylogenetic approaches may offer insight into possible adaptive radiations in crown-group Crocodylomorpha during the Palaeogene.

The effect of Cenozoic climate change on the macroevolution of vertebrates is a topic in need of further study. Anthropogenic climate change gives this subject greater urgency. Cenozoic climate change is the most accessible analogue for anthropogenic climate change in terms of available rock and fossil records. Cenozoic fossil ecosystems are easier to reconstruct than older examples, since their constituent taxa are closely related to extant species. The impact of Cenozoic climate change on endotherms such as mammals would be of specific interest, since vertebrate macroevolution so far has commonly focused on ectotherms and extinct clades with an uncertain physiology. Further, the loss of many megafauna since the Pliocene may perhaps be attributed to interactions between body size evolution and climate change. Definitively testing for changes in morphology, disparity and diversity with environmental data is only possible through analysis of morphological data from fossils. This highlights the importance of fossil palaeontology to evolutionary biology, climate science and conservation, and cannot be replaced with biomolecular approaches.

Decoupling of diversity and disparity is difficult to diagnose. Currently qualitative observations of time-series distributions are the most effective way. Developing new comparative phylogenetic approaches to test for diversity- or disparity-first models would represent a significant improvement. The occurrence of decoupling between diversity and disparity warrants further study. Decoupling of diversity and disparity may vary according to physiology, reproductive strategy or ecology. Similarly the degree of decoupling may be subject to biological interactions or extrinsic environmental changes, similar to diversification under the red queen or court jester regimes.

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Appendix 1

Here are captions associated with figures S1-S4 in the supplementary information.

Figure S1. Matrix representation parsimony supertree of the Crocodylomorpha. The sampled treespace is represented here by a strict consensus of the 92 most parsimonious trees recovered by a New Technology search using TNT.

Figure S2. Matrix representation parsimony supertree of the Crocodylomorpha. The sampled treespace is represented here by a strict consensus of the 97 most parsimonious trees recovered by a New Technology search using TNT. The crown-group topology has been constrained to a topology estimated from analysis of molecular data (See main text).

Figure S3. Maximum parsimony supermatrix tree of the Crocodylomorpha. The sampled treespace is represented here by a strict consensus of the 95 most parsimonious trees recovered by a New Technology search using TNT.

Figure S4. Maximum parsimony supermatrix tree of the Crocodylomorpha. The sampled treespace is represented here by a strict consensus of the 93 most parsimonious trees recovered by a New Technology search using TNT. The crown-group topology has been constrained to a topology estimated from analysis of molecular data (See main text).