A multi-disciplinary approach to the analysis of crocodylian phylogeny, diversity and biogeographic history in Deep Time

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Declaration

I, Selina Groh, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.
Abstract

Crocodylomorpha are one of the oldest extant clades on the planet, having originated over 200 million years ago in the Triassic. Their large fossil diversity stands in contrast to only 23 living species, providing a rich source for evolutionary study. In addition, they illustrate the influence of homoplasy on phylogenetic reconstruction: an elongated snout form ('longirostry') arose multiple times throughout their history, causing erroneous clade clustering inconsistent with the stratigraphic record in phylogenetic analyses.

For this thesis, the largest dataset to date was assembled for Neosuchia, a crocodylomorph clade consisting of all extant and several extinct families. 569 characters (82 continuous and 487 discrete) were scored for 106 taxa and analysed using Bayesian and parsimony methods (with and without Extended Implied Weighting (EIW)). The resulting phylogenies were evaluated using stratigraphic congruence, dated with four different methods (cal3, FBD, sGLA and Extended Hedman), and analysed for their biogeographical patterns.

The results show that using both EIW and continuous characters successfully resolves the issue of homoplasy, producing the most stratigraphically congruent trees. They confirm the position of Diplocynodontinae, Goniopholididae and Tethysuchia as non-eusuchian neosuchians and resolve the three major eusuchian superfamilies, Crocodyloidea, Gavialoidea and Alligatoroidea, although Alligatorinae emerge as non-monophyletic. Character tracing reveals that similar modifications in the anterior of the skull underpin the evolution of longirostry.
in all clades, coupled with more clade-specific modifications of the posterior skull.

Divergence age estimation places the emergence of Neosuchia in the late Triassic, confirming that all three major eusuchian clades were present before the K/Pg-boundary. Cal3 and FBD emerged as the most accurate divergence age estimation methods. Biogeographical analyses showed that neosuchian biogeography is complicated, but most clades emerged on the Laurasian continents, with a definite European origin for Alligatoroidea. Founder event speciation and transoceanic dispersal played an important role in neosuchian evolution.
Impact statement

Inside academia, one of the strongest impacts is provided by the methodological advances brought forward in this thesis. Chapter 2 provides a novel way of dealing with strong homoplasy in the reconstruction of phylogenetic trees, a problem that has been an issue especially in crocodylian phylogenetics for several decades. The findings of this chapter have been submitted for publication and will provide helpful notes on methodology for future researchers dealing with the same problem.

In addition to phylogenetic reconstruction, this thesis also assessed four different methods for divergence dating that hadn’t previously been compared in Chapter 3. The divergence age estimates from the four methods were evaluated not only for different phylogenetic clades, but also amongst several sets of phylogenetic trees in order to assess their vulnerability to minor and major differences in tree topology. As such, this thesis provides a detailed evaluation of the four most common divergence age methods and their advantages and disadvantages depending on different factors. A paper detailing these results and making them available for the wider scientific community is currently in preparation.

Similarly to the divergence dating methods, four different ways of biogeographic analyses are compared and evaluated for their usefulness in elucidating crocodylian biogeography in Chapter 4. This includes a new method published this year which has been used only once before. The results of this comparison
will be made available in a third published paper that is currently in preparation as well.

Finally, this thesis delivers new insights not only into methodology, but also in the evolutionary history of Neosuchia itself: the new morphological character list provides a revision of the last decades' research on neosuchian phylogeny with coherent and standardised character descriptions and 150 novel character illustrations (Appendix A). It strongly increases the reproducibility of the study and will serve as basis for many future neosuchian researchers once the paper (currently under review) is published.

In addition, the new phylogenies increased the knowledge about the evolution of Neosuchia. They confirmed the composition and placement of all major neosuchian clades and that the three major superfamilies containing extant species (alligators, gharials and crocodiles) were present before the K/Pg-boundary. The biogeographic analyses confirmed that transoceanic dispersal plays an important role in neosuchian biogeography and many extinct species were likely saltwater tolerant (these findings are currently in the process of being turned into papers and published). This additional knowledge will serve as basis for future studies in all areas of neosuchian evolution.

The increased knowledge about neosuchian evolution is carried further for impact outside academia. The author has been part of several public engagement activities, mostly at the Natural History Museum (Science Uncovered, Museum Lates and Nature Live), informing visitors of all ages about the evolutionary history of crocodylians. Not only did it serve to increase people’s knowledge about a rather enigmatic animal group and raise awareness for their protection (the majority of extant crocodylians are on the IUCN Red List), but also furthered their interest in natural history and science in general.
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Chapter 1

Introduction

Crocodylomorpha, including all current species of crocodiles, alligators and gharials, originated at least 230 million years ago (mya) (Irmis et al., 2013). Despite the low number of extant crocodylomorphs [23 species] (Oaks, 2011), this clade has a rich fossil record composed of over 600 species (Alroy, 1998). It was once a much more diverse and widespread group, which occupied a range of key ecological niches (Brochu, 2003). Crocodylomorpha comprise a paraphyletic stem array of early diverging taxa (‘sphenosuchians’) and Crocodyliformes (Brochu et al., 2009), with the latter including the three extant crocodylian families. Although living crocodylians are often referred to as 'living fossils' because of their apparently conservative anatomy (Buckland, 1836; Meyer, 1984), recent studies have demonstrated that Crocodylomorpha exhibited considerable morphological disparity throughout its evolutionary history (Brochu, 2003). Many of the major constituent clades within Crocodylomorpha diverged early in its evolutionary history and exhibit numerous unique modifications to their ancestral bauplan. Species range from fully terrestrial (Tennant et al., 2016a) through amphibious to fully marine (De Andrade & Sayão, 2014) and, although predominantly carnivorous, some extinct species are suggested to have been herbivorous (Ösi et al., 2007) or omnivorous (Sereno & Larsson, 2009). In addition, several species exhibit unusual snout shapes (Gasparini et al., 2006), from

'pug-nosed' forms such as *Simosuchus* (Buckley *et al.*, 2000) to extremely long-snouted taxa such as *Dyrosaurus* and the gharial (Fig. ??). Body sizes ranged from <1m, as in the Atoposauridae (Schwarz-Wings *et al.*, 2011) to giant forms such as *Sarcosuchus imperator* with body lengths >11m (Sereno *et al.*, 2001).

This study is limited to the crocodylomorph group Neosuchia as this clade represents most of the long, intricate evolutionary history of the clade. Neosuchia, defined as 'Atoposauridae, Goniopholidae [sic], Pholidosauridae, Dyrosauridae, Bernissartia, Shamosuchus, and eusuchians' by Benton & Clark (1988, p. 27), currently contains 480 species, including the 23 extant crocodylians, all of which are under close scrutiny given their current conservation status (Oaks, 2011). Whilst almost all extant crocodylians are on the IUCN Red List, seven out of these 23 species are currently marked as 'critically endangered'

The morphological and ecological diversity of Crocodylomorpha is paralleled by expansions and contractions in geographical ranges that occurred in the Mesozoic and early Cenozoic, especially during periods of higher global temperatures such as the Eocene (Brochu, 2003), as well as marked changes in species richness through time (Mannion *et al.*, 2015). Crocodylian diversity, in particular, is coupled strongly with peaks in global thermal maxima (Brochu, 2013).

### 1.1 Definition of higher neosuchian groups

Neosuchian groups as defined by SG (except ‘Neosuchia’) for the purpose of this study.

**Neosuchia:** ‘Atoposauridae, Goniopholididae [sic], Pholidosauridae, Dyrosauridae, *Bernissartia, Shamosuchus,* and eusuchians’ (Benton & Clark, 1988, p. 27). Last common ancestor of *Dyrosaurus phosphaticus* and *Melanosuchus niger* and all its descendants.

**Eusuchia:** the most recent common ancestor of *Hylaeochampsa vectiana* and *Melanosuchus niger* and all its descendants.

**Tethysuchia:** *Dyrosaurus phosphaticus* and all neosuchians closer to it than to *Goniopholis simus.*

**Goniopholididae:** *Goniopholis simus* and all neosuchians closer to it than to *Bernissartia fagesii.*

‘derived’ **Goniopholididae:** all species of *Goniopholis, Anteophthalmosthus* and *Amphicotylus.*

**Crocodylia:** *Melanosuchus niger* and all eusuchians closer to it than to *Hylaeochampsa vectiana.*

**Gavialoidea:** *Gavialis gangeticus* and all crocodylians closer to it than to
Melanosuchus niger.

**Gavialinae:** all species of *Gavialis* and *Eogavialis*.

**Brevirostres:** the most recent common ancestor of *Melanosuchus niger* and *Crocodylus niloticus* and all its descendants.

**Crocodyloidea:** *Crocodylus niloticus* and all brevirostrans closer to it than to *Melanosuchus niger*.

**Crocodylidae:** the most recent common ancestor of *Tomistoma schlegelii* and *Crocodylus niloticus* and all its descendants.

**Crocodylinae:** *Crocodylus niloticus* and all crocodylids closer to it than to *Tomistoma schlegelii*.

**Tomistominae:** *Tomistoma schlegelii* and all crocodylids closer to it than to *Crocodylus niloticus*.

**Alligatoroidea:** the most recent common ancestor of *Melanosuchus niger* and *Diplocynodon remensis*.

**Globidonta:** *Melanosuchus niger* and all alligatoroids closer to it than to *Diplocynodon remensis*.

**Diplocynodontinae:** *Diplocynodon remensis* and all globidontans closer to it than to *Melanosuchus niger*.

**Caimaninae:** *Melanosuchus niger* and all alligatoroids closer to it than to *Alligator sinensis*.

### 1.2 The neosuchian clades

Neosuchia is composed of several smaller clades and Eusuchia, with the latter containing the three major extant crocodylomorph superfamilies: Gavialoidea, Crocodyloidea and Alligatoroidea (see Fig. 1.6 for differing phylogenetic hypotheses).

Tethysuchia is one of the oldest neosuchian clades and is unique in that it contains several marine species (Khosla *et al.*, 2009). Its interrelationships have
been subject to debate: two families are usually recognised within Tethysuchia, Dyrosauridae and Pholidosauridae (Fortier et al., 2011; Young et al., 2014). However, the placement and monophyly of Pholidosauridae has recently been questioned (De Andrade et al., 2011; Meunier & Larsson, 2016) and some authors have proposed the resurrection of Elosuchidae, taking Elosuchus out of Dyrosauridae (De Andrade et al., 2011). Tethysuchia is a widely distributed clade, with the majority of its species from Africa but additional occurrences in South America, Europe and North America (De Andrade et al., 2011). Several of its members, in particular marine species of Dyrosaurus (Fig. 1.3) and its close relatives, possess an elongated snout (longirostry) that is thought to be an adaptation for piscivory (Iordansky, 1973; Pooley & Gans, 1976). Tethysuchia also contains some of the largest known neosuchian taxa with Sarcosuchus reaching a length of up to 11m (Sereno et al., 2001). Tethysuchia originated during the Jurassic (Martin, 2010; De Andrade et al., 2011; Turner et al., 2017), and was present throughout the Cretaceous and early Paleogene, having survived the K/Pg mass extinction. A second longirostrine crocodylomorph clade, Thalattosuchia, is not discussed here, as it has been resolved in various different positions within and outside Neosuchia (Benton & Clark, 1988; Wu et al., 2001; Pol & Gasparini, 2009; Young & De Andrade, 2009; Wilberg, 2015) and is currently being worked on by other research teams (pers. comm).

The second major neosuchian clade outside Eusuchia is Goniopholididae (Fig. 1.2). Similar in size to medium modern crocodilians and semi-aquatic (Farlow et al., 2005; De Andrade et al., 2011), goniopholidid fossils have been found throughout Laurasia and span the time from the earliest Jurassic to the end of the Cretaceous (De Andrade et al., 2011; Turner et al., 2017). In addition to Tethysuchia and Goniopholididae, there are a number of smaller clades, represented by only a few taxa, and single species plesions: Susisuchidae (a Gondwanan clade from the Early and ‘middle’ Cretaceous) (Turner & Pritchard, 2015), Stomatosuchidae (an African clade from the Late Cretaceous) (Sereno &
Figure 1.2: Two species from extinct neosuchian clades: A, the goniopholidid *Goniopholis* sp. † (IRSNB EFR 47), skull in dorsal view; B, the diplocynodont *Diplocynodon remensis* † (MNHN F BR 4020), skull in dorsal view. All photographs in this thesis taken by SG.
Larsson, 2009), Bernissartiidae (a European clade from the Early Cretaceous) (Sweetman et al., 2014), Atoposauridae (a clade of miniaturised European taxa from the Late Jurassic to the Early Cretaceous) and Paralligatoridae (a second Laurasian clade of miniaturised taxa from the Late Jurassic and Cretaceous) (Tennant et al., 2016a), to name the most significant.

Eusuchia, the largest of the neosuchian clades, is a global group estimated to have originated in the Early Cretaceous (Salisbury et al., 2006; Martin & Delfino, 2010; Lee & Yates, 2018) although its biogeographical origin is unclear (Salisbury et al., 2006). In addition to a number of smaller species and clades, e.g. Hylaeochampsidae (a Cretaceous European clade) (Buscalioni et al., 2011) and Planocraniidae (a Laurasian clade from the Paleocene and Eocene) (Brochu, 2013), it is dominated by the three major superfamilies that are commonly referred to as Crocodylia: Crocodyloidea, Gavialoidea and Alligatoroidea.

Gavialoidea is the clade with the most debated position within Eusuchia (Piras et al., 2010). Morphological phylogenies place it at the base of Crocodylia, separate from Tomistominae and as the sister group to both Crocodyloidea and Alligatoroidea (Bronzati et al., 2012). In contrast, molecular analyses resolve Gavialoidea as the sister clade of Crocodyloidea, with Tomistominae as part of the gavialoids (Oaks, 2011; Roos et al., 2007). Recently, the monophyly of Gavialoidea has been questioned, with Lee & Yates (2018) removing thoracosaursa from this clade (where they were the sister group of Gavialinae) and placing them separately at the base of Crocodylia.

Together with Tomistominae, Gavialoidea is one of the two major longirostrine clades within Eusuchia (Fig. 1.3). The history of Gavialoidea begins before the K/Pg-boundary, with fossils found globally since its origination during the Late Cretaceous (Martin & Delfino, 2010; Oaks, 2011; Turner et al., 2017). *Gavialis gangeticus* from India is the only extant member of the clade, although past species were considerably more widespread (Jouve et al., 2008b). Although
Figure 1.3: Examples of longirostrine neosuchians: A, False Gharial (*Tomistoma schlegelii*); B, *Tomistoma petrolica*† (unnumbered IVPP specimen), skull in dorsal view; C, *Dyrosaurus phosphaticus*† (unnumbered MNHN specimen), skull in dorsal view; D, Gharial (*Gavialis gangeticus*, unnumbered NHMUK specimen), skull in dorso-lateral view.
the extant gharial inhabits mainly freshwater habitats, it is highly likely that past gavialoids were considerably more saltwater tolerant (Delfino & Vos, 2010).

Crocodyloidea is the eusuchian clade with the largest number of extant species, with 13 in the subfamily Crocodylinae (in the genera Crocodylus, Osteolaemus, and Mecistops) and one in the subfamily Tomistominae (Tomistoma schlegelii) based on morphological phylogenies (Brochu, 2003; Piras et al., 2010) (Fig. 1.4). Both subfamilies are thought to have originated after the K/Pg-boundary (Salisbury et al., 2006; Oaks, 2011; Puértolas et al., 2011). Although the false gharial, the only extant member of Tomistominae, exclusively occupies Asian habitats, the clade itself is much more widespread, with fossils found on all major continents except Antarctica (Piras, 2007). Similarly to Gavialis, its long snout is regarded as an adaptation to piscivory (Iordansky, 1973) (Fig. 1.3).

Extant crocodyline species have achieved a pantropical distribution and their fossils have been found on all continents except Antarctica. Crocodyloidea originated during the Late Cretaceous (Martin & Delfino, 2010; Puértolas et al., 2011; Lee & Yates, 2018) and their high saltwater tolerance was likely a major factor in their widespread distribution (Brochu, 2003, 2007). Extant species can grow up to a length of 6m (Whitaker & Whitaker, 2008) and inhabit preferentially fresh- or brackish water habitats, although some species, such as Crocodylus porosus, have been recorded in marine areas up to 200km from the nearest shore (Bustard & Choudhury, 1980). Although extant crocodylians are carnivorous, there is substantial evidence for facultative frugivory in at least 13 species (Platt et al., 2013).

The third major eusuchian clade is Alligatoroidea, which is usually subdivided into Globidonta (which contains all extant members of the clade) and Diplcynodontinae. Similar to Gavialoidea and Crocodyloidea, Alligatoroidea is thought to have originated during the Late Cretaceous before the K/Pg-boundary (Salisbury et al., 2006; Puértolas et al., 2011; Lee & Yates, 2018), although its
Figure 1.4: Examples of crocodylid species: A, Nile Crocodile (*Crocodylus niloticus*); B, *Crocodylus sivalensis*† (NHMUK PV R 39705), skull in dorsal view; C, African Dwarf Crocodile (*Osteolaemus tetraspis*, NHMUK 1862.6.30.5), skull in dorsal view.
Diplacynodontinae is a low diversity Laurasian clade that has been suggested to have originated during the Eocene (Salisbury et al., 2006; Lee & Yates, 2018) (Fig. 1.2). Globidonta (Fig. 1.5) is more widespread, with fossils found in South America, North America, Europe and Asia. It contains a few minor taxa and Alligatoridae, which, in turn, is subdivided into Alligatorinae (including the two extant Alligator species) and Caimaninae (containing all extant caimans) (Fig. 1.5). Caimaninae is the youngest of the globidontan clades,
although there is now evidence for its origin just before the K/Pg-boundary (Brochu, 2011; Pinheiro et al., 2013). The distribution of extant caimans is restricted to South America, but fossil caimanins have also been found in North America (Brochu & Carbot-Chanona, 2015). Alligatorinae are more widespread with a similar fossil distribution to Globidonta as a whole, although its extant species are restricted to North America (Alligator mississippiensis) and China (A. sinensis). While Alligator specimens can grow to over 4m in length (Woodward et al., 1995), caimans are typically smaller, reaching only 1m in the dwarf caiman Paleosuchus palpebrosus (Campos et al., 2010). The diets of both alligators and caimans are highly variable and dependent on size, ranging from small arthropods, snails, crabs, and shrimp to larger vertebrates, mainly fish (Delany et al., 1999; Borteiro et al., 2009).

1.3 History of neosuchian evolutionary studies

The first detailed phylogenetic analyses of Crocodylomorpha (including Neosuchia) were undertaken during the 1980s (e.g. Clark 1986; Benton & Clark 1988; Buscalioni & Sanz 1988). These were followed by further studies that led to analyses with marked increases in character and species numbers, with numerous new phylogenetic hypotheses proposed during the 1990s and early 2000s (e.g. Norell & Clark, 1990; Gasparini et al., 1991; Clark, 1994; Wu et al., 1994, 1997; Ortega et al., 1996; Gomani, 1997; Brochu, 1999, 2001, 2003; Buckley & Brochu, 1999; Ortega et al., 2000; Larsson & Gado, 2000; Buscalioni et al., 2001; Sereno et al., 2001; Tykoski et al., 2002; Martinelli, 2003; Pol, 2003; Pol & Norell, 2004; Turner, 2004; Jouve et al., 2005). The vast majority of phylogenetic studies that followed ultimately derived most of their morphological characters from these earlier works, often without critical re-examination of the characters and scores used (e.g. Hill et al., 2008; Lauprasert et al., 2009; Hastings et al., 2010; De Andrade et al., 2011; Puértolas et al., 2011; Holliday 22
This wide variety of studies has generated a multitude of phylogenetic hypotheses (Fig. 1.6; for details see Section 2.2.2 in Chapter 2). One of the major problems in neosuchian phylogenetics is posed by the evolution of longirostrine taxa: several neosuchian clades contain members with a markedly elongated snout (Fig. 1.3). In phylogenetic analyses, this superficial similarity between taxa can cause artificial clustering of these longirostrine species (Fig. 2.1) into clades whose branching patterns are incongruent with their stratigraphic record (Clark, 1994; Jouve, 2009; Meunier & Larsson, 2016). However, despite the strong homoplasic signal in characters associated with the longirostrine condition, they still retain potential phylogenetic information. In this thesis, several novel methods will be employed in order to deal with the 'longirostrine problem'. These include the application of continuous characters instead of more subjective discrete character states (see Section 2.3.2 in Chapter 2) and the use of methods such as Extended Implied Weighting in parsimony analyses (see Section 2.3.4 in Chapter 2).

In addition to phylogenetic reconstructions, there have been a number of both molecular and morphological studies attempting to estimate divergence times for various parts of the neosuchian tree, including Brochu (2000); Salisbury et al. (2006); Roos et al. (2007); Martin (2010); De Andrade et al. (2011); Oaks (2011); Puértolas et al. (2011) and Lee & Yates (2018) (see Table 3.1). The divergence age estimates obtained vary substantially for some groups like Eusuchia (with estimates ranging from 120 to 170 mya) and there is debate on whether several groups were present before the K/Pg-boundary or not, including Crocodylidae and Globidonta. Furthermore, there is a dichotomy between age estimates based on molecular and morphological studies, with dated trees based on molecular data providing younger estimates for some clades than palaeontological data (e.g. Globidonta and Crocodylinae: see also Brochu
Figure 1.6: Summary of the competing hypotheses of neosuchian and eusuchian phylogenetic relationships. The topologies are based on the following analyses: A, Brochu (2013); B, Bronzati et al. (2012); C, Buscalioni et al. (2011) and Puértolas et al. (2011); D, Sereno & Larsson (2009).
A few biogeographical analyses of Neosuchia use quantitative methods, chiefly Turner (2004) and Hastings et al. (2014). However, all other studies (e.g. Salisbury et al. 2006; Jouve et al. 2008a; Hastings et al. 2010; De Andrade et al. 2011; Holliday & Gardner 2012; Halliday et al. 2013; Young et al. 2016) postulate ancestral areas based on fossil occurrences mapped onto phylogenetic trees, without statistical analyses. Neosuchian biogeography is further confused by the unknown capacity for saltwater tolerance in extinct taxa and thus their potential to cross oceanic barriers, especially among alligatoroids (Brochu, 1999; Martin & Delfino, 2010). Therefore, the ancestral areas of several clades have either never been statistically investigated (Neosuchia, Eusuchia) and/or are strongly debated (Eusuchia, Goniopholididae, Crocodylidae, Tomistominae, Alligatoroidea, Alligatoridae).

1.4 Study aims

This thesis aims to investigate the following areas of neosuchian evolution in order to shed light on a number of issues:

1. A new, comprehensive character list for Neosuchia. After critical re-appraisal of previously constructed morphological characters and an evaluation of their use in deducing neosuchian phylogeny, a new character list for Neosuchia is generated with uniformly worded, clearly defined and illustrated character states and also including continuous characters.

2. A new neosuchian phylogeny. The new character list is re-scored and the new resulting dataset used to reconstruct a new neosuchian phylogeny that will be compared with previous topologies.

3. Evaluation of phylogenetic methods in the presence of strong homoplasy. Since homoplasy has been shown to pose a significant obstacle in neo-
suchian phylogenetics, different methods are used and evaluated during phylogenetic reconstruction in order to investigate their influence on tree topology using homoplastic characters.

4. Revised divergence age estimations of all major neosuchian clades. On the basis of the new phylogenetic hypotheses for Neosuchia, divergence ages will be estimated for the major clades in order to solve the question of how many neosuchian clades crossed the K/Pg-boundary and to assess when major origination and diversification events took place.

5. Evaluation of different divergence dating methods. Several methods are currently being used for divergence age estimations. So far, there has been no evaluation of these methods with regard to their vulnerability to changes in tree topology, sampling, etc. Therefore, this thesis aims to compare these different methods to assess their usefulness for divergence date estimation, in particular with respect to Neosuchia.

6. Revised ancestral area estimations and biogeographic history of Neosuchia. The dated generated here are used to assess the biogeographic history of Neosuchia. In particular, these new analyses shed light on contested areas of neosuchian biogeography, such as the geographical origins of Neosuchia, Eusuchia and Alligatoroidea.

1.5 Abbreviations

**Methodological abbreviations**

CI, Consistency Index; EIW, Extended Implied Weighting; FAD, First Appearance Date; FBD, Fossilised-Birth-Death Model; GER, Gap Excess Ratio; sGLA, smoothed Ghost-Lineage-Analysis; LAD, Last Appearance Date; mya, million years ago; MP, Maximum Parsimony; MPTs, Most Parsimonious Trees; MSM*,
Manhattan Stratigraphic Measure; **NTS**, New Technology Search; **OTU**, Operational Taxonomic Unit; **RCI**, Relative Completeness Index; **RI**, Retention Index; **TL**, Tree Length.

**Anatomical abbreviations**


**List of institutions**

Chapter 2

Neosuchian phylogeny

2.1 Abstract

Neosuchia have undergone a large amount of evolutionary change in their 200 million year history, resulting in a wide range of body types, diets and environmental preferences. One of this clade’s most striking features is a strongly elongated snout, which is usually regarded as an adaptation to piscivory. However, this longirostrine condition is likely to have arisen convergently on many occasions and so the morphological characters associated with longirostry can cause erroneous clustering of longirostrine groups in phylogenetic analyses, potentially obscuring true relationships. This study employs a supermatrix approach, coupled with new data, to capture as much evidence on their relationships as possible and to synthesize previous work on their systematics. I have compiled the largest ever dataset for examining neosuchian relationships (569 morphological characters for 19 extant and 87 extinct taxa), based on a comprehensive review of previous studies and personal observations of original specimens. In addition to 487 discrete characters, the dataset contains 82 continuous characters to capture the quantitative nature of several evolutionary traits more accurately. These data were analysed using both maximum parsimony (with and without extended implied weighting [EIW]) and Bayesian infer-
ence. Maximum parsimony coupled with EIW performed better than both equal weights parsimony and Bayesian analyses, with higher stratigraphic congruence of the resulting trees and no homoplasy-driven clustering of longirostrine clades. The resulting topologies resolved all major neosuchian clades and confirmed the placement of tethysuchians as non-eusuchian neosuchians. The tree topologies suggest that the longirostrine condition evolved independently in three major clades within Neosuchia (Tethysuchia, Gavialoidea and Tomistominae) and on at least three further occasions in phylogenetically isolated longirostrine species that occur in otherwise brevirostrine clades (e.g. Mecistops cataphractus and Euthecodon arambourgi). Character optimisations reveal that all longirostrine snouts were assembled similarly, with modifications mainly in the maxilla and premaxilla. In all longirostrine groups these changes of the anterior skull region are accompanied by modifications of the posterior skull, which are often unique to each of the clades and might represent adaptations to their different habitats. EIW and continuous characters are thus shown to be valuable tools for resolving relationships using morphological datasets in the presence of strong homoplasy.

2.2 Introduction

A robustly constructed phylogenetic tree serves as the basis for further evolutionary studies, ranging from biogeographic analyses, through macroevolutionary studies of trait evolution, to clade richness through time among many other issues. Three major methods are used currently for phylogenetic reconstruction based on either molecular or morphological data: Bayesian phylogenetics, Maximum Parsimony and Maximum Likelihood. Whilse there are a number of different algorithms for the analysis of molecular data (Yang & Rannala, 2012), maximum parsimony is still the most commonly used method in morphological phylogenetics (Wright & Hillis, 2014). Methods other than parsimony postu-
late uniform branch length across the phylogenetic tree since they often feature algorithms derived from molecular models (Felsenstein, 1978; Farris, 1983). Goloboff (1993) first proposed the implied weighting algorithm to add to maximum parsimony methods based on Farris (1969), which was implemented in the most commonly used maximum parsimony program, TNT in Goloboff et al. (2008b) and further elaborated upon in Goloboff (2014). Although Congreve & Lamsdell (2016) argued that unweighted parsimony performs better than implied weights, extended implied weighting was found to be the most effective method for phylogenetic reconstruction (Goloboff et al., 2017).

Likelihood is used little in morphological phylogenetics, although the Markov model has been developed for its use (Lewis, 2001). The same Markov model used for likelihood can also be implemented in a Bayesian framework (Ronquist & Huelsenbeck, 2003; Wright & Hillis, 2014). According to O’Reilly and colleagues (e.g. Wright & Hillis 2014; O’Reilly et al. 2016; Puttick et al. 2017; O’Reilly et al. 2018a,b), this Bayesian method outperforms all others, albeit with lower resolution in the resulting phylogenies. By contrast, Goloboff et al. (2017, 2018) found that extended implied weighting applied together with maximum parsimony delivers the most accurate phylogenies. Therefore, this study will applying a multitude of different statistical methods to the dataset here, including both Bayesian analyses and maximum parsimony.

Neosuchian phylogenetics

For a full overview of previous phylogenetic studies involving Neosuchia, see Section 1.3 in Chapter 1 and Table 2.1. An attempt has been made to generate a consensus of these multiple phylogenetic hypotheses using supertrees (Bronzati et al., 2012). However, although they can be useful tools for integrating previous hypotheses, supertrees have been criticised because robust methods to assess these phylogenies are lacking and their topologies can be strongly influenced by the potential non-independence of the source trees (Gatesy &
Springer, 2004; Haeseler, 2012). In addition, taxa with uncertain phylogenetic affinities such as *Borealosuchus* (as mentioned above) can be placed in compromise positions in the supertree as a result of widely differing placements in the source trees.

In addition, the affinities of various taxa within Neosuchia remain unclear, despite the large number of studies available (Fig. 1.6). This includes the positions of early diverging neosuchians such as *Bernissartia* and *Mahajangasuchus* (Lauprasert *et al*., 2009; De Andrade *et al*., 2011) and early branching eusuchians, such as *Hylaeochampsia* and *Alloposuchus* (Buscalioni *et al*., 2011). The placements of *Boverisuchus* and *Borealosuchus* are also contested. *Boverisuchus* is often associated with either Crocodylia (Bronzati *et al*., 2012) or Planocraenidae (Brochu, 2013). The position of *Borealosuchus* is unclear in its relation to the Gavialoidea, being resolved either as the latter’s sister taxon (Buscalioni *et al*., 2011; Puértolas *et al*., 2011) or outside Crocodylia (Bronzati *et al*., 2012).

The phylogenetic studies listed also vary widely in terms of character sampling, construction and treatment. For example, all previous analyses have discretised quantitative characters rather than treating them as continuous data. Continuous data are less influenced by worker subjectivity (Parins-Fukuchi, 2017) and are a more accurate representation of evolutionary processes, which usually occur along a sliding scale rather than in separate, distinct stages (Wiens & Brower, 2001). Furthermore, many previous datasets contain multiple examples of problematic characters, such as complex multistate composite characters. According to Sereno (2007) and Brazeau (2011), such characters should be converted into several binary characters. Therefore, a detailed examination and re-evaluation of the available characters for elucidating crocodylomorph phylogeny is long overdue.

An added difficulty with phylogenetic reconstruction in Neosuchia is the so-
<table>
<thead>
<tr>
<th>Authors</th>
<th>Clade</th>
<th>Number of taxa</th>
<th>Number of characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clark (1994)</td>
<td>Crocodyliformes</td>
<td>39</td>
<td>101</td>
</tr>
<tr>
<td>Brochu (1999)</td>
<td>Crocodylia</td>
<td>69</td>
<td>164</td>
</tr>
<tr>
<td>Sereno <em>et al.</em> (2001)</td>
<td>Mesoeucrocodilia</td>
<td>20</td>
<td>72</td>
</tr>
<tr>
<td>Wu <em>et al.</em> (2001)</td>
<td>Crocodyliformes</td>
<td>32</td>
<td>131</td>
</tr>
<tr>
<td>Jouve (2009)</td>
<td>Crocodyliformes</td>
<td>75</td>
<td>143</td>
</tr>
<tr>
<td>Hastings <em>et al.</em> (2010)</td>
<td>Dyrosauridae</td>
<td>16</td>
<td>82</td>
</tr>
<tr>
<td>Brochu <em>et al.</em> (2012)</td>
<td>Eusuchia</td>
<td>96</td>
<td>179</td>
</tr>
<tr>
<td>Bronzati <em>et al.</em> (2012)*</td>
<td>Crocodyliformes</td>
<td>184</td>
<td>-</td>
</tr>
<tr>
<td>Montefeltro <em>et al.</em> (2013)</td>
<td>Neosuchia</td>
<td>90</td>
<td>484</td>
</tr>
<tr>
<td>Adams (2014)</td>
<td>Crocodyliformes</td>
<td>90</td>
<td>301</td>
</tr>
</tbody>
</table>

Table 2.1: The clades, character numbers and number of taxa analysed in exemplar previous studies. *Bronzati *et al.* (2012) constructed a supertree, rather than using a character-based matrix.

called ‘longirostrine problem’. Various unrelated neosuchian taxa, such as *Gavialis*, *Mecistops* and *Dyrosaurus*, possess a very elongated snout morphology (Fig. 1.3) that is thought to be an adaptation to piscivory (Iordansky, 1973) (for the exact definition of ‘longirostrine’ used here, see Section 2.3.4). The superficial similarity between the morphology of the different longirostrine species causes a number of characters, in particular those related to snout shape, to be scored identically. This homoplastic signal leads to artificial clades in phylogenetic reconstructions that contain all longirostrine species in the analysis (Clark, 1994; Jouve, 2009). Several ways of coping with the longirostrine problem have been suggested by Jouve (2009), including the removal of morphological characters affected by the longirostrine problem and of all of the longirostrine taxa in the affected analysis.

This study aims to provide new insights into the effectiveness of different methods of phylogenetic reconstruction, the longirostrine problem and the phy-
logenetic relationships of neosuchians. It will do so by re-examining established morphological characters and analysing them with several different phylogenetic methods, including maximum parsimony analyses (with and without Extended Implied Weighting) and Bayesian approaches, as well as the application of methods that analyse continuous characters.

2.3 Materials and Methods

Data Collection

Morphological characters were scored from 150 specimens representing 106 different taxa. As outgroup choice has been shown to influence taxon placement in all phylogenetic analyses (Wilberg, 2015) multiple outgroups were employed. *Protosuchus richardsoni* was set as the outgroup to all other taxa. A further four outgroups were included (*Araripesuchus gomesii*, *Comahuesuchus brachybucaulis*, *Notosuchus terrestris*, *Sebecus icaeorhinus*) because they are representative of a range of clades that the current consensus regards to be outside Neosuchia, but more closely related to Neosuchia than *Protosuchus* (Bronzati et al., 2012). The analysis also included 19 extant taxa (from local museum collections) representing all three crocodylian families.

Continuous character measurements were obtained firsthand. Where possible, measurements were taken from multiple specimens of the same species and later entered as ranges in the dataset to minimise collection error, with a maximum of four specimens per species. Only adult specimens were measured, but as crocodylians show little to no sexual dimorphism (Grigg & Gans, 1993), potential differences between males and females are not accounted for.

All measurements and character scores were recorded in Microsoft Office Excel. The ratios between two measurements representing the continuous characters were calculated using Excel before being transferred into a .tnt file.
Character list assembly and data matrices

An initial character list was assembled following a comprehensive literature search, with characters taken from Brochu (1999), Sereno et al. (2001), Wu et al. (2001), Pol & Norell (2004), Jouve et al. (2006), Salisbury et al. (2006), Hill et al. (2008), Jouve (2009), Hastings et al. (2010), Bronzati et al. (2012), Montefeltro et al. (2013) and references therein (Table 2.1). These characters were traced back to their original descriptions and new characters were added based on personal observations and a survey of more recent literature. Each morphological character was evaluated to establish that it described unique morphological features, in order to avoid accidental duplication. Each character was re-worded to fit the character construction schemes proposed by Sereno (2007) and Brazeau (2011) in order to enhance clarity and repeatability.

After removing obvious duplicates the original character list contained 1419 discrete characters. All of these characters were then identified using specimens of extant crocodylians in the collections of the LDUCZ and the NHMUK and individually re-evaluated for their utility. This led to numerous characters being discarded for three major reasons: 1) they represented autapomorphies for OTUs in the dataset and were thus found to be uninformative in resolving neosuchian phylogeny; 2) they were found to be hidden duplicates of already used characters, describing the same morphological features with different wordings; 3) they were describing unclear morphological variation which did not work when applied to real specimens.

A list of these discarded characters, with justification for their exclusion, can be found in Appendix C.3.

In addition, 23 new characters were generated, nine of which were based on personal observation of specimens and 14 of which were based on features identified in other systematic descriptions (Wu et al., 2001; Brochu, 2007, 2010, 2011; Jouve et al., 2008a; Martin et al., 2010; Buscalioni et al., 2011; Hastings
The original character list contained a number of complex multistate compound characters. One example is character 6 in Pol & Norell (2004) (originally from Clark (1994)): "External nares facing: anterolaterally or anteriorly (0), dorsally not separated by premaxillary bar from anterior edge of rostrum (1), or dorsally separated by premaxillary bar (2)". According to Sereno (2007) and Brazeau (2011), such characters should be converted into several binary characters. In this case, the two binary characters separate the orientation of the external nares from the state of the premaxillary bar (see characters 95 and 96 in this character list, available in full in Appendix A).

Further problems in character scoring and repeatability have been caused not only by unclear wording, but also by the use of character states that are vague and difficult to operationalise, for example those that employ qualitative, poorly defined terms such as 'small' and 'large' in lieu of exact state descriptions. Character states using these and other similar terms introduce subjectivity into the analysis and have the potential to affect repeatability. Since evolutionary change often occurs along a sliding scale rather than via distinct stages (Wiens & Brower, 2001) it is also more appropriate to convert discretised quantitative characters into continuous ones, especially since these can now be analysed phylogenetically, using raw measurement data converted into ratios rather than pre-defined and often arbitrary character state boundaries (Goloboff et al., 2006). Despite potential problems of covariance (Adams & Felice, 2014; Uyeda et al., 2015) and arbitrariness in measurements (Koch et al., 2015), continuous characters have been demonstrated to provide useful phylogenetic information (Wiens & Brower, 2001; Goloboff et al., 2006), performing better than discrete characters under certain circumstances, such as under regimes of high evolutionary rates (Parins-Fukuchi, 2017). Here, quantitative characters with arbitrarily defined state boundaries were converted into continuous characters (see Goloboff et al. (2006)), wherever possible, using the ratio of two clearly
defined linear or angular measurements. Several previous studies have employed additional sources of data for neosuchian phylogenetic inference, such as: Piras et al. (2010) who used a dataset consisting entirely of 3D landmark data collected from crocodylian skulls; Chamero et al. (2014) who applied 3D morphometrics to the skull and the cervico-thoracic region of Crocodylia; and Gold et al. (2014) who utilised geometric morphometrics to analyse eusuchian braincase structure. These studies, however, focused only on very limited parts of the neosuchian tree.

In order to examine the interdependence and covariance of continuous characters, Principal Components Analysis (PCA) (Brocklehurst et al., 2016) was applied using pcaMethods (Stacklies et al., 2007) in R v. 3.4.2 (R Core Team, 2017). This was applied to all continuous characters and to a subset of 10 continuous characters related to the longirostrine conditions in Neosuchia (continuous character numbers 1, 11, 12, 13, 16, 28, 37, 52, 53a and 54a). The longirostrine condition is defined for the purpose of this study by the following two conditions applying together: a) the snout length (measure from anterior-most point of orbit to most anterior point of skull) being at least twice as long, or longer, than the remaining skull length (measured from anteriormost point of orbit to posteriormost point of skull), b) a very narrow snout whose lateral margins stay parallel for more than half its length. This corresponds to a ratio of 0.67 or larger in character 16 of the character list. For the purposes of the PCA, taxa with more than four missing character states were deleted due to the sensitivity of this method to missing data. NipalsPCA (implemented in the R environment, based on an algorithm by Wold 1966) was used for the analysis of both total continuous data and the longirostrine subset of characters, minimising the impact of missing data. Analyses were unsuccessful for the complete continuous dataset of 84 characters due to the high proportion of missing information that could not be excluded (>15% missing data). As a result, all characters clustered in the same place in the resulting PCA plots, preventing me from drawing
conclusions as to character dependency. However, for longirostrine continuous characters only, the results showed a clear clustering of characters 52, 53a and 54a, suggesting that they are not independent from each other. Therefore, the original characters 53a and 54a were excluded and are marked as such in the full character list. The character numbers listed below refer to the dataset with characters 53a and 54a excluded (corresponding to the character numbers in the full character list).

The final full morphological character list used as the basis for the subsequent analysis contains 569 characters (487 discrete and 82 continuous) and is available in full in Appendix A. To facilitate the use of this character list, 163 of the characters have been illustrated in order to enhance clarity and repeatability of character state scoring in future analyses.

A second dataset was assembled to investigate problems related to potential homoplasy caused by the longirostrine condition. All of the characters related to the longirostrine condition were removed, based on character descriptions and synapomorphies plotted on the first tree results obtained, in which longirostrine groups to cluster together. The characters excluded were as follows: 1, 11, 12, 13, 16, 28, 37, 52, 53, 54, 108, 127, 128, 147, 150, 152, 178, 201, 216, 224, 379, 386, 391, 397, 400, 401, 402, 419, 424, 427, 428 and 468. The resulting dataset contained 539 characters, with 74 continuous and 465 discrete characters.

In addition, datasets containing only the continuous and discrete characters respectively were generated to assess their viability for phylogenetic analysis. Lastly, a version of the full dataset was assembled in which all continuous characters were rediscernised into separate states according to their original character descriptions.

All datasets and the numbers of characters they contain are listed in Table 2.2. The full data matrix for dataset 1 is available in Appendix B.
Table 2.2: The types of datasets analysed and the number of characters contained in each.

<table>
<thead>
<tr>
<th>Dataset number</th>
<th>Continuous characters form</th>
<th>Discrete characters</th>
<th>Longirostrine characters</th>
<th>Number of characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>continuous</td>
<td>present</td>
<td>present</td>
<td>569</td>
</tr>
<tr>
<td>2</td>
<td>continuous</td>
<td>present</td>
<td>absent</td>
<td>539</td>
</tr>
<tr>
<td>3</td>
<td>continuous</td>
<td>absent</td>
<td>present</td>
<td>82</td>
</tr>
<tr>
<td>4</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>487</td>
</tr>
<tr>
<td>5</td>
<td>discretised</td>
<td>present</td>
<td>present</td>
<td>531</td>
</tr>
<tr>
<td>6</td>
<td>discretised</td>
<td>present</td>
<td>absent</td>
<td>504</td>
</tr>
</tbody>
</table>

Data transformations and character settings

It is necessary to adjust the relative weights of quantitative characters when expressed as continuous data (e.g. ratios) (Goloboff et al., 2006). In order to ensure that continuous characters were weighted equally in proportion to discrete characters, each character was set to have an initial weight of 100. The weightings of continuous characters were then adjusted as follows:

1. the total range of the continuous character value was calculated for each character, e.g. 0.5 for character X with values ranging from 0.2 to 0.7;

2. 1 was divided by said total range to obtain a weighting factor, in the case of character X this would be 2;

3. since the initial character weight is 100, the weighting factor was multiplied by 100 to obtain a unique weight for each continuous character (e.g. 200 in the case of character X).

These unique weights were entered manually into the .tnt file to adjust all weightings. In addition, 40 of the 57 discrete multi-state characters were treated as ordered as their states represent potential transformation series (Brazeau, 2011): 86, 87, 92, 108, 120, 122, 125, 152, 155, 178, 188, 190, 193, 211, 217, 241, 247, 254, 265, 274, 285, 290, 363, 394, 400, 415, 416, 425, 443, 461, 483,
490, 508, 522, 527, 530, 547, 549, 551 and 552. These ordered characters are also marked in the full character list in Appendix A.

**Phylogenetic Analyses**

Maximum parsimony analyses were performed in TNT v. 1.5 (Goloboff & Catalano, 2016). Phylogenies were generated from the different datasets described above with and without the use of extended implied weighting (EIW) in TNT (for the exact algorithm, see Goloboff 2014). New Technology Search (NTS) was used with sectorial searches, ratchet, drifting and tree fusing algorithms enabled. The consensus was required to stabilise at least five times with factor 75 before completing the search. The optimal topologies found by these initial new technology searches were then used as starting trees for a traditional TBR search, following the protocol outlined by Mannion et al. (2013). For extended implied weighting, analyses were carried out with three different K-values, K=3, K=6 and K=12 in order to explore the influence of different weighting strengths on the resulting phylogenies. According to Goloboff et al. (2017), higher K-values do not downweight potentially homoplastic characters as strongly as lower values.

In order to identify unstable taxa and the characters responsible for their instability, the command `pcrprune` (Goloboff & Szumik, 2015) was used which is based on the `iterpcr` script by Pol & Escapa (2009). Further analysis of unstable taxa was carried out using RogueNaRok v. 1.0 (Aberer et al., 2013). Bremer support was calculated using the script `Bremer.run`, and CI and RI were calculated using the script `Stats.run`, both supplied with TNT. Character statistics were calculated using the `Charstats.run` script by Martin Ramírez, made available online on `sites.google.com/site/teosiste/tp/archivos`. Bootstrap and jackknife supports were generated using NTS with 1000 and 100 replicates respectively to avoid excessively high runtime.

Bayesian Inference using Mr. Bayes v. 3.2 (Ronquist et al., 2012b) was per-
formed as well. Since MrBayes does not allow for the use of continuous
variables, only the discrete and rediscretised versions of the dataset were analysed
using this approach. The data sets were analysed using the following com-
mands: lset nst=1 rates=gamma (denoting the use of the GTR model (nst=1)
and proper analysis of morphological character data (which usually display
gamma-shaped variation, see Ronquist et al. (2012b)) and mcmc ngen=1000000
samplefreq=10000 printfreq=10000 diagnfreq=10000. After the initial num-
ber of 1,000,000 generations, the standard deviation (SD) still proved too high
(above 0.01). SD never dropped below 0.2 so the analyses were stopped after
10,000,000 generations, with a burnin of 1,000,000.

Stratigraphic congruence

Stratigraphic congruence for each of the resulting trees was calculated using
the package strap (Bell & Lloyd, 2014) in the R environment and the command
StratPhyloCongruence with 1,000 permutations each for resampled and ran-
domly generated trees. Taxon ages for the analysis were taken from the Palaeo-
biology Database (PBDB) (Alroy, 1998) and the literature and are listed in full
in Table 3.2 in Chapter 3. For those taxa with only one occurrence in the fossil
record uncertainties in dating were taken into account by using midpoint ages
of their stratigraphic ranges. Several taxa such as Dyrosaurus phosphaticus,
however, displayed genuine stratigraphic ranges with multiple occurrences in
the fossil record and were entered into the ages file as such. All MPTs ob-
tained as result from each analysis were run through strap to obtain a range of
stratigraphic congruence values from best to worst.

Stratigraphic congruence was calculated for three major measures: Relative
Completeness Index (RCI) (Benton & Storrs, 1994), Manhattan Stratigraphic
Measure (MSM*) (Siddall, 1998; Pol & Norell, 2001) and Gap Excess Ratio
(GER) (Wills, 1999). RCI is based on the ratios between the observed age
ranges of taxa with the lengths of their inferred ghost ranges (i.e. the remaining
branch lengths of the tree). Thus it functions similarly to a completeness metric, by determining how much of a time-scaled tree’s total branch length can be explained by actual taxonomic ranges. MSM* is based on similar algorithms to the character consistency index (Kluge & Farris, 1969) where the ages of terminal taxa are represented as Sankoff characters. In contrast to RCI, it compares a hypothetical tree with optimal stratigraphic congruence to the actual topology. GER is similar to MSM* in that it operates with a hypothetical tree of best stratigraphic congruence and the actual topology. However, it also takes into account suboptimal trees and calculates stratigraphic congruence with optimal and suboptimal tree topologies compared to the actual time-scaled tree.

2.4 Analyses and results

Phylogenetic analyses

The results of the tree searches (Table 2.3) generally fell into three different categories (Fig. 2.1): topologies where the longirostrine groups were clustered together (analyses I, VI and IX); topologies where they were resolved as sep-
### Table 2.3: Tree statistics for the twelve parsimony analyses and three Bayesian analyses. TL, CI and RI are based on the MPTs for maximum parsimony analyses, values for Bayesian analyses are based on the shortest trees resulting from the analysis. Dataset numbers correspond to Table 2.2. (CI, Consistency Index; EIW, Extended Implied Weighting; MPTs, Most Parsimonious Trees; RI, Retention Index; TL, Tree Length)

<table>
<thead>
<tr>
<th>Analysis number</th>
<th>Dataset number</th>
<th>EIW</th>
<th>k-value</th>
<th>TL</th>
<th>CI</th>
<th>RI</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1</td>
<td>no</td>
<td>-</td>
<td>213909.8</td>
<td>0.282</td>
<td>0.606</td>
</tr>
<tr>
<td>II</td>
<td>1</td>
<td>yes</td>
<td>3</td>
<td>221468.5</td>
<td>0.273</td>
<td>0.586</td>
</tr>
<tr>
<td>III</td>
<td>2</td>
<td>no</td>
<td>-</td>
<td>191350.8</td>
<td>0.298</td>
<td>0.596</td>
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<tr>
<td>IV</td>
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<td>3</td>
<td>195742.5</td>
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<td>0.586</td>
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<tr>
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<td>193793.5</td>
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<td>192414.8</td>
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<td>0.593</td>
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<td>22169.4</td>
<td>0.300</td>
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<td>2142</td>
<td>0.276</td>
<td>0.591</td>
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<td>X</td>
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<td>3</td>
<td>2207</td>
<td>0.268</td>
<td>0.592</td>
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<tr>
<td>XI</td>
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<td>-</td>
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<td>0.293</td>
<td>0.594</td>
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<tr>
<td>XII</td>
<td>6</td>
<td>yes</td>
<td>3</td>
<td>1933</td>
<td>0.286</td>
<td>0.579</td>
</tr>
<tr>
<td>Bayesian I</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>1949</td>
<td>0.277</td>
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<tr>
<td>Bayesian II</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>2211</td>
<td>0.267</td>
<td>0.591</td>
</tr>
<tr>
<td>Bayesian III</td>
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<td>-</td>
<td>-</td>
<td>1931</td>
<td>0.286</td>
<td>0.580</td>
</tr>
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</table>

The results of the various analyses conducted can be summarised as follows:

- **Analysis I** (*full dataset*): all longirostrine clades clustering together; *Hyloechampsia, Bernissartia* and *Borealosuchus* in monophyletic group with Goniopholididae (Fig. 2.1A).

- **Analysis II** (*full dataset + EIW*): longirostrine clades resolved individually; all tethysuchian taxa + *Steneosaurus* in one clade; the tomistomines *Kentisuchus* and *Gavialosuchus antiquus* are grouped within Gavialoidea.
Figure 2.2: Summary of the six strict consensus trees with the best stratigraphic congruence value from the analyses in this study. The topologies are based on the following analyses: A, analysis II; B, analysis III; C, analysis IV; D, analysis VIII; E, analysis X; F, analysis XII.
• **Analysis III** *(full dataset, longirostrine characters removed)*: longirostrine clades resolved individually; Tethysuchia paraphyletic to remaining Neosuchia; a number of species associated with different clades than in their current classification, such as *Elosuchus* grouped with Goniopholididae and *Tomistoma dowsoni* with Gavialoidea; all *Alligator* species as monophyletic sister group to Caimaninae (Fig. 2.2B).

• **Analysis IV** *(full dataset, longirostrine characters removed + EIW)*: longirostrine clades resolved individually; *Hyposaurus* and *Terminonaris* outside Tethysuchia; Planocraniidae resolved; *Maroccosuchus* grouped with Gavialoidea (Fig. 2.2C).

• **Analysis V** *(continuous characters only)*: One large polytomy; no clades resolved.

• **Analysis VI** *(continuous characters only + EIW)*: all longirostrine clades clustered together; other clades are resolved but not with currently known species associations (Fig. 2.1A).

• **Analysis VII** *(discrete characters only)*: large polytomy; the only resolved clades are outgroups, Goniopholididae, Caimaninae and several taxon groupings.

• **Analysis VIII** *(discrete characters only + EIW)*: all longirostrine clades resolved individually; all tethysuchian taxa (except *Sarcosuchus*)+ *Ste-neosaurus* in one clade; *Nannosuchus* and *Vectisuchus* outside Goniopholididae; *Elosuchus* within Gavialoidea (Fig. 2.2D).

• **Analysis IX** *(rediscretised dataset)*: all longirostrine clades clustered together; Crocodyloidea paraphyletic to remaining Eusuchia; *Hylaeochamps* and *Bernissarta* in monophyletic group with Goniopholididae (Fig. 2.1A).


- **Analysis X** (*rediscretised dataset + EIW*): all longirostrine clades resolved individually; all tethysuchian taxa (except *Sarcosuchus*+ *Steneosaurus*) in one clade; *Kentisuchus*, *Tomistoma dowsoni* and *Gavialosuchus* grouped with Gavialoidea (Fig. 2.2E).

- **Analysis XI** (*rediscretised dataset, longirostrine characters removed*): large polytomy, few clades truly resolved; all extant Crocodylinae resolved as monophyletic.

- **Analysis XII** (*rediscretised dataset, longirostrine characters removed + EIW*): all longirostrine clades resolved individually; all tethysuchian taxa (except *Sarcosuchus*)+ *Steneosaurus* in one clade; *Tomistoma dowsoni*, *Elosuchus* and *Gavialosuchus* grouped with Gavialoidea (Fig. 2.2F).

- **Bayesian Analysis I** (*discrete characters only*): large polytomy; Diplocynodontinae resolved as monophyletic polytomy; Gavialidae resolved; Alligatoridae resolved as monophyletic group; Caimainae fully resolved.

- **Bayesian Analysis II** (*rediscretised dataset*): all longirostrine clades clustering together; remainder of tree with large polytomies; Caimainae, extant Alligatorinae and Crocodylinae are resolved, as well as most derived Goniopholididae and Diplocynodontinae (the latter as polytomy).

- **Bayesian Analysis III** (*rediscretised dataset, longirostrine characters removed*): large polytomy; Caimainae, extant Alligatoridae and Crocodylinae are resolved, as well as most derived Goniopholididae, Gavialidae and Diplocynodontinae (the latter as polytomy).

Taxon pruning and the use of RogueNaRok yielded limited and unclear results as tree resolution was not significantly improved following the removal of potential 'wildcard' taxa: only a handful of taxa were shown to affect tree topology when removed. These taxa were either member of the Tethysuchia (*Dy-
rosaurus, Rhabdognathus, Pholidosaurus) or Crocodyloidea (Crocodylus affinis, C. elliotti, C. cf. clavis and C. megarhinus all of which have similar character scores).

A combined analysis that included molecular data (nuclear and RNA) in addition to the different morphological datasets yielded a further clustering of longirostrine taxa in the resulting topologies, similar to analyses I, VI and IX (Fig. 2.1).

Stratigraphic congruence

Table 2.4 summarises the results of the stratigraphic congruence analyses. RCI, GER and MSM* values for the stratigraphically best and worst fitting trees are given. The p-values for all stratigraphic congruence values (not shown) were all p <0.05. Analysis IV (continuous and discrete characters, longirostrine characters removed, with EIW) yielded the best results according to stratigraphic congruence, with analyses II (continuous and discrete characters, EIW) and XII (rediscretised dataset, longirostrine characters removed, EIW) performing similarly well. Analysis XI yields trees with a number of differing topologies and thus a large range of stratigraphic congruence values. Analyses I, VI and IX, which yielded different topologies (Fig. 1.6) performed notably worse in terms of stratigraphic congruence, all with RCI values below -590. Bayesian analyses showed less resolution and thus all performed worse in terms of stratigraphic congruence than their parsimony counterparts with EIW, but better than equally weighted parsimony.

Differences between trees

The full strict consensus trees for each analysis in this study are available in Appendix C.4. Differences in support for several of the clades obtained across the various analyses are illustrated in Fig. 2.2. All major clades are resolved in the six analyses illustrated; however, minor clades differ greatly in their positions or
Figure 2.3: Full strict consensus tree obtained from analysis IV (see Table 2.4). The 2x3 matrix boxes adjacent to the branches indicate whether those branches were supported/not supported by the other analyses yielding similar topologies (black square = similar branch supported in other analyses; white square = branch not supported). Analysis numbers correspond to those listed in Table 2.4 and are, from top left to bottom right: analysis II, III, IV, VIII, X and XII. Support values shown on the tree are those derived from analysis IV in the following order: Bootstrap/Jackknife/Bremer. Consensus tree properties: TL=196964.189, CI=0.146.

Support values:
Bootstrap/Jackknife/Bremer

Analysis numbers

II III IV
VIII X XII
Table 2.4: The results of the stratigraphic congruence analyses for each parsimony and Bayesian analysis performed. Dataset numbers correspond to Table 2.2.

<table>
<thead>
<tr>
<th>Analysis number</th>
<th>Dataset</th>
<th>EIW</th>
<th>RCI k-value</th>
<th>GER Best tree</th>
<th>GER Worst tree</th>
<th>MSM* Best tree</th>
<th>MSM* Worst tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1 no</td>
<td>-</td>
<td>-740.4</td>
<td>0.659</td>
<td>0.648</td>
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<td>0.037</td>
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<tr>
<td>II</td>
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<td>3</td>
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<td>0.828</td>
<td>0.822</td>
<td>0.073</td>
<td>0.071</td>
</tr>
<tr>
<td>III</td>
<td>2 no</td>
<td>-</td>
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<td>0.767</td>
<td>0.760</td>
<td>0.055</td>
<td>0.053</td>
</tr>
<tr>
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<td>0.826</td>
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<td>0.072</td>
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<tr>
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<td>0.060</td>
</tr>
<tr>
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<tr>
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<tr>
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<td>0.028</td>
</tr>
<tr>
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</tr>
<tr>
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<td>0.654</td>
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<td>3</td>
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<td>0.045</td>
<td>0.033</td>
</tr>
<tr>
<td>Bayesian III</td>
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<td>0.579</td>
<td>0.043</td>
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</tr>
</tbody>
</table>

internal structure. For example, relationships between taxa within Tethysuchia vary between different analyses, such as the placement of *Elosuchus* and *Hyposaurus* in the tree. *Susisuchus anatoceps* is placed in various positions, as the sister group to Goniopholididae as in analyses IV, X and XII, more deeply nested within Gonipholididae (analysis II) or outside Eusuchia (analyses III and VIII). Similarly, *Crocodilaemus robustus* is resolved in several different positions within both Neosuchia and Eusuchia. Planocraniidae, as currently defined ([*Planocrania* and *Boverisuchus vorax]*) is resolved only in analysis IV. Other analyses place *Planocrania* as the sister taxon to Diplocynodontinae (analyses III and X) or the sister group to Crocodylidae (analyses II, VIII and XII).

Other differences between the analyses include: the affiliation of *Leidyosuchus* with Diplocynodontinae (in only half of the analyses); the positions of *Marocosuchus* and the oldest gavialoids; and the placements of the oldest tomistomines. The relationships of species within Crocodylinae also vary strongly from analysis to analysis, with the members of the genus *Crocodylus* being resolved in different positions with each analysis, especially *C. intermedius*, *C.*
siamensis, C. novaguineae, and C. palustris.

Preferred phylogeny (Analysis IV)

The evolutionary relationships supported by analysis IV (Fig. 2.3) are the most congruent with stratigraphy. In addition, the topology is based on the dataset including both continuous and discrete characters, with the continuous data treated as such and not rediscrétised. Given that it is not feasible to explore the implications of all, or even most, of the numerous topologies produced by the different analyses, the results of analysis IV were adopted as the preferred tree (see Discussion for further details and justification). The tree search in TNT for this analysis produced five MPTs and the strict consensus tree (TL=195742.505 steps, Cl=0.291 for trees 1-5, Cl=0.289 for consensus, RI=0.586 for trees 1-5, RI=0.579 for the consensus).

Previously proposed major phylogenetic groups within Neosuchia were all resolved; however, support values for the tree are low overall, with only a few clades receiving high support values across all three methods used. The best supported clades are Notosuchia (consisting of Araripesuchus, Noto- suchus and Comahuesuchus) (bootstrap = 74, jackknife = 85, Bremer support = 37.93), the clade formed by two species of Allognathosuchus (bootstrap = 73, jackknife = 81, Bremer support = 2.34) and the Caimaninae (bootstrap = 61, jackknife = 61, Bremer support = 5.29). Other clades receive high Bremer support values, but low bootstrap or jackknife support, including Planocraniidae with Boverisuchus and Planocrania (Bremer support = 13.48), Alligatoroidea (Bremer support = 43.49), Crocodylinae (Bremer support = 50.83), and 'derived' Goniopholididae (Amphicotylus, Anteophthalmosuchus and Goniopholis) (Bremer support = 18.66).
2.5 Discussion

Methodological implications

*Extended Implied Weighting*

All three stratigraphic congruence values (RCI, GER and MSM*) showed the same pattern of high and low support across the different datasets. Extended Implied Weighting consistently yielded results with better stratigraphic congruence than the same dataset analysed without EIW (Table 2.4). Almost all analyses using EIW resolved Tethysuchia, Gavialoidea and Tomistominae as separate longirostrine clades. The same datasets analysed without EIW often yielded a single longirostrine clade including all long-snouted taxa (see Fig. 2.1 for the different topologies). It is apparent that the usage of EIW plays a key role in obtaining trees whose topologies are less determined by homoplastic features, such as those associated with convergent instances of snout elongation.

Despite Goloboff *et al.* (2017) arguing for the use of higher K-values (with K=12 given as the optimum), the results display higher stratigraphic congruence for those analyses conducted with lower K-values. Analysis IV with K=3 (RCI= -283.1) yielded the best results, better than the K=6 (RCI = -349.5) and K=12 (RCI = -351.7) trees (Table 2.4). This result might reflect a high degree of homoplasy in neosuchians since lower K-values are known to downweight homoplastic characters more strongly (Goloboff *et al.*, 2017). Thus, the preferred tree (Fig. 2.3) selected for character mapping and a more detailed discussion of neosuchian evolution was obtained using a K-value of 3.

Parsimony is the most commonly used method in reconstructing phylogenies using morphological data, although it has been argued that it is due to force of habit rather than the best method available (Congreve & Lamsdell, 2016). Recent debate has begun to question the usefulness of parsimony in
phylogenetic reconstruction in comparison with Bayesian methods. For example, Wright & Hillis (2014) found that Bayesian models outperform parsimony, a result that was repeated by O’Reilly et al. (2016) and Puttick et al. (2017). However, O’Reilly et al. (2016) also noted that Bayesian analyses frequently produce less resolution than parsimony analyses. In addition, O’Reilly et al. (2016) and Puttick et al. (2017) stated that implied weighting (implemented by Goloboff et al. 2008a based on the algorithms by Farris 1969 and Goloboff 1993) performed worse than both equal-weights parsimony and Bayesian models. Congreve & Lamsdell (2016) obtained the same result, suggesting again that unweighted parsimony outperforms implied weights parsimony. However, Goloboff et al. (2017) argued that the improved version of implied weighting (i.e. EIW) outperforms all other methods, including Bayesian analyses. EIW is superior to the implied weighting algorithm used in the previous studies as it is not as heavily influenced by missing data according to Goloboff (2014). Bayesian analyses have also recently been criticised for being overly confident in choosing one hypothesis over another in molecular phylogenetic analyses, resulting in posterior probabilities that are too high (Yang & Zhu, 2018). Although caution is required when extrapolating from the single case study presented here, it is interesting to note that the results herein broadly support the utility of EIW and the potential problems of applying Bayesian analysis to morphological data. Here, the merits of EIW in resolving potentially more accurate morphology-based phylogenies are demonstrated when a high amount of homoplasy is present. Bayesian analyses of the same datasets produced large numbers of polytomies and trees where longirostrine clades cluster together.

**Longirostrine characters**

Analysing the datasets that excluded the 32 characters associated with the longirostrine condition in Neosuchia with EIW (analysis IV) resulted in the phylogenetic trees with the highest stratigraphic congruence (Table 2.4). However,
although this result implies that identifying and removing characters related to homoplasy *a priori* yields the most stratigraphically congruent trees, it should be cautioned against using this approach too liberally. *A priori* deletion of characters has the inherent danger of increased subjectivity when creating and analysing dataset. Such a measure should only be considered after extensive exploration of the full dataset demonstrates that homoplasy is so rife and coherent that it repeatedly disrupts accurate phylogenetic reconstruction.

As shown below, other methods can take the phylogenetic information in such homoplastic characters into account and produce tree topologies of only slightly worse stratigraphic congruence.

**Continuous characters**

In addition to the datasets with longirostrine characters removed (analyses IV and XII), the full dataset with continuous characters (including longirostrine characters, analysis II) performed similarly well under EIW with respect to stratigraphic congruence.

Continuous characters analysed on their own (analyses V and VI) result in tree topologies with large polytomies and low stratigraphic congruence. However, when continuous characters are analysed as such together with discrete characters (analyses I, II, III and IV) stratigraphic congruence is markedly higher in the analyses with EIW (II and IV) than without (I and III). In addition, despite the presence of characters associated with the longirostrine condition, analysis II resolves all longirostrine clades separately (Fig. 2.1). Under the use of EIW, the datasets with continuous characters analysed as such (analyses II and IV) perform better than their rediscretised counterparts (analyses X and XII respectively) in terms of stratigraphic congruence.

In short, there appear to be two ways to deal with homoplasy in general and the longirostrine problem in particular:
1. Remove longirostrine characters from any dataset *a priori* and analyse with EIW.

2. Use a full dataset containing both continuous and discrete characters and analyse with EIW.

Thus the use of EIW and continuous characters together provides a valid alternative to the *a priori* deletion of possible homoplastic characters and the loss of potentially relevant phylogenetic information that such characters might still contain.

**Implications for neosuchian phylogeny and systematics**

All of the major neosuchian clades proposed by previous phylogenetic studies were also resolved by the preferred analyses herein. The internal structure of Neosuchia differs mostly in the placement of several rogue taxa and the interrelationships of taxa within Crocodylinae and Alligatorinae (see below).

*Tethysuchia*

The interrelationships of Tethysuchia have been controversial (De Andrade *et al.*, 2011; Young *et al.*, 2014; Martin *et al.*, 2016b; Meunier & Larsson, 2016) (Fig. 2.4). The analyses support the placement of Tethysuchia as an early diverging neosuchian clade rather than more deeply nested within Eusuchia (contra Rogers (2003)). In addition to being proposed as the sister clade of Dyrosauridae (Fortier *et al.*, 2011; Young *et al.*, 2014), pholidosaurids have also been suggested to be paraphyletic within Tethysuchia (De Andrade *et al.*, 2011), closely related to Goniopholididae (Martin *et al.*, 2016b) or grouped together only by longirostrine characters (Meunier & Larsson, 2016). The results clearly refute the latter two hypotheses, with Tethysuchia being resolved as monophyletic in almost all analyses with high stratigraphic congruence. The monophyletic tethysuchian group in this analysis is united by the existence of
medial tubercles on the posterior margin of external nares (character 99), a zigzag-shaped frontoparietal suture on their interfenestral bar (character 195) and a long and acute anterolateral process of the postorbitals (character 200). Furthermore, none of the analyses including longirostrine characters (analyses II and X) resolved a monophyletic Pholidosauridae.

*Hyposaurus natator* and *Terminonaris robusta*, which are usually classified as tethysuchians, group with the thalattosuchian *Steneosaurus bollensis*, (Fig. 2.3) which might result from the high amounts of missing data in all three of these taxa. Despite possessing relatively complete skulls, many features were unscorable in these taxa and there is only a single thalattosuchian in this dataset. *Congosaurus* is also resolved outside Tethysuchia in analysis IV, in varying positions near the base of the neosuchian tree.

Internal relationships within Tethysuchia vary markedly between the different analyses (Fig. 2.3). *Dyrosaurus, Congosaurus, Rhabdognathus* and *Hyposaurus* often form a polytomy (analyses VIII, X, and XII) that cannot be resolved further. *Dyrosaurus phosphaticus* and the two species of *Rhabdognathus* were resolved as part of Dyrosauridae in analysis IV (Fig. 2.3), but *Elosuchus/Fortignathus felixi* is not, in contrast to the results presented by Young et al. (2016). *Elosuchus* is grouped with *Sarcosuchus* and *Pholidosaurus* on the basis of medial tubercles on posterior margin of their external nares being in ventral position (character 100); and the posterior part of the dentary tooth row undulating in dorsal view (character 413).

Moreover, *Elosuchus* does not form a clade with *Vectisuchus* (Elosuchidae), in contrast to the tree of De Andrade et al. (2011). In accordance with previous literature (e.g. Tykoski et al. (2002)) *Vectisuchus* is referred to Goniopholididae in the preferred tree, although the snout of the specimen examined for this study was not preserved. It shares a notable depression on the posterolateral surface of the maxillae (character 134) with the other goniopholids, as well as thick and vertical lateral margins of its osteoderms (character 555).
Figure 2.4: Summary of the competing hypotheses of tethysuchian phylogenetic relationships. The topologies are based on the following analyses: A, De Andrade et al. (2011); B, Young et al. (2014) in Young et al. (2016); C, Martin et al. (2016b) and Puértolas et al. (2011); D, Fortier et al. (2011); E, Hastings et al. (2010) in Young et al. (2016).
Increased sampling of tethysuchian and thalattosuchian species is required to resolve these disagreements and to determine whether the relationships supported here are indeed more accurate than those proposed by previous studies based on smaller datasets.

**Unstable early diverging neosuchian taxa**

In addition to limited sampling, which can often lead to issues associated with long branch attraction (Bergsten, 2005), the most prevalent problem in this study is the high proportion of missing data. The dataset contains 49.7% missing data, the most complete taxon being *Crocodylus porosus* (7.7% missing data) and most incomplete being *Congosaurus compressus* (extremely fragmentary material with 94.3% missing data). It is possible that this factor has lead to the resolution of relationships that are incongruent with previously published studies, such as the association between *Bernissartia fagesii* (a non-eusuchian neosuchian) and *Hylaeochampsasa* (an early diverging eusuchian and the single sampled member of the family Hylaeochampsidae: Buscalioni et al., 2011) in a single early diverging eusuchian clade in all analyses (Fig. 2.3). This is further corroborated by the fact that all of their uniting characters in this phylogeny are in the loss of certain features: ventralmost foramina on maxillae and premaxillae close to teeth (character 124); palatal process of maxillae next to anterior border of suborbital fenestrae absent (character 140); jugal does not exceed the anterior margin of orbit (character 253); boss on posterior surface of paroccipital process absent (character 298); and paroccipital process of exoccipital being short, lateral to cranioquadrate opening (character 299).

*Shamosuchus djadochtaensis* (an early diverging neosuchian according to Pol et al. (2009)), *Crocodilaemus robustus* (a pholidosaur according to Young et al. (2011a)) and *Theriosuchus pusillus* (an early diverging neosuchian recently removed from Atoposauridae (Tennant et al., 2016a)) are also affected by these problems. Each of these taxa are resolved in multiple different posi-
tions around the neosuchian root across the different analyses.

**Goniopholididae and Susisuchus**

The phylogenetic relationships of Goniopholididae resolved herein are very similar to those presented by De Andrade *et al.* (2011). *Sunosuchus* and *Vextisuchus* are identified as one of the earliest diverging goniopholids in contrast to Martin *et al.* (2016b) where *Sunosuchus* was placed as a more derived goniopholid. One novel aspect of the results of this study is the identification of *Susisuchus anatoceps* as the sister taxon of Goniopholididae in three of six of the analyses with high stratigraphic congruence (analyses IV, X and XII). However, there are only two characters supporting this relationship, both of which are not synapomorphies of Goniopholididae: quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (character 265); and caudal vertebrae with amphicoelus centra from second vertebra onward (character 503).

*Susisuchus* has previously been resolved outside Neosuchia (Jouve, 2009), as part of Susisuchidae at the base of Neosuchia (Fortier & Schultz, 2009; Turner & Pritchard, 2015) or as part of Eusuchia (Leite & Fortier, 2018). The latter placement is broadly similar to the position resolved in analyses III and VIII, albeit with much lower stratigraphic congruence in both cases. Adding *Isisfordia duncani* as a second member of the Susichidae to this dataset could potentially help to clarify the phylogenetic position of this species in the neosuchian tree and eventually strengthen or remove the association of the Susisuchidae with Goniopholididae.

**Borealosuchus and Planocraniidae**

As in Pol *et al.* (2009), *Borealosuchus* is resolved as one of the earliest diverging eusuchian groups in four out of the six analyses with the highest stratigraphic congruence (analyses III, IV, X and XII). This is in contrast to the results of Holliday & Gardner (2012) where *Borealosuchus* was in a polytomy
with Gavialoidea and Puértolas et al. (2011) where it was resolved as the sister group to Gavialoidea. The characters uniting the two species of Borealosuchus and placing the genus in its own clade in this analysis are: anterior median pala-
tine process into maxilla in form of thin wedge (character 371); dentary alveoli
of teeth 3 and 4 confluent (character 420); surangulars extend to posterior end
of retroarticular process (character 450); and height of peduncle of neural arch
on posterior cervical vertebrae taller (ratio larger than 1:1) compared to pedicel
height of other vertebrae (character 568).

Analysis IV also resolved Planocraniidae with the same species composition
(both Planocrania and Boverisuchus) as Brochu (2013). However, the other
analyses do not support this clade, placing Planocrania as the sister group of
either Diplocynodontinae or Crocodylidae instead, while Boverisuchus remains
as an early diverging eusuchian taxon in all analyses.

Gavialoidea

In line with the majority of recent morphological phylogenies for Crocodylomor-
phha (with the notable exception of Halliday et al. 2013), Gavialoidea and Tomis-
tominae are here resolved as separate clades. Gavialoidea appears as the
sister clade of Brevirostres (Fig. 2.3) and Tomistominae as the sister clade of
Crocodylinae, nested within Crocodyloidea. The separation of Thoracosaurus
from Gavialoidea found in Lee & Yates (2018) is not supported. The over-
all branching pattern within Gavialoidea is similar to that proposed by Brochu
(2004) and Jouve et al. (2015) with the exception of Piscogavialis jugali-perfo-
ratus, which is resolved in a earlier diverging position in a monophyletic group
with Rhamphosuchus and Eosuchus compared with these previous analyses.
The Piscogavialis+Rhamphosuchus+Eosuchus grouping is united by the pres-
ence of a posterior ventral extension of the maxilla devoid of teeth (character
143) and an ectopterygoid that is broadly separated from the maxillary toothrow
by the maxilla (character 327). However, there is only one character separating
this group from the remaining Gavialoidea: skull table surface slopes ventrally from sagittal axis (character 89).

Two taxa are grouped within Gavialoidea in analysis IV (Fig. 2.3) despite their previous referrals to Tomistominae: *Maroccosuchus zennaroi* (an early diverging tomistomine according to Jouve et al. 2015) and *Gavialosuchus antiquus* (a tomistomine according to Brochu & Storrs 2012). *Gavialosuchus* is grouped together with the Gavialidae+ *Thoracosaurus* on the basis of the shared presence of a ventrally sloping skull table surface (character 89). In contrast, *Maroccosuchus* has a number of characters uniting it with the Gavialoidea: premaxillo-maxillary contact without ventral opening on ventral edge (character 118); dorsal and ventral rims of groove for external ear valve musculature flaring anteriorly (character 230); spina quadratojugalis prominent (more than 10% of infratemporal fenestrae length) (character 269); large bilateral pendulous tubera present on basioccipital (character 305); and interalveolar space between third and fourth dentary alveoli roughly equal to that between second and third (character 418). However, the other analyses in this study with high stratigraphic congruence resolve *Maroccosuchus* as either a member of Tomistominae (analyses II, VIII, X and XII) or Crocodylidae (analysis III).

**Crocodyloidea**

Crocodyloidea is composed of three clades in all of the analyses herein: Tomistominae, Crocodylinae and an early diverging crocodyloid clade consisting of *Brachyuranochampsia, Crocodylus affinis, C. elliotti, C. cf. clavis* and *Prodiplocynodon* (Fig. 2.3), consistent across five of the six most stratigraphically congruent analyses (II, IV, VIII, X and XII). This cluster of taxa is united by: foramen for the palatine ramus of CN-V very large (at least 50% or more of adjacent alveolus length) (character 137); frontoparietal suture linear (character 194); basisphenoid not exposed laterally on braincase (character 317); and anterior median palatine process into maxilla does not extend beyond anterior
end of the suborbital fenestrae (character 370).

The relationships within Tomistominae resolved herein are similar to those found by Brochu (1999), Jouve et al. (2008b) and Buscalioni et al. (2011). However, unlike the Brochu (2004) and Jouve et al. (2015) analyses, all four of the *Tomistoma* species that were scored for this dataset were resolved as the most derived tomistomines in the majority of analyses, including *T. petrolica*, which had been placed in an earlier diverging position elsewhere (Brochu & Storrs, 2012). These tomistomines are clustered together because they share: the absence of a parieto-postorbital suture from skull roof (character 244) and a horizontal position of the paroccipital process in occipital view (character 290).

The interrelationships presented here for Crocodylinae are highly variable across the different analyses conducted in this study and are weakly supported overall. The topology based on analysis IV (Fig. 2.3) shows the greatest similarity to some older morphological trees (e.g. Brochu 1999), but is dissimilar from more recent phylogenies, both morphological (Brochu & Storrs, 2012) and molecular (Meredith et al., 2011; Oaks, 2011) (Fig. 2.5) and also does not cluster species along geographic borders (e.g. old world and new world groups as in Meredith et al. (2011)).

**Alligatoroidea**

All of the analyses in this study support the traditional split of Globidonta and Diplocynodontinae (Fig. 2.3).

*Leidyosuchus gilmorei* + *Leidyosuchus canadensis* is resolved as the sister group of Diplocynodontinae in half of the analyses with high stratigraphic congruence, clustered together by their frontoparietal suture being placed deeply within the supratemporal fenestra (character 193) and the dentary alveoli of teeth 3 and 4 being confluent (character 420). This is in contrast to the relationship proposed by Delfino & Smith (2012) where *Leidyosuchus* is placed as the sister taxon to Diplocynodontinae + Globidonta. However, the results here
Figure 2.5: Summary of the competing hypotheses of crocodyloid phylogenetic relationships. The topologies are based on the following analyses: A, Brochu & Storrs (2012), morphological; B, Brochu (1999), morphological; C, Meredith et al. (2011), molecular, mitochondrial DNA; D, Oaks (2011), molecular, mitochondrial & nuclear DNA.
agree with Delfino & Smith (2012) that *Baryphracta deponiae* is nested deeply within *Diplocynodon*.

The results of this study agree with Wu *et al.* (2017) that *Eoalligator* and *Asiatosuchus* are separate taxa and not synonymous, in contrast to the proposal of Wang *et al.* (2016). The findings here corroborate the resolution of *Asiatosuchus* as a crocodyloid (Delfino & Smith, 2009; Wang *et al.*, 2016). However, *Eoalligator chunyi* is resolved as an early diverging alligatoroid based on the dorsal margin of its supraoccipital being lower than that of the squamosal (character 288) and *Eoalligator huiningensis* as the sister taxon of *Alligator sinensis*, in contrast to Wu *et al.* (2017) who placed *E. chunyi* as a crocodyloid. *Eoalligator huiningensis* and the remaining Alligatoridae form a group that is united by a number of synapomorphies: preorbital ridges on dorsal skull surface reduced (character 87); single enlarged foramen medial to row of small foramina along alveolar margin of palatal surface present (character 138); foramina on medial parietal wall of supratemporal fenestrae (character 223); anterior opening of temporal canal hidden in dorsal view and overlapped by squamosal rim of supratemporal fossa (character 226); jugal and lacrimal with no notch at anterior contact (character 250); and first premaxillary teeth more closely spaced to each other than to second alveoli (character 378).

The relationships within Globidonta display the largest differences between the results in this study and those of previous analyses. Although Caimaninae is resolved as monophyletic, Alligatorinae is not, unlike recent analyses such as those by Brochu (2013) and all of its derivates (e.g. Skutschas *et al.* 2014; Wang *et al.* 2016 (Fig. 2.3). The overall relationships of Alligatorinae resemble those in Wu *et al.* (1996), although the latter did not include any members of the Caimaninae in their dataset. The presence of an Alligatorinae that is paraphyletic with respect to Caimaninae is consistent across all analyses with one exception (analysis III). Further study of the fossil material and the revised characters should shed light on this issue in the future.
Evolution of longirostry

The longirostrine problem, and the probably inaccurate taxon clustering it creates in crocodylomorph phylogenies, has been recognised for several decades (Clark, 1994; Jouve, 2009; Meunier & Larsson, 2016). One of the most striking examples of for the impact of longirostrine characters on phylogenetic topology is illustrated by the position of Thalattosuchia. This group has been placed almost everywhere in the crocodylomorph tree from highly nested within Neosuchia (often in association with other longirostrine clades such as members of the Tethysuchia) (Pol & Gasparini, 2009; Bronzati et al., 2012) to a position outside Neosuchia (Benton & Clark, 1988; Sereno et al., 2001; Wu et al., 2001; Young & De Andrade, 2009; Holliday & Gardner, 2012). Similar patterns are observed in the analyses in this study, with Tethysuchia clustering with other longirostrine clades in several of the trees here (Fig. 2.1). One of the methods used here, the a priori deletion of characters associated with the longirostrine condition, has been used before in order to deal with the longirostrine problem (Jouve, 2009). Other methods used by the same authors included the deletion of several longirostrine taxa from the analysis to avoid artificial associations, although the loss of information from such a drastic deletion is noted (Jouve, 2009).

The results of this study agree with Brochu (2001) that long-snouted forms evolved on at least three major occasions within Neosuchia: Gavialoidea, Tomistominae and Tethysuchia. Additionally, longirostry evolved independently in three more of the examined taxa within short snouted families: Euthodon arambourgi, Mecistops cataphractus, and Crocodylus johnstoni (N.B. the latter was not examined firsthand and is thus missing from this dataset). However, in contrast to Brochu (2001), the crocodyline taxon Crocodylus intermedius is not a truly longirostrine taxon as defined in the current study (see Section 2.2 above). Molecular studies reduce the number of independent origins of the lon-
Figure 2.6: Characters associated with the evolution of the longirostrine condition mapped onto a simplified version of the neosuchian tree in this study. Note that character numbers do not necessarily indicate synapomorphies for the clades; rather, these refer to characters that character tracing has revealed to be in common between longirostrine clades. See Table 2.5 for detailed character state descriptions.

Longirostrine condition by at least one, with Gavialoidea and Tomistominae usually forming a clade (Piras et al., 2010). Despite the attention paid to the longirostrine problem as outlined above, no previous study has examined in detail the character state changes that occurred during the parallel assembly of elongate snouts in neosuchians. A previous study found that different selection pressures led to similar snout morphologies in different metriorhynchid (a thalattosuchian group outside Neosuchia) clades, causing functional divergence (Young et al., 2011b).

Character tracing carried out in Mesquite v. 3.2 (Maddison & Maddison, 2017) on the strict consensus tree produced by analysis IV (Fig. 2.3) revealed that at least 24 characters are associated with the evolution longirostrine clades (Fig. 2.6, see Table 2.5 for detailed character descriptions). Thirteen of these characters appear to be linked to the evolution of longirostry in all three clades, as well as in the three other independently occurring longirostrine species. These features include skull and mandibular characters, approximately equally. Preorbital ridges are lost at the base of all longirostrine clades and several oth-
ers, such as Goniopholididae (character 87). The longirostrine snout is formed mainly from elongation of the premaxilla and maxilla, leading to straight ventral and lateral margins of the maxilla (characters 127 and 128). This is accompanied by the absence of raised alveolar walls relative to the ventral surface of the maxilla (character 131) and a change in the ventral structure of the premaxillary-maxillary contact, with one median projection of the premaxilla extending into the maxilla, often in the form of a sharp process (characters 122 and 123). Furthermore, the maxillary teeth all remain the same size, including that in the usually enlarged third alveolus (characters 386 and 391). There is less involvement from the nasal bones in snout elongation, because they lose contact with the external nares (character 149). Similar changes occur in the mandible: the shape of the dentary, symphysis and involvement of the splenial in the symphysis (characters 400, 401, 402, 438 and 468) play a large role. The splenial is usually involved extensively in the symphysis together with a relatively straight and long dentary, leading to the characteristic 'Y'-shape of the mandibular symphysis in all longirostrine taxa. All of these changes occur at the basis of the longirostrine clades, pointing to a sudden shift in snout morphology rather than slower assembly across several nodes.
<table>
<thead>
<tr>
<th>Present in</th>
<th>Character number</th>
<th>Character state</th>
<th>Character description</th>
<th>Details of position</th>
</tr>
</thead>
<tbody>
<tr>
<td>all longirostrine clades</td>
<td>87</td>
<td>0</td>
<td>Preorbital ridges absent</td>
<td>ancestral for all longirostrine clades, plus Alligatoroidea and Diplocynodontinae</td>
</tr>
<tr>
<td></td>
<td>122</td>
<td>1</td>
<td>One median projection of premaxilla at premaxillo-maxillary contact</td>
<td>ancestral for all longirostrine clades and Diplocynodontinae</td>
</tr>
<tr>
<td></td>
<td>123</td>
<td>1</td>
<td>Median projection of premaxilla at premaxillo-maxillary contact with sharp tips</td>
<td>in all longirostrine clades as well as Eusthenodon and Mecistacps</td>
</tr>
<tr>
<td></td>
<td>127</td>
<td>0</td>
<td>Lateral margins of snout linear, not festooned in dorsal view</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>128</td>
<td>0</td>
<td>Ventral edge of maxilla is straight in lateral view</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>149</td>
<td>0</td>
<td>Nasal not in contact with external nare</td>
<td>in all longirostrine clades and Goniopholididae</td>
</tr>
<tr>
<td></td>
<td>386</td>
<td>0</td>
<td>All maxillary teeth of similar size</td>
<td>in all longirostrine clades and Euthecodon</td>
</tr>
<tr>
<td></td>
<td>391</td>
<td>1</td>
<td>Third maxillary alveolus not enlarged in comparison with second and third</td>
<td>in all longirostrine clades and Eusthenodon</td>
</tr>
<tr>
<td></td>
<td>400</td>
<td>2</td>
<td>Extensions of symphysis beyond fifth alveolus</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>401</td>
<td>2</td>
<td>Anterior edge of symphysis transversally oriented, lateral edges longitudinal</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>402</td>
<td>0</td>
<td>Dorsal edge of dentary straight or slightly concave</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>428</td>
<td>2</td>
<td>Splenial involved extensively in symphysis</td>
<td>in all longirostrine clades</td>
</tr>
<tr>
<td></td>
<td>468</td>
<td>1</td>
<td>Mandible broadly Y-shaped</td>
<td>in all longirostrine clades and Goniopholididae</td>
</tr>
</tbody>
</table>

| Tethysuchia | 118 | 0 | No ventral opening on ventral edge of premaxillo-maxillary contact | in all Tethysuchia and Alligatoroidea |
| | 195 | 1 | Frontoparietal suture on interfenestral bar zigzag in shape | in all Tethysuchia and Tomistoma |
| | 200 | 1 | Well developed anterolateral process on postorbital | in all Tethysuchia |
| | 208 | 0 | 'Complx' supratemporal roof dorsal surface | in all Tethysuchia |
| | 254 | 0 | Postorbital bar placed anterolaterally on jugal | in all Tethysuchia |

| Tethysuchia & Gavialoidea | 89 | 0 | Skull table surface slopes ventrally at maturity | in derived Gavialoidea and Pholidosaurus and Dyrosaurus |
| | 224 | 0 | Supratemporal fenestrae large, covering more than 50% of skull roof | in all Tethysuchia and several gavialoids |
| | 257 | 1 | Jugal shaped rod-like beneath infra-temporal fenestra | in most Tethysuchia and Gavialidae + Thoracosaurus |
| | 305 | 1 | Basioccipital with large bilateral pendulous tubera | in all Tethysuchia and Gavialoidea |
| | 479 | 1 | Hypapophysis of axis with deep fork | in all scored Tethysuchia and Gavialoidea |

| Gavialoidea & Tomistominae | 131 | 1 | Alveolar walls of maxillary level with ventral surface | in all Gavialoidea and Tomistominae, plus Elasmosuchus and Rhabdognathus and several goniopholidids |
| | 230 | 1 | Groove for external ear valve musculature flaring anteriorly | in all Gavialoidea and Tomistominae |
| | 304 | 0 | No midline crest on basioccipital below opisthodiscal condyle | in Gavialidae, Tomistoma, Elasmosuchus and several single other taxa |
| | 371 | 1 | Anterior median process of palatines into maxilla in form of thin wedge | in all Gavialoidea and Tomistominae |
| | 397 | 1 | Thin and long teeth which are at least three times longer than wide | Ancestral state retained outside Eusauchia and within Gavialoidea and Tomistominae |

| Gavialis & Tomistoma | 384 | 1 | Flat depressions the size of small alveoli between maxillary and premaxillary alveoli | only in Gavialis, Gavialisosuchus and Tomistoma |
| | 397 | 1 | Thin and long teeth which are at least three times longer than wide | Ancestral state retained outside Eusauchia and within Gavialoidea and Tomistoma |

Table 2.5: Characters revealed by character tracing to be common to one or several longirostrine clades with details of character state, character description and exact occurrence in the phylogenetic tree. Based on the consensus tree of Analysis IV (Fig. 2.3).
In contrast to the anterior snout and mandible, far fewer posterior skull characters contribute to the independent derivation of the longirostrine condition in each of the separate long-snouted groups. Tethysuchia in particular possesses several supratemporal roof characters associated with their longirostrine condition that are not seen in the other 'longirostrine' clades (characters 127, 195 and 200), indicating increased modification of the skull roof in these taxa as their snouts evolved. It is possible that these changes were related to the more marine lifestyles of many tethysuchians which were almost unique to this clade within Neosuchia (Hill et al., 2008). These features include the zigzag shape of the frontoparietal suture on the interfenestral bar (character 195); the anterolateral process of the postorbital (the presence of which is typical for Dyrosauridae) (character 200); and a complex skull roof surface (character 208). In addition to the other skull roof changes, the placement of the postorbital is more anterior compared to other Neosuchia (character 254) and tethysuchians also share the absence of a ventral opening on the premaxilla-maxilla contact (character 118) with Alligatoridae.

Modifications of the posterior part of the skull also played some role in the evolution of gavialoid longirostry. Relatively large supratemporal fenestrae (character 224) and a ventrally sloping skull roof surface (character 89) are shared by both gavialoids and tethysuchians. These changes are accompanied by a much more rod-like jugal beneath the infratemporal fenestra (character 257) and larger bilateral tubera of the basioccipital (character 305), as well as a deep fork in the hypapophysis of the axis (character 479) in both Tethysuchia and Gavialoidea.

Gavialoids and tomistomines share three characters that are potentially related to the formation of a long snout in the posterior part of the skull. The groove for the external ear valve musculature is flared anteriorly in both clades (character 230) and a midline crest below the occipital condyle is missing on the basioccipital (character 304). Furthermore, the anterior process of the palatines
into the maxilla takes the form of a thin wedge (character 371). There are two characters, number 384 and 397 with shared character states between Gavialis and Tomistoma but are absent in their direct ancestors (Table 2.5). This further corroborates the hypothesis of their long-snoutedness as a homoplastic condition, in direct contrast to hypotheses derived from molecular evidence alone (Piras et al., 2010).

Overall, the evolution of the longirostrine condition seems to have been remarkably constrained and to have occurred in a broadly similar fashion in each of these different clades. Modifications to the premaxilla, maxilla, dentary and splenial were those that were of primary importance in the convergent construction of the long-snouted condition. In contrast, the median parts of the skull and mandible between anterior and posterior parts remained mostly unchanged. Moreover, the posterior part of the skull evolved in a less constrained manner with separate adaptations present in each of the longirostrine clades. These unique posterior skull features potentially represent adaptations to different habitats and feeding styles.

For example, it is notable that tethysuchians possess a much larger number of unique character states related to the acquisition of the long snout than the other 'longirostrine' clades, which might be linked to their marine lifestyle. Furthermore, Tethysuchia and Gavialoidea exhibit more similarities in their snout assembly than Gavialoidea and Tomistominae. Once again, this emphasises the dissimilarities between the latter two groups. In order to assess these results further, it would be interesting to conduct developmental studies of snout assembly in both Gavialis and Tomistoma, which could provide new data that would be potentially critical in resolving the ongoing Gavialis-Tomistoma debate (Gatesy et al., 2003; Piras et al., 2010; Gold et al., 2014).
2.6 Conclusion

This case study has demonstrated that the combined application of continuous data treated as such and EIW together can result in improved stratigraphic fit of the resulting phylogenetic trees in the presence of strong homoplasy. Despite several studies confirming their utility (see Parins-Fukuchi (2017)), the influence of continuous characters on large scale-phylogenetic studies is still largely unexplored and future work should concentrate on determining the effect of continuous characters and EIW in more taxonomic datasets. Despite the large number of morphological characters used in this study, character quality is equally important and this work highlights the need to construct characters more critically and to assess them rigorously before including them within phylogenetic analyses.

The new neosuchian phylogeny is generally congruent with those derived from previous phylogenetic analyses, confirming the placement of Tethysuchia at the base of Neosuchia. However, it deviates from established phylogenetic hypotheses in the identification of alligatorine paraphyly and in the lack of resolution within Crocodylinae. Future datasets should aim to include additional members of clades that were either unrepresented or represented by only a single taxon in this phylogeny, including Atoposauridae, Susisuchidae, Hylaeochampsidae and Thalattosuchia.

Character tracing reveals that the long snout was assembled in similar ways across the neosuchian tree by transformation of the anterior portions of the snout and mandible. Posterior skull transformations, however, are often unique to individual longirostrine clades, and might represent adaptations to their different habitats and life styles. Future work should be aimed at both the genetic mechanisms that underlie long snout evolution and the particular ways in which evolution of longirostry was influenced by differing environments.
Chapter 3

Divergence dating of neosuchian trees

3.1 Abstract

The times of origin of the major neosuchian clades have long been debated, with different estimates yielded by molecular and morphological studies and particular disagreement over the number of clades present before the K/Pg-boundary. In addition, there have been several recent advances in methodology for divergence dating although no study has yet compared all of the major techniques available. In order to evaluate these different dating methods and to obtain a clearer picture of neosuchian divergence times, this study used four different methods (cal3, Extended Hedman, smoothed Ghost-Lineage-Analysis (sGLA) and the Fossilised Birth-Death model (FBD)) on four different phylogenetic tree sets for neosuchians. Cal3 and FBD provided the most accurate divergence date estimates, whilst Extended Hedman dates were generally too old. SGLA and Extended Hedman are more vulnerable to both minor and major changes in tree topology. Neosuchia originated before or around the Early Jurassic and all three extant clades (Crocodyloidea, Alligatoidea and
Gavialoidea) were present before the K/Pg-boundary. In addition both Diplo-
cynodontinae and the alligatoroid subfamily Caimaninae originated before the
K/Pg-boundary, while both Gavialinae and Tomistominae date back to the Pale-
ogene. A detailed understanding of phylogeny and good taxonomic coverage of
clades (in particular the inclusion of the oldest taxa in each clade) is essential
when evaluating the results of these studies.

3.2 Introduction

Estimating divergence dates assists in determining the tempo of clade evolu-
tion and enables the correlation of taxonomic events such as the origination of
new clades with other events, such as climatic or palaeographic change (e.g.
Springer et al. 2011; Hastings et al. 2013; Patiño & Vanderpoorten 2015). How-
ever, a variety of methods can be used for divergence date estimation, all with
different requirements and suitabilities for different datasets.

The first attempts at divergence dating were based on trees generated from
molecular sequence data and positive correlations between changes in se-
quence and changes in time: a ‘molecular clock’ that can be calibrated us-
ing fossils with a node-dating approach (Zuckerkandl & Pauling, 1962, 1965).
However, these approaches assume a single constant rate of evolution on all
branches of the evolutionary tree, an assumption that is usually violated by
real data (e.g. Britten 1986). This assumption of a constant evolutionary rate
negatively influences divergence date estimations especially when molecular
phylogenies have only a few fossil calibration points (Yoder & Yang, 2000), lead-
ing to inaccurate divergence time estimates. To account for this shortcoming,
new clock models (‘relaxed clocks’) were developed that allowed different evo-
lutionary rates throughout the tree, usually set within a Bayesian framework that
coupled phylogenetic inference with divergence date estimations (Thorne et al.,
1998; Drummond et al., 2006).
However, major issues emerge when the datasets in question are based largely on fossil taxa, and incorporate only partial or no molecular sequences. In terms of divergence data estimation, fossils have been used mainly for calibrating ‘key events’, such as the emergence of new clades signified by the earliest fossil to possess its features. These fossil taxa were situated at internal nodes within molecular phylogenies (e.g. Yoder & Yang 2000; Xiong et al. 2009; Agnarsson et al. 2011). Many living groups, however, have a larger proportion of extinct species than extant species, as with Neosuchia, which forms the basis for this study (Brochu, 2003). Work on such groups has led to fossil taxa being incorporated more often and critically into divergence time estimations, especially those using Bayesian inference, such as the Fossilised Birth-Death model (FBD) (Stadler, 2010; Heath et al., 2014) as implemented in BEAST2 (Bouckaert et al., 2014). The FBD allows for the incorporation of fossils as tips in phylogenetic trees and randomises both speciation and extinction probabilities over time. It was further refined to allow more flexibility for fossil assignments and model parameters by Gavryushkina et al. (2014). Although using these serially sampled birth-death models can lead to long ghost lineages (Turner et al., 2017), incorporating birth, death and sampling rates renders the results more accurate than models without these rates, as the latter tend to yield estimates that are too old (Matzke & Wright, 2016).

In addition to Bayesian approaches, other methods for divergence time estimation have been proposed more recently. These are often aimed specifically at, or at least to facilitate, the dating of fossil-only trees. Methods to produce the first time-scaled phylogenies with a major fossil component were developed in the 1990s (Norell, 1992; Smith, 1994). These basic algorithms used the ages of taxa bracketing a clade to assign a minimum age to the clade in question, but this can lead to the inference of long ghost ranges (Turner et al., 2017). Moreover, this method frequently creates branches of zero length, due to gaps in the fossil record (Hunt & Carrano, 2010). Several methods for scaling these
branches have now been developed (e.g. Ruta et al. 2006; Brusatte et al. 2008; Laurin et al. 2009; Brusatte 2011) and these ‘basic’ algorithms are still in use for some stratigraphic dating algorithms (e.g. Bell & Lloyd 2014). Following the terminology of Turner et al. (2017), these methods will be referred to as ‘Ghost-Lineage-Analysis’ (GLA) from here on. However, none of these algorithms take into account the stochastic uncertainty of node ages (since the stratigraphic record usually does not allow for a single age to be given but a range of possible ages instead) and provide only a minimum age for each clade. New methods have been devised to take such uncertainty into account, including that implemented in the R package cal3 (Bapst, 2013, 2014), and, most recently, Extended Hedman based again on Bayesian algorithms (Lloyd et al., 2016) (see below for detailed method descriptions).

In order to cope with the problems in both molecular-only and fossil-only studies, several authors have suggested the use of ‘total evidence’ approaches, especially since fossil-only approaches can be subject to many uncertainties such as the underestimation of clade origination times (Turner et al., 2017) and studies using fossils for node calibrations are strongly dependent on the correct stratigraphic and phylogenetic categorisation of extinct taxa (Pyron, 2011). In total evidence dating, phylogenies and divergence time estimates are obtained simultaneously using datasets consisting of combined molecular and morphological data, such as those of Pyron (2011) for Lissamphibia and Ronquist et al. (2012a) for Hymenoptera (re-examined in O’Reilly & Donoghue 2016). As with all dating approaches, divergence date estimation still depends on obtaining the ‘correct’ phylogenetic tree, especially from the morphological portion of the data (Pyron, 2011). In the case of Neosuchia, however, combined molecular and morphological phylogenetic analyses produced trees where longirostrine taxa clustered together in ways that were incompatible with the stratigraphic record, so this avenue was not pursued further in this thesis (see Chapter 2).

Most of the above mentioned methods can be sorted into two distinct modes
of dating algorithms: tip-dating and node-dating approaches. In tip-dating (such as cal3 and GLA), divergence ages are estimated based solely on the actual ages provided for the operational taxonomic units (OTUs) used in the phylogenetic studies, i.e. the tips of the tree branches. In contrast, node-dating methods (such as those employed by many of the Bayesian approaches) work with the a priori calibration of tree nodes, often based on estimated molecular and/or morphological clock rates and the ages of fossils. Opinions regarding the accuracy of these different methods differ: tip-dating alone is thought to lead to estimates that are too old as it compounds uncertainty in age estimates with closer proximity to the tree root (O’Reilly & Donoghue, 2016). Its usefulness is also heavily dependent on the nature of the dataset and is influenced by such factors as low numbers of characters, low numbers of fossils near the tree root, preservation bias, strongly fluctuating changes in evolutionary rate, using only a small sampled proportion of total fossil diversity and the presence of worldwide radiations, mass extinctions and subsequent diversifications (Matzke & Wright, 2016). Node-dating, however, suffers from different problems: the phylogenetic associations of the fossils used for calibration have to be known with absolute certainty and both the phylogenetic and stratigraphic uncertainty of many fossil taxon ages is difficult to incorporate into node age restrictions (Ronquist et al., 2012a; O’Reilly et al., 2016). In addition, node calibrations can lead to a circular argument — many divergence time estimations, such as in this study, are carried out to obtain age estimates for certain nodes. If these are defined a priori this purpose is nullified (Matzke & Wright, 2016).

Although neosuchians suffer from the aforementioned problem of worldwide radiations and diversifications, tip-dating methods were used predominantly for this study, comparing four different methods: cal3, Extended Hedman, sGLA (a derivate of GLA) and FBD. The majority of the algorithms used here (cal3, Extended Hedman, sGLA) do not provide node-dating approaches. The aims of this study are twofold: 1) to obtain age estimates of crucial points in neosuchian
evolution and 2) to provide comparisons between these four divergence date estimation algorithms which has been strongly encouraged by previous authors (Bapst et al., 2016), but not yet attempted. As a result, exclusively a posteriori time scaling approaches are adopted here that make use of stratigraphic taxon ranges that are imposed on the phylogenies obtained in Chapter 2, but do not incorporate any tree building algorithms.

**Previous neosuchian divergence estimates**

A number of studies have attempted node age estimations for the various neosuchian clades. Despite the existence of early divergence time estimations studies (e.g. Brochu 2000), a large number of phylogenies map the taxa contained therein onto a time scale without dating the tree in question using mathematical methods. Recently, with the emergence of the new methods mentioned above, molecular and morphological studies using different dating algorithms have become available (Table 3.1). There used to be a stark difference in the age estimates obtained from molecular and morphological methods, with younger molecular divergence time estimates (Brochu, 2000), as exemplified by the dates for Crocodylinae shown in Table 3.1. However, more recent studies often provide a more even spread in age estimates, especially amongst older clades such as Crocodylia (Table 3.1), where molecular estimates lie within the age estimates provided by morphological studies. The younger estimates provided by the two molecular studies featured here, Oaks (2011) and Roos et al. (2007), are found mostly for Crocodylinae, Globidonta and Caimaninae. They can be explained by a lack of calibration points (only one calibration point within Neosuchia: Roos et al. 2007) and rather young age restrictions for older clades (90 and 100 mya for the emergence of Crocodylia: Oaks 2011). Furthermore, the different placements of *Gavialis* and *Tomistoma* and the necessary absence of both entire extinct clades (e.g. Diplocynodontinae) and older extinct species of dated families (e.g. old 'Crocodylus' species) from the molecular trees bi-
<table>
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<tr>
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<th>BEAST**</th>
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</tr>
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<td>Martin et al. 2010</td>
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<tr>
<td>Turner et al. 2017</td>
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<td></td>
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<th>Tethysuchia</th>
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<th>'derived' Goniopholididae</th>
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<th>Gavialoidea</th>
<th>Gavialinae</th>
<th>Brevirostres</th>
<th>Crocodyloidea</th>
<th>Crocodylidae</th>
<th>Crocodylinae</th>
<th>Tomistominae</th>
<th>Alligatoroidea</th>
<th>Diplocynodontinae + Leidyosuchus</th>
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<th>Globidonta</th>
<th>Caimaninae</th>
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<td>73–73</td>
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<td>59–59</td>
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<td>44–44</td>
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</table>

Table 3.1: Ages obtained by previous authors of the neosuchian clades dated in this study. Ages given in millions of years. *molecular studies. **total evidence Bayesian tip dating.
ases estimates towards younger dates.

So far there has been no study that dates the emergence points of all major neosuchian clades comprehensively, a gap that this study aims to fill. In addition, this study aims to obtain more accurate estimates for the number of neosuchian clades that existed before and crossed the K/Pg-boundary, attempting to resolve the differences between molecular and morphological estimates.

### 3.3 Materials and Methods

**Taxon ages**

The initial taxon age estimates were taken from the Paleobiology Database (PBDB) (Alroy (1998), http://fossilworks.org/), adjusted for the more recently revised ages established in the International Chronostratigraphic (ICS) chart (Cohen et al., 2013). Several species (such as *Alligator mcgrewi*) were dated using the North American Land Mammal Ages provided in their original descriptions (see Table 3.2). For methods requiring non-overlapping time bins (e.g. cal3), these occurrences were integrated into the existing ICS standard stages and epochs (the complete time bin list is available in Appendix C.5). The Holocene was used as the time bin for those taxa without a known fossil record.

For analysis in BEAST, only one age can be given for each taxon for divergence dating. Following Lloyd et al. (2016) the last appearance dates (LAD) were used in order to deal with uncertainty in the stratigraphic record. Using the LAD ages ensures that all species were definitely present by the time indicated. However, it should be noted that this potentially skews node age estimates towards younger ages.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Time period</th>
<th>FAD</th>
<th>LAD</th>
<th>Singleton</th>
</tr>
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<tbody>
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<td>16</td>
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<td>Time period</td>
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<tr>
<td><em>Alligator mefferdi</em></td>
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<td>145</td>
<td>x</td>
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</tr>
<tr>
<td>Eoalligator huiningensis</td>
<td>Danian</td>
<td>66</td>
<td>61.6</td>
<td>x</td>
</tr>
<tr>
<td>Eocaiman cavernensis</td>
<td>Barrancan</td>
<td>41.3</td>
<td>38</td>
<td>x</td>
</tr>
<tr>
<td>Eogavialis africanum</td>
<td>Priabonian</td>
<td>38</td>
<td>33.9</td>
<td>x</td>
</tr>
<tr>
<td>Eogavialis gavialoides</td>
<td>Rupelian</td>
<td>33.9</td>
<td>28.1</td>
<td>x</td>
</tr>
<tr>
<td>Eosuchus lerichei</td>
<td>Eocene</td>
<td>56</td>
<td>33.9</td>
<td></td>
</tr>
<tr>
<td>Eosuchus minor</td>
<td>Ypresian</td>
<td>56</td>
<td>47.8</td>
<td></td>
</tr>
<tr>
<td>Euthedon arambourgi</td>
<td>Early Miocene</td>
<td>23</td>
<td>16</td>
<td>x</td>
</tr>
<tr>
<td>Eutretauranosuchus delphi</td>
<td>Kimmeridgian</td>
<td>157.3</td>
<td>152.1</td>
<td></td>
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<tr>
<td>Gavialis gangeticus</td>
<td>extant</td>
<td>2.6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Gavialis hysudricus</td>
<td>Zanclean</td>
<td>5.3</td>
<td>3.6</td>
<td></td>
</tr>
<tr>
<td>Gavialis lewisi</td>
<td>Zanclean</td>
<td>5.3</td>
<td>3.6</td>
<td></td>
</tr>
<tr>
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<td>Burdigalian to Messinian</td>
<td>20.4</td>
<td>5.3</td>
<td></td>
</tr>
<tr>
<td>Gavialosuchus antiquus</td>
<td>Langhian to Messinian</td>
<td>16</td>
<td>5.3</td>
<td></td>
</tr>
<tr>
<td>Gavialosuchus eggenburgensis</td>
<td>Burdigalian</td>
<td>20.4</td>
<td>16</td>
<td>x</td>
</tr>
<tr>
<td>Goniopholis simus</td>
<td>Berriasian</td>
<td>145</td>
<td>139.8</td>
<td></td>
</tr>
<tr>
<td>Hylaeochampsa vectiana</td>
<td>Barremian</td>
<td>129.4</td>
<td>125</td>
<td>x</td>
</tr>
<tr>
<td>Hyposaurus natator</td>
<td>Maastrichtian to Danian</td>
<td>72.1</td>
<td>61.6</td>
<td></td>
</tr>
<tr>
<td>Species name</td>
<td>Time period</td>
<td>FAD</td>
<td>LAD</td>
<td>Singleton</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-------------------</td>
<td>-----</td>
<td>-----</td>
<td>-----------</td>
</tr>
<tr>
<td><em>Kentisuchus spenceri</em></td>
<td>Ypresian</td>
<td>56</td>
<td>47.8</td>
<td></td>
</tr>
<tr>
<td><em>Leidyosuchus canadensis</em></td>
<td>Santonian to Campanian</td>
<td>85.8</td>
<td>72.1</td>
<td></td>
</tr>
<tr>
<td><em>Leidyosuchus gilmorei</em></td>
<td>Santonian to Campanian</td>
<td>85.8</td>
<td>72.1</td>
<td></td>
</tr>
<tr>
<td><em>Leidyosuchus multidentatus</em></td>
<td>Late Danian</td>
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<td>61.6</td>
<td>x</td>
</tr>
<tr>
<td><em>Maroccosuchus zennaroi</em></td>
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<td>56</td>
<td>47.8</td>
<td></td>
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<tr>
<td><em>Mecistops cataphractus</em></td>
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<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Melanosuchus niger</em></td>
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<td>0.1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Nannosuchus gracilidens</em></td>
<td>Early Cretaceous</td>
<td>145</td>
<td>125</td>
<td></td>
</tr>
<tr>
<td><em>Navajosuchus novomexicanus</em></td>
<td>Danian</td>
<td>66</td>
<td>61.6</td>
<td></td>
</tr>
<tr>
<td><em>Notosuchus terrestris</em></td>
<td>Santonian</td>
<td>85.8</td>
<td>83.6</td>
<td></td>
</tr>
<tr>
<td><em>Osteolaemus tetraspis</em></td>
<td>extant</td>
<td>11.6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Paleosuchus trigonatus</em></td>
<td>extant</td>
<td>13.8</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Pholidosaurus purbeckensis</em></td>
<td>Berriasian</td>
<td>145</td>
<td>139.8</td>
<td></td>
</tr>
<tr>
<td><em>Piscogavialis jugaliperforatus</em></td>
<td>Messinian</td>
<td>7.3</td>
<td>5.3</td>
<td></td>
</tr>
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<td><em>Planocrania datangensis</em></td>
<td>Selandian</td>
<td>61.6</td>
<td>59.2</td>
<td>x</td>
</tr>
<tr>
<td><em>Planocrania hengdongensis</em></td>
<td>Thanetian</td>
<td>59.2</td>
<td>56</td>
<td>x</td>
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<tr>
<td><em>Prodiplocynodon langi</em></td>
<td>Maastrichtian</td>
<td>72.1</td>
<td>66</td>
<td>x</td>
</tr>
<tr>
<td><em>Protosuchus richardsoni</em></td>
<td>Hettangian</td>
<td>201.6</td>
<td>199.1</td>
<td></td>
</tr>
<tr>
<td><em>Rhabdognathus keiniensis</em></td>
<td>Paleocene</td>
<td>66</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td><em>Rhabdognathus sp.</em></td>
<td>Paleocene</td>
<td>66</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td><em>Rhamphosuchus crassidens</em></td>
<td>Zanclean</td>
<td>5.3</td>
<td>3.6</td>
<td></td>
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<tr>
<td><em>Sarcosuchus imperator</em></td>
<td>Albian</td>
<td>113</td>
<td>100.5</td>
<td></td>
</tr>
<tr>
<td><em>Sebecus icaeorhinus</em></td>
<td>Casamayoran</td>
<td>53</td>
<td>47.8</td>
<td></td>
</tr>
<tr>
<td><em>Shamosuchus djadochaensis</em></td>
<td>Campanian</td>
<td>83.6</td>
<td>72.1</td>
<td></td>
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<tr>
<td><em>Steneosaurus bollensis</em></td>
<td>Toarcian</td>
<td>182.7</td>
<td>174.1</td>
<td></td>
</tr>
<tr>
<td>Species name</td>
<td>Time period</td>
<td>FAD</td>
<td>LAD</td>
<td>Singleton</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-------------------</td>
<td>-------</td>
<td>-------</td>
<td>-----------</td>
</tr>
<tr>
<td>Sunosuchus junggarensis</td>
<td>Oxfordian</td>
<td>163.5</td>
<td>157.3</td>
<td>x</td>
</tr>
<tr>
<td>Sunosuchus miaoi</td>
<td>Late Jurassic</td>
<td>163.5</td>
<td>145</td>
<td></td>
</tr>
<tr>
<td>Susisuchus anatoceps</td>
<td>Albian</td>
<td>113</td>
<td>100.5</td>
<td></td>
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<tr>
<td>Terminonoras robusta</td>
<td>Turonian</td>
<td>93.9</td>
<td>89.5</td>
<td></td>
</tr>
<tr>
<td>Theriosuchus pusillus</td>
<td>Berriasian</td>
<td>145</td>
<td>139.8</td>
<td></td>
</tr>
<tr>
<td>Thoracosaurus macrorhynchus</td>
<td>Paleocene</td>
<td>66</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>Thoracosaurus neocesariensis</td>
<td>Late Cretaceous</td>
<td>72.1</td>
<td>50.3</td>
<td></td>
</tr>
<tr>
<td>Tomistoma cairensense</td>
<td>Lutetian</td>
<td>47.8</td>
<td>41.3</td>
<td>x</td>
</tr>
<tr>
<td>Tomistoma dowsoni</td>
<td>Langhian to</td>
<td>16</td>
<td>11.6</td>
<td></td>
</tr>
<tr>
<td>Tomistoma petrolica</td>
<td>Priabonian</td>
<td>38</td>
<td>33.9</td>
<td></td>
</tr>
<tr>
<td>Tomistoma schlegelii</td>
<td>extant</td>
<td>2.6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Vectisuchus leptognathus</td>
<td>Barremian</td>
<td>129.4</td>
<td>125</td>
<td>x</td>
</tr>
<tr>
<td>Voay robustus</td>
<td>Holocene</td>
<td>0.1</td>
<td>0.01</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.2: First (FAD) and last (LAD) appearance dates of all neosuchian species used in the time list file (Appendix C.5) in this study. Ages in million years.

Node ages were extracted for the following 18 phylogenetic groups (for the definitions of these groups see Chapter 1, Section 1.1): Neosuchia, Eu-suchia, Tethysuchia, Goniopholididae, 'derived' Goniopholididae, Crocodylia, Gavialoidea, Gavialinae, Brevirostres, Crocodyloidea, Crocodylidae, Crocodyli-nae, Tomistominae, Globidonta, Diplocynodontinae + Leidyosuchus, Diplocynodontinae, Alligatoroidea and Caimaninae.
**Phylogenetic trees used**

The phylogenetic analyses from Chapter 2 were used to generate divergence time estimates, using only those trees that were the most stratigraphically congruent (see Chapter 2, Section 2.4.2) for downstream analyses. All most parsimonious trees (MPTs) from the following analyses were dated (analyses numbers are the same as in Table 2.3):

- **Analysis II (7 MPTs):** Discrete & continuous characters + EIW
- **Analysis IV (5 MPTs):** Discrete & continuous characters + EIW, longirostrine characters removed
- **Analysis X (5 MPTs):** Rediscretised characters + EIW
- **Analysis XII (23 MPTs):** Rediscretised characters + EIW, longirostrine characters removed

Analyses X and XII both featured 'rogue' taxa that were far older than the rest of the clades they were recovered with, thus skewing the results: analysis X recovered *Crocodilaemus robustus* (a pholidosaur according to Young *et al.* (2011a)) as part of Alligatoridae. Analysis XII recovered *Nannosuchus gracilidens* (a goniopholidid according to De Andrade *et al.* (2011)) as part of the Alligatoridae. Both taxa were removed from all MPTs in their respective analyses and the divergence time estimates re-run. In addition, neither analysis X nor analysis XII resolved 'Gavialinae' and 'Diplocynodontinae + Leidyosuchus' (see Chapter 1 for exact definitions) as monophyletic, therefore these groups were not dated.

**Divergence dating methods**

In order to obtain a wide range of age estimates and enable comparison between a variety of methods, four different methods were chosen for dating the above phylogenetic trees.
**cal3**

Cal3 is a tip-dating method first described by Bapst (2013), and further elaborated in Bapst (2014). Instead of carrying out only a single divergence time estimation, cal3 employs repeated stochastic sampling of node ages from a given distribution, enabling the assessment of uncertainty of obtained estimations for node ages. To create this distribution of possible node ages, three different rates have to be defined *a priori*: branching (=speciation) rate, extinction rate and sampling rate. This prior estimation, however, makes the cal3 method vulnerable to the presence of singletons because these can skew the estimates of branching and extinction rates (which are usually assumed to be equal). The neosuchian dataset here contains only 19.8% singletons (21 out of 106 species), thus node ages should only be skewed minimally.

Cal3 and the algorithms to estimate its rates are implemented in the R package *paleotree* (Bapst, 2012) and were executed in the environment of R v. 3.4.3 (R Core Team, 2017). In order to estimate the branching, extinction and sampling rates the function `make_durationFreqDisc` was used. Following Bapst’s recommendations written in the annotated cal3 code, several iterations of the time intervals file were compared as the method is potentially sensitive to large differences in individual time interval lengths. In addition to a version of the time intervals corresponding to time periods in the ICS chart (Cohen *et al.*, 2013), a second version of the time interval file was generated where all intervals were broken up into equally-sized time slices of 2-3 million years’ (Myr) length. Several other iterations of the time intervals file with multiple overlapping slices representing the different occurrence periods of the taxa in this dataset were also assessed (see ‘Taxon ages’ below). Finally, the rates obtained from these files were compared to those reported by Tennant *et al.* (2016b) to assess their accuracy. Since rate estimates were very similar across the different time interval files (and showed little difference in node age estimates during later divergence dating), the following rates from the 2-3 million year time intervals file were used:
Table 3.3: Ages of additional outgroup taxa for Extended Hedman, based on the phylogenetic relationships in Nesbitt (2011). Ages given in millions of years, based on PBDB (Alroy, 1998) and adjusted for the ICS chart (Cohen et al., 2013).

<table>
<thead>
<tr>
<th>Age</th>
<th>Taxon</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>201.3</td>
<td><em>Terrestrisuchus gracilis</em></td>
<td>early Crocodylomorpha</td>
</tr>
<tr>
<td>208.5</td>
<td><em>Dromicosuchus grallator</em></td>
<td>early Crocodylomorpha</td>
</tr>
<tr>
<td>208.5</td>
<td><em>Rauisuchus tiradentes</em></td>
<td>Rauisuchidae</td>
</tr>
<tr>
<td>227</td>
<td><em>Saurosuchus galilei</em></td>
<td>Loricata</td>
</tr>
<tr>
<td>237</td>
<td><em>Batrachotomus kuperzellensis</em></td>
<td>Loricata</td>
</tr>
<tr>
<td>237</td>
<td><em>Gracilisuchus stipanicicorum</em></td>
<td>early Pseudosuchia</td>
</tr>
<tr>
<td>242</td>
<td><em>Ticinosuchus ferox</em></td>
<td>Suchia</td>
</tr>
<tr>
<td>242</td>
<td><em>Turfanosuchus dabanensis</em></td>
<td>Gracilisuchidae</td>
</tr>
<tr>
<td>247</td>
<td><em>Proterosuchus fergusi</em></td>
<td>Archosauriformes</td>
</tr>
<tr>
<td>251</td>
<td><em>Prolacerta broomi</em></td>
<td>Archosauromorpha</td>
</tr>
</tbody>
</table>

branching rate = 0.1350148, extinction rate = 0.1350148 and sampling rate = 0.3653429. For divergence dating, the original time list file with the ICS chart interval lengths was used.

Every MPT from each analysis was analysed 100 times in order to obtain a distribution of different age estimates. Node ages were extracted using the functions `FindAncestor` and `GetNodeAges` in the R package `Claddis` (Lloyd, 2016). Adding further outgroup ages as suggested by Lloyd et al. (2016), in order to enable comparison with the node ages obtained by the Extended Hedman method (below), did not alter the obtained age estimates.

**Extended Hedman**

Whole Tree Extension of the Hedman Algorithm (‘Extended Hedman’) is a recent tip-dating method described by Lloyd et al. (2016), based on an algorithm for the dating of single nodes first described by Hedman (2010). It makes use of Bayesian algorithms to date nodes based on the ages of their successive outgroups. As such, additional outgroup ages have to be added to enable the dating of all nodes in the phylogenetic trees supplied.
The Extended Hedman algorithm has been implemented in the R environment (R Core Team, 2017) and a modified version of the script supplied by Lloyd et al. (2016) was used for the node estimates in this study. Ten new outgroup ages were added to the tree (Table 3.3). Varying these outgroup ages did not lead to significant differences in the dates obtained. Different versions of the occurrence file specifying the age intervals and occurrences of neosuchian taxa in these intervals were generated to assess the resilience of the method. These files included a) time intervals spliced into 2-3 million year intervals to mirror the time list used to calculate the cal3 rates and b) an adjustment so that the number of occurrences was 1 per taxon per time slice. The obtained node ages only showed small differences between the two files. Therefore, the original occurrences file with age intervals following the ICS chart (Cohen et al., 2013) and actual number of occurrences (taken from the PBDB (Alroy, 1998)) was used. One thousand dates were estimated for each node of which 100 were sampled. Node ages were extracted using Claddis as outlined above.

**Smoothed Ghost-Lineage-Analysis (sGLA)**

‘Smoothed Ghost-Lineage-Analysis’ (GLA) was used by Turner et al. (2017) to describe the simplest type of tip-dating divergence dating analysis where each node is assigned a minimum emergence age equivalent to that of the oldest member of its sister group. However, the presence of several old fossil taxa can lead to the introduction of zero branch lengths and multiple extremely short branches upon time scaling. Therefore, the temporally ‘smoothed’ version of GLA makes use of a modified version of an algorithm originally described by Ruta et al. (2006) wherein the zero length branches are assigned lengths based on the time between unconstrained nodes. This algorithm was used and implemented by Brusatte (2011) and Lloyd et al. (2012). Although GLA is influenced by clustered occurrences over time (Turner et al., 2017) and potentially biased towards minimum age estimates (Lloyd et al. 2016, Supplementary), it has been
widely used for age estimates because it is implemented in both the R packages `paleotree` (Bapst, 2012) and `strap` (Bell & Lloyd, 2014). For this study, the "equal" option of `bin_timePaleoPhy` was used in order to include sGLA comparison with the other three methods. sGLA was run with three different vartimes variables, vartime=1, =5 and =10 for the first analysis. As the results proved similar for all three, vartime=1 was used for the remaining analyses.

The time list file of temporal species occurrences used was the same as in the cal3 analysis, with time bins following the ICS chart (Cohen et al., 2013). Each analysis was carried out 100 times for each MPT to obtain 100 different estimates and the R package `Claddis` (Lloyd, 2016) was used for extracting node ages.

**Fossilised Birth-Death-Model (FBD)**

The FBD was developed by Stadler (2010) and Heath et al. (2014), and further expanded by Gavryushkina et al. (2014) as part of BEAST2 (Bouckaert et al., 2014). It allows for the direct incorporation of fossils into Bayesian age estimation models, randomising both speciation and extinction probabilities over time. When using FBD in BEAST2 the right choice of tree prior is of paramount importance (Matzke & Wright, 2016), more so than the choice of clock model (Turner et al., 2017). Depending on the tree, the performance of FBD is influenced little by additional node calibrations (Matzke & Wright, 2016). In order to keep the results of this method comparable to the three other time scaling methods used here, nodes were not additionally constrained and no tree building was carried out in BEAST2, restricting the analysis to the previously supplied MPTs. Log normal priors were used throughout the analysis, with 199.1 as offset for the original tree (corresponding to the age of the oldest taxon) and M = 21.0, S =1.0. Diversification rate was set to 1.0, turnover & sampling rates to 0.5, and Rho was 1.0. Each MPT was inserted separately into the xml file generated by BEAUTi 2.4.8 (part of the BEAST2 package), analysed with BEAST2 2.4.8
(Bouckaert et al., 2014) and the sampled ancestors (SA) package (Gavryushkina et al., 2014). Burnin was set to 20% and the dated trees were combined and annotated using Log Combiner 2.4.8 and TreeAnnotator 2.4.8.

For the first five trees, analyses were carried out with and without the use of priors. Using priors only ignores the sequence data that has to be supplied in order to run analyses with BEAST2, taking only the supplied trees and fossils into account. As such, the results presented below stemmed from the analyses with priors only.

The resulting dated trees were transferred into the R environment and node ages extracted using Claddis (Lloyd, 2016).

### 3.4 Analyses and results

The results of the different divergence dating methods for the selected taxonomic groups (Table 3.4 and Fig. 3.1) highlight variation in the age estimates obtained from different dating methods depending on the group examined.

Key results include the discovery that the means of all age estimates for Neosuchia, Eusuchia, Tethysuchia, Goniopholididae, ‘derived’ Goniopholididae and Diplocynodontinae + Leidyosuchus show low variation across all dating analyses, with variation between mean ages in millions of years between 10 and 30%, Brevirostres, Gavialoidea, Alligatoroidea, Diplocynodontinae, Globidonta and Caimaninae show higher variation between means across dating analyses, between 40 and 60%, and Crocodylia, Gavialinae, Crocodyloidea, Crocodylidae, Crocodylinae and Tomistominae display a high amount of variation between the means of different dating analyses, 60 to 90%.

Differences in tree topology have a smaller impact on variation in age estimates than differences in divergence estimation methods, with several exceptions. Cal3 shows high variation between the four different tree set in Crocodylia (70 Myr), Alligatoroidea (60 Myr) and Tomistominae (47 Myr). The age esti-
### Table 3.4: The results of all the divergence age estimation analyses across the four different types of tree sets (see Table 2.3 in Chapter 2) and the four dating different methods. Node ages are given as means with standard deviation estimates. Ages in millions of years.

<table>
<thead>
<tr>
<th></th>
<th>Analysis II</th>
<th>Analysis IV</th>
<th>Analysis X</th>
<th>Analysis XII</th>
</tr>
</thead>
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<td>180.3±2.1</td>
<td>180.0±2.0</td>
<td>180.4±2.1</td>
<td>180.2±2.1</td>
</tr>
<tr>
<td>Eusuchia</td>
<td>144.6±2.5</td>
<td>144.4±2.5</td>
<td>144.6±2.5</td>
<td>157.7±2.5</td>
</tr>
<tr>
<td>Tethysuchia</td>
<td>180.0±2.0</td>
<td>145.5±2.5</td>
<td>181.6±2.5</td>
<td>194.4±7.3</td>
</tr>
<tr>
<td>Gonioholidae</td>
<td>169.8±3.1</td>
<td>169.2±3.2</td>
<td>169.2±3.2</td>
<td>188.8±7.6</td>
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<tr>
<td>Derived Gonioholida</td>
<td>155.7±2.6</td>
<td>155.0±2.6</td>
<td>155.5±1.2</td>
<td>160.0±9.1</td>
</tr>
<tr>
<td>Crocodylia</td>
<td>100.3±2.5</td>
<td>84.4±2.5</td>
<td>84.2±2.3</td>
<td>156.4±1.5</td>
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<td>Gavialoidea</td>
<td>80.1±4.0</td>
<td>79.1±3.0</td>
<td>79.1±3.0</td>
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<td>38.9±2.7</td>
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<td>85.2±20.7</td>
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<td>Brevoortes</td>
<td>98.4±1.5</td>
<td>82.0±1.6</td>
<td>82.0±1.6</td>
<td>142.8±1.7</td>
</tr>
<tr>
<td>Crocodyloidea</td>
<td>98.4±1.5</td>
<td>72.3±2.5</td>
<td>72.4±2.7</td>
<td>141.8±10.7</td>
</tr>
<tr>
<td>Crocodylidae</td>
<td>98.4±1.5</td>
<td>63.1±2.2</td>
<td>63.2±2.1</td>
<td>61.9±1.1</td>
</tr>
<tr>
<td>Crocodylinae</td>
<td>63.1±2.4</td>
<td>61.7±1.2</td>
<td>61.7±1.1</td>
<td>61.3±0.8</td>
</tr>
<tr>
<td>Tomistominae</td>
<td>98.4±1.5</td>
<td>51.5±2.3</td>
<td>51.4±2.4</td>
<td>132.1±14.4</td>
</tr>
<tr>
<td>Alligatoroidea</td>
<td>84.1±3.0</td>
<td>81.8±1.6</td>
<td>81.8±1.6</td>
<td>142.6±1.5</td>
</tr>
<tr>
<td>Diplocaulus / Leidyosuchus</td>
<td>82.5±2.1</td>
<td>81.5±1.8</td>
<td>-</td>
<td>110.6±17.6</td>
</tr>
<tr>
<td>Diplocaulus / Caimaninae</td>
<td>60.3±2.4</td>
<td>60.2±2.3</td>
<td>59.6±1.4</td>
<td>60.3±2.4</td>
</tr>
<tr>
<td>Globoidea</td>
<td>79.5±3.3</td>
<td>79.1±3.0</td>
<td>78.8±3.0</td>
<td>67.0±1.7</td>
</tr>
<tr>
<td>Caimaninae</td>
<td>45.3±2.0</td>
<td>45.6±2.2</td>
<td>45.5±2.2</td>
<td>46.2±2.7</td>
</tr>
</tbody>
</table>

The four dating different methods. Node ages are given as means with standard deviation estimates. Ages in millions of years.
mates obtained with Extended Hedman generally show a larger variation between the four tree sets than the other three methods, with an especially large variation in Tomistominae (73 Myr for EH, 50 Myr in cal3 and sGLA, 30 Myr in FBD). The estimates of sGLA show low variation between the different tree sets (usually within 20 Myr), except for sets II and XII which display different, often higher age estimates for certain groups (Crocodyloidea, Crocodylidae, Crocodylinae and Tomistominae for analysis II and Crocodylia, Gavialoidea, and Alligatoroidea for analysis XII). Ages obtained with FBD typically show a low amount of variation between the different tree sets (within 20 Myr). Estimates from sets II (in Crocodylidae, Crocodylinae and Tomistominae) and XII (in Eusuchia, Crocodylia, Gavialoidea, Brevirostres) occasionally deviate from the low variation of the mean in the other tree sets (Fig. 3.1).

The cal3 age estimates are consistently the youngest across almost all taxonomic groups (with the exception of Caimaninae, the two groups of Goniocephalidae and Tethysuchia) whilst the overall highest mean is usually given by Extended Hedman estimates.

**Taxonomic groups**

See Chapter 1, Section 1.1 for phylogenetic definitions of the clades examined.

**Neosuchia**

Age estimates for the origin of Neosuchia vary between 180.0±2.0 Million years ago (mya) minimum (cal3, analysis IV) and 201.1±6.1 mya (Extended Hedman, analysis II) (Table 3.4). The results of the different tree sets in each method cluster closely together, with sets IV and II providing the consistently lowest and highest estimates respectively (Fig. 3.1).

**Eusuchia**

The eusuchian clade is estimated to have emerged between 144.4±2.5 (cal3,
Figure 3.1: Age estimates for all dated neosuchian groups. Median, upper and lower quartiles, minimum and maximum values for all MPT estimates within a single tree set are given. Results are shown for each of the four tree sets for each dating method: cal3, cal3; EH, Extended Hedman; sGLA, smoothed Ghost Lineage Analysis; FBD, Fossilised Birth-Death Model. Ages given in millions of years.
Estimates for the trees stemming from tree sets II and IV are similar across the dating methods whereas the ages estimates provided by the trees from set XII are older (at least 10 Myr compared to sets II and IV) than the others (Fig. 3.1).

**Tethysuchia**

Tethysuchia are estimated to have emerged between 145.5±2.5 (cal3, analysis IV) and 194.4±7.3 (Extended Hedman, analysis II) mya (Table 3.4). The vast majority of estimated ages lies between 160 and 195 mya, with the exception of the cal3 estimation of tree set IV. All tree set IV MPTs provide younger age estimates than the other tree sets estimated using the same dating method (Fig. 3.1).

**Goniopholididae**

Estimates for the emergence of Goniopholididae vary between 166.0±0.2 (FBD, analysis IV) and 188.8±7.6 (Extended Hedman, analysis II) mya (Table 3.4). The results within a single dating method are very uniform, varying not more than 10 Myr between the means of the different tree sets, with larger variation between dating methods (Fig. 3.1).

**'Derived' Goniopholididae**

The more 'derived' Goniopholididae are estimated to have their emergence dates between 150.4±0.1 (FBD, analysis X) and 172.6±9.6 (Extended Hedman, analysis XII) mya (Table 3.4). The results are less uniform than those of the entire goniopholidid clade, with tree sets IV and XII consistently providing older estimates than tree sets II and X across all dating methods (Fig. 3.1).

**Crocodylia**

The estimated emergence dates for Crocodylia vary markedly across both dating methods and tree sets, ranging from 84.2±2.3 (cal3, analysis X) to
175.0±9.3 (Extended Hedman, analysis XII) mya (Table 3.4). The estimates given by tree set XII are far older (>20 Myr) than those of the other tree sets, with tree set II always giving the youngest estimates across all dating methods (Fig. 3.1).

**Gavialoidea**

Gavialoidea are estimated to have emerged between 79.1±3.0 (cal3, analysis IV) and 149.9±13.5 (Extended Hedman, analysis XII) mya (Table 3.4). Tree set XII provides the oldest age estimates across all dating methods, whereas the other tree sets vary. Tree set IV analysed with sGLA provides a low median with an almost invisible lower quartile. Here, all obtained age estimates cluster around two different points in time, 80 mya and 110ma, with slightly more estimates around 80 mya (Fig. 3.1).

**Gavialinae**

Similarly to Gavialoidea, there is a relatively wide range of age estimates for Gavialinae: between 38.9±2.7 (cal3, analysis IV) and 85.2±20.7 mya (Extended Hedman, analysis II) (Table 3.4). Estimates vary strongly between the different dating methods used but little across tree sets (Fig. 3.1).

**Brevirostres**

Brevirostres are estimated to have emerged between 82.0±1.6 (cal 3, analyses IV and VIII) and 145.1±10.6 (Extended Hedman, analysis II) Myr (Table 3.4). Estimates show a large variation both within and between the different dating methods, with tree set XII providing the oldest and tree set IV providing the youngest estimates for each method (Fig. 3.1).

**Crocodyloidea**

The emergence age estimates for Crocodyloidea vary between 72.2±2.6 (cal3, analysis XII) and 141.8±10.7 (Extended Hedman, analysis II) mya (Table 3.4).
Age estimates are moderately uniform between tree sets IV, X and XII within each method (age difference <20 Myr), with tree set II providing markedly older emergence time estimates than the other tree sets across all dating methods (Fig. 3.1).

**Crocodylidae**

Crocodylidae are estimated to have emerged between 61.9±1.1 (cal3, analysis XII) and 135.8±13.4 (Extended Hedman, analysis II) Myr (Table 3.4). Similarly to Crocodyloidea, variation between the different dating methods is large, with tree sets IV, X and XII showing very similar estimates within the respective dating methods and tree set II providing markedly older estimates (Fig. 3.1).

**Crocodylinae**

The variation between the different age estimates for Crocodylinae is slightly less pronounced that in Crocodyloidea and Crocodylidae, reaching from 61.3±0.8 (cal3, analysis XII) to 128.2±15.1 (Extended Hedman, analysis II) mya (Table 3.4). As above, the patterns between and within the four different dating methods are very similar, if less pronounced, to those in Crocodylidae and Crocodyloidea (Fig. 3.1).

**Tomistominae**

The emergence date of Tomistominae lies between 51.4±2.4 (cal3, analysis X) and 132.1±14.4 (Extended Hedman, analysis II) Myr (Table 3.4). While tree sets IV, X and XII deliver relatively similar divergence time estimations across all dating methods (around 20 Myr difference), tree set II gives far older estimates (>30 Myr older than the others) (Fig. 3.1).

**Alligatoroidea**

Emergence date estimates for Alligatoroidea vary between 81.8±1.6 (cal3, analyses IV and X) and 129.9±14.0 (Extended Hedman, analysis II) mya (Table
There is strong variation in date estimates both between and within dating methods, with tree set XII providing much earlier emergence estimates in all methods except Extended Hedman (Fig. 3.1).

*Diplocynodontinae + Leidyosuchus*

If *Leidyosuchus* is included in Diplocynodontinae as several of the phylogenies obtained in Chapter 2 indicated, their emergence date is estimated to fall between 81.5±1.8 (cal3, analysis IV) and 110.6±17.6 (Extended Hedman, analysis II) mya (Table 3.4). Whilst the two estimates obtained with Extended Hedman vary strongly (close to 20 Myr difference), there is much larger variation between the other dating methods than between tree sets (Fig. 3.1).

*Diplocynodontinae*

With the exception of one estimate, emergence date estimates for Diplocynodontinae (without *Leidyosuchus*) are lower than the estimates obtained if *Leidyosuchus* is included, varying between 59.6±1.4 (cal3, analysis X) and 109.6±20.1 (Extended Hedman, analysis XII) mya (Table 3.4). Although the estimates obtained by cal3 are extremely similar across all tree sets, the age estimates show more variation when using Extended Hedman and sGLA, although no single tree set delivers generally younger or older estimates (Fig. 3.1).

*Globidonta*

Globidonta are estimated to have emerged between 67.0±1.7 (cal3, analysis X) and 115.5±15.7 (Extended Hedman, analysis II) mya (Table 3.4). Tree set XII always gives the youngest age estimates whilst the other three tree sets are more uniform in their emergence age estimations. Cal3 and sGLA show almost no variation in tree sets II, IV and X with similar estimates across both dating methods, whilst Extended Hedman and FBD exhibit more variation between the three tree sets (Fig. 3.1).
Caimaninae

Caimaninae is the youngest of the neosuchian clades examined here and is estimated to have originated between $44.2^{\pm}0.2$ (FBD, analysis II) and $63.9^{\pm}12.1$ (Extended Hedman, analysis X) mya (Table 3.4) (Table 3.4). Although there is some variation between the different dating methods, age estimates are remarkably uniform across all tree sets within a single method (Fig. 3.1).

3.5 Discussion

Overall, many of the estimates for clade divergences within Neosuchia obtained by this study are similar to those found by previous authors (Table 3.1). In some cases, however, estimates generated herein included far older emergence times than have been postulated before, even though the oldest known taxa from several clades (e.g. Caimaninae) were not included in the phylogenetic analysis (see Table 3.5). In general, age estimates are strongly dependent on the dating method applied and set of source trees used. Estimated emergence ages based on the combined evidence presented below can be found in Table 3.6.

Methodologies

cal3

Cal3 generally delivered the youngest age estimates in this study. The reason lies in the workings of the algorithm - the youngest possible age for a node is initially set as the FAD of the oldest member of the clade that is to be dated and the probability distribution of potential node ages is determined from this starting point, moving from root to shallowest node (Bapst, 2013). This dependence on using the oldest possible taxon age within the clade to be dated, however, makes cal3 particularly vulnerable to the assumption that the oldest known taxa of a tree are part of the phylogeny that is to be dated, because younger taxon ages cause a significant shift towards lower nodes ages, especially with the low
standard deviations on ages.

Cal3 is more robust to minor differences in tree topology, where other methods, especially Extended Hedman (see below) are far more vulnerable. This probably stems from the combination of the above mentioned method of determining the minimal dates - if the order of taxa within a clade changes slightly, the overall initial minimum clade age will remain the same - and the additional a priori determination of rates that is needed for cal3. The probability distribution of the node ages themselves are determined by extinction, branching (=speciation) and sampling rate, although the results in this study showed that changes in these rates only had minor influence on the obtained node ages. Since these rates are applied equally to the entire phylogeny it renders standard variation and the difference in dates between relatively similar phylogenies rather low in the neosuchian dataset.

**Extended Hedman**

The Extended Hedman estimates obtained in this study are starkly different from those produced by other dating methods. The standard deviation is far greater than in cal3, sGLA or FBD. A striking example is the Extended Hedman estimates for Gavialoidea where the maximum and minimum ages obtained by Extended Hedman span over 100 Myr and the difference in medians between the various input tree sets is over 30 Myr. A similar result was also observed by Lloyd *et al.* (2016) in their analyses of dinosaur divergence times. In addition, these authors found that higher phylogenetic uncertainty led to higher variance in age estimates. However, the latter cannot be confirmed here - most of the phylogenetic uncertainty in the neosuchian trees lies within Tethysuchia and yet here both the standard deviation as well as minimum/maximum values and quantiles for Extended Hedman are lower than for many other estimated clades. In fact, the Extended Hedman standard deviations generally increase with distance from the tree root instead.
In several cases, Extended Hedman was also more vulnerable to variation in tree topology, with a large differences in medians between the tree sets, more so than in other methods (e.g. for 'derived' Goniopholididae, Gavialinae, Tomistominae and Globidonta). Extended Hedman estimates are extremely dependent on the taxon ages of the immediately older sister taxa of the dated clade (instead of the FAD of the oldest taxon in the dated clade as in e.g. cal3). Therefore, differences in phylogeny have a much larger effect, especially when moving further away from the root where there is a larger likelihood of these immediate sister taxa changing position in the phylogenetic tree (even amongst the MPTs of the same phylogenetic analysis). Standard deviation of the age estimates, however, is not dependent on the number of MPTs, as analysis XII which has by far the most MPTs in this study has similar standard deviations as the other tree sets.

Finally, Extended Hedman also delivered consistently older ages than all of the other methods. Changing the outgroup ages did not alter the resulting age estimates significantly (see above) in this study, although it has been reported that the order and age of outgroups have significant influence on Extended Hedman (Lloyd et al., 2016). In addition, these authors recovered markedly younger cal3 age estimates in only 2 of their dated nodes, unlike this study (the effect persisted even when the same outgroups were added to the cal3 analysis). This age difference compared to the other methods remains even when taxa causing artificially old ages in some groups are removed (e.g. the thalattosuchian *Steneosurus* from Tethysuchia in analyses II, X and XII, see below for details).

One reason for the older estimates might lie within the workings of the method itself: Extended Hedman depends strongly on the youngest possible ages of not only one, but successive 'outgroups' of the dated clade. Therefore, if the 'outgroups' of the dated clade are all of similar age to the oldest taxon in the clade (as would happen with well-sampled groups that contain multiple
species for each time bin as, for example, in the Alligatoroidea surrounding the Caimaninae in this study), Extended Hedman will produce lower age estimates. In contrast, the older the possible ages for the successive 'outgroups' to the dated clades, the older the obtained ages - such as, for example, Crocodyloidea in this study where its immediate outgroups are sparsely sampled and cover a wide range of ages, especially with *Bernissartia* and *Hylaeochampsia*. Whilst the proportion of sampled taxa poses a caveat for all divergence age estimation studies, Extended Hedman seems particularly vulnerable to both lower taxon coverage and stratigraphic bias.

**sGLA**

The results obtained using sGLA constitute an intermittent age estimate between those given by cal3 and Extended Hedman, but are mostly older than those from FBD (with the exception of the divergence dates for Brevirostres, Crocodyloidea, Crocodylidae and Crocodylinae). These results contrast with some of those obtained by Turner *et al.* (2017), who found that sGLA provided older age estimates than FBD for clades that contained closely related fossil taxa situated on seemingly long ghost lineages (similar to Crocodylinae in this study, although the ghost lineages here are shorter). Equally, the statement that age estimates with sGLA become older than those of FBD with decreasing distance to the tree root (Turner *et al.*, 2017) cannot be confirmed here: sGLA estimates are older than those of FBD by the same amount in Neosuchia (closest to the root) as, for example, in Caimaninae (furthest from the root).

This can be explained by examining the algorithms upon which sGLA is based: as with cal3, a minimum possible age estimate is assigned to each node according to the FAD of taxa within the tree. However, instead of using the oldest taxon within the clade for dating, the minimum age estimate is based on the oldest taxon within the closest sister clade to that being dated. For sGLA, these minimum node ages are then scaled up in accordance with the age of
earlier nodes. As cal3 makes use of the oldest ages within the dated clade and Extended Hedman estimates divergence ages according to the ages of several successive ‘outgroups’, it is plausible that sGLA estimates lie between the two given they are more closely bound to the minimum ages of older sister taxa/groups than Extended Hedman.

In addition, sGLA is more vulnerable to minor changes in phylogeny (e.g. a taxon swapping position within a clade) than cal3, although less so than Extended Hedman. However, larger phylogenetic differences between tree sets (such as for Crocodyloidea and Crocodylinae in tree set 2 of this study) have a much greater influence on sGLA age estimates than they do on cal3 derived ages, in several instances even larger than in Extended Hedman. Once again, this can be explained by the sGLA algorithm — similar to Extended Hedman, the age estimates are adjusted towards older ages. The amount of adjustment is directly related to the age of the next oldest sister taxon. In the case of old rogue taxa being recovered as next older sister taxon/’outgroup’ to Crocodyloidea, for example, this leads to a much stronger shift towards older estimates than in cal3. As in Extended Hedman, this makes sGLA vulnerable to incomplete taxon sampling and more strongly dependent on phylogenetic topology.

**FBD**

Despite the fact that the FBD age estimates in this study are potentially skewed towards younger dates (see Section 3.3.3), the youngest node ages were found mostly by cal3, not FBD. This is in contrast to the findings of Bapst et al. (2016), although the authors examined different phylogenies for cal3 and FBD, having used FBD for phylogeny reconstruction as well as divergence date estimation. In this thesis, FBD provides the second youngest estimates in most cases. In addition, the standard deviation values of the age means are much lower than those calculated by the other dating methods, although this can be attributed to the very low sample sizes for age estimates compared to cal3, Extended
Hedman and sGLA.

In contrast to the other three methods applied herein, the FDB model used here calculates node ages by using priors to determine the rates of evolution along the entire tree (which are changeable throughout different time intervals under the skyline version of FBD: Gavryushkina et al. (2014)) and the variation between taxon ages. Therefore, FBD is not reliant on the identity of the oldest taxon within or immediately next to the clade to be dated. This makes it more vulnerable to minor changes in phylogeny than cal3 and sGLA, but less vulnerable to major phylogenetic differences, even less so than cal3 in several instances (e.g. divergence date for Brevirostres).

The reason for the younger sGLA age estimates probably reflects the algorithms of the different methods. For example, amongst Crocodyloidea, the oldest taxa of the different sister groups (Crocodylidae and ‘early diverging’ Crocodyloidea discussed in Chapter 2, Section 2.5.2) are of very similar age (within 10 Myr of each other). Similarly, the three large superfamilies within Brevirostres all evolved within a relatively short time frame before the K/Pg boundary (see below). Since sGLA uses the oldest ages of the next earlier diverging sister group (‘early diverging Crocodyloidea’ in the case of Crocodylidae, Gavialoidea and Alligatoroidea in the case of Crocodyloidea, etc.) these minimum node ages are not significantly scaled back in time. In contrast, FBD assumes constant change amongst phylogenetic branches over time and accordingly, scales node ages even of successive nodes further back in time. This is confirmed when looking at the divergence dates of Crocodylidae and Crocodylinae, for example: sGLA node ages are almost the same for both nodes whereas FBD operates on the assumption of a larger amount of change and thus more passed time between the two nodes.
<table>
<thead>
<tr>
<th>Clade</th>
<th>Taxon</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neosuchia</td>
<td>Calsoyasuchus valliceps*</td>
<td>199.3–190.8</td>
</tr>
<tr>
<td>Eusuchia</td>
<td>Hylaeochampsa vectiana</td>
<td>129.4–125.0</td>
</tr>
<tr>
<td>Tethysuchia</td>
<td>Meridiosaurus vallisparadisi*</td>
<td>157.3–152.1</td>
</tr>
<tr>
<td>Goniopholididae</td>
<td>Calsoyasuchus valliceps*</td>
<td>199.3–190.8</td>
</tr>
<tr>
<td>‘derived’ Gonio-</td>
<td><em>Goniopholis</em> sp.</td>
<td>168.3–166.1</td>
</tr>
<tr>
<td>pholididae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crocodylia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gavialoidea</td>
<td>Thoracosaurus sp.</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Gavialinae</td>
<td>Eogavialis africanum</td>
<td>37.8–33.9</td>
</tr>
<tr>
<td>Brevirostres</td>
<td>? Crocodylus sp.</td>
<td>100.5–93.9</td>
</tr>
<tr>
<td>Crocodyloidea</td>
<td>? Crocodylus sp.</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Crocodylidae</td>
<td>? Crocodylus sp.</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Crocodylinae</td>
<td>? Crocodylus sp.</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Tomistomininae</td>
<td>Thecachampsa antiqua*</td>
<td>59.2–56.0</td>
</tr>
<tr>
<td>Alligatoroidea</td>
<td>Albertochampsa langstoni*</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Diplocynodontinae +</td>
<td>Leidyosuchus canadensis</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Leidyosuchus</td>
<td></td>
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<tr>
<td>Diplocynodontinae</td>
<td>? Diplocynodon sp.</td>
<td>72.1–66.0</td>
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<tr>
<td>Globidonta</td>
<td>Albertochampsa langstoni*</td>
<td>83.6–72.1</td>
</tr>
<tr>
<td>Caimaninae</td>
<td>Eocaiman palaeocenicus*</td>
<td>66.0–61.6</td>
</tr>
</tbody>
</table>

Table 3.5: Ages of the oldest known taxon in each phylogenetic group dated for this study. Taxon names and ages taken from PBDB (Alroy, 1998) and adjusted for ICS ages, in millions of years. *denotes taxa not present in the phylogenetic analyses used here.
Taxonomic clade age estimates

Neosuchia

Except for Extended Hedman, the majority of origination time estimates obtained here for Neosuchia are younger than those given by Turner et al. (2017) (189–209 mya) and De Andrade et al. (2011) (208 mya). These younger estimates are probably caused by the oldest taxon (*Calsoyasuchus valliceps*, 190.8–199.3 Myr old) not being included in the phylogenetic analysis. The preferred phylogenies from the previous chapter, tree sets IV, yielded results between 180 and 200 mya. These results corroborate the hypotheses of both above mentioned studies as well as those of Pol et al. (2009) and Montefeltro et al. (2013) that Neosuchia originated in the Early Jurassic or possibly the very latest Triassic.

Eusuchia

All the divergence estimates obtained in this study for Eusuchia are older than the oldest species *Hylaeochamps'a vectiana*, sometimes by a large margin (several Extended Hedman estimates are 50 Myr older). It also contradicts the work of previous authors, such as Salisbury et al. (2006), Pol et al. (2009), Martin et al. (2010), Puértolas et al. (2011) and Lee & Yates (2018) who all place the eusuchian origin within the Early Cretaceous, between 120-140 mya. In contrast, the ages obtained by De Andrade et al. (2011) and Turner et al. (2017) suggest a Late Jurassic origin for Eusuchia, between 150–172 mya which is more in line with the ages estimated here. However, the older age estimates in this study are likely attributable to clustering of *Bernissartia*, a non-eusuchian neosuchian from the beginning of the Cretaceous, with *Hylaeochamps'a*, the oldest known eusuchian. Removing *Bernissartia* from the phylogenies does result in a younger estimate under cal3 (128.6±2.4 for the youngest), but does not change the older estimates under Extended Hedman (183.2±8.6 for the
oldest). Tree set XII always gives older ages than the remaining phylogenies because of the placement of the Late Jurassic pholidosaurid *Crocodilaemus* as part of Eusuchia.

Tree set IV, based on the preferred analysis from Chapter 2, estimates eusuchian divergence dates to lie between 144 (128 with the removal of *Bernissartia*) and 158 mya, pointing towards a Late Jurassic or possibly Early Cretaceous origin of Eusuchia.

**Tethysuchia**

Tethysuchia have previously been estimated to have emerged either in the Late Jurassic, around 145–150 mya (Martin *et al.*, 2010; De Andrade *et al.*, 2011) or in the Early/Middle Jurassic, 156–187 mya (Turner *et al.*, 2017). All of the estimates in this study (except tree set IV under cal3) fall into the latter category and are in line with the oldest definite tethysuchian remains of *Meridosaurus* from the Kimmeridgian (which was not included in this analysis). There has been speculation about the presence of pholidosaurids from the Middle Jurassic of China (Young, 1939) which would be in line with most of the older estimates obtained here. However, the identity of these remains is still unconfirmed. The much younger estimates that are consistently found by tree set IV result from the position of the thalattosuchian *Steneosaurus*. This non-tethysuchian taxon from the Early/Middle Jurassic is resolved as part of Tethysuchia in tree sets II, X and XII and as part of a mixed tethysuchian-thalattosuchian sister group to Tethysuchia in tree set IV. However, if *Steneosaurus* is removed from the analysis yielding providing the oldest age estimate (Extended Hedman, analysis II), the resulting divergence date, 185.8±11.4, is still situated in the Early Jurassic.

Tree set IV estimates for tethysuchian origins run between 145–184 mya, with one estimate in the Early Jurassic (Extended Hedman), two estimates in the Middle Jurassic (sGLA and FBD) and one in the Late Jurassic (cal3). Tak-
Table 3.6: Estimated emergence ages of all eighteen neosuchian clades in this study. Ages based on the results from the preferred methods (mostly cal3 and FBD).

<table>
<thead>
<tr>
<th>Clade</th>
<th>Estimated age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neosuchia</td>
<td>Early Jurassic/very Late Triassic</td>
</tr>
<tr>
<td>Eusuchia</td>
<td>Late Jurassic/Early Cretaceous</td>
</tr>
<tr>
<td>Tethysuchia</td>
<td>Middle Jurassic</td>
</tr>
<tr>
<td>Goniopholididae</td>
<td>early Early Jurassic</td>
</tr>
<tr>
<td>‘derived’ Goniopholididae</td>
<td>Middle Jurassic</td>
</tr>
<tr>
<td>Crocodylia</td>
<td>late Early Cretaceous</td>
</tr>
<tr>
<td>Gavialoidea</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Gavialinae</td>
<td>Eocene</td>
</tr>
<tr>
<td>Brevirostres</td>
<td>late Early Cretaceous</td>
</tr>
<tr>
<td>Crocodyloidea</td>
<td>late Early Cretaceous</td>
</tr>
<tr>
<td>Crocodylidae</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Crocodylinae</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Tomistominae</td>
<td>Paleocene</td>
</tr>
<tr>
<td>Alligatoroidea</td>
<td>early Late Cretaceous/late Early Cretaceous</td>
</tr>
<tr>
<td>Diplocynodontinae + Leidyosuchus</td>
<td>early Late Cretaceous</td>
</tr>
<tr>
<td>Diplocynodontinae</td>
<td>late Late Cretaceous</td>
</tr>
<tr>
<td>Globidonta</td>
<td>early Late Cretaceous</td>
</tr>
<tr>
<td>Caimaninae</td>
<td>Late Cretaceous</td>
</tr>
</tbody>
</table>

The earliest neosuchian, *Calsoyasuchus valliceps* is also thought to be the earliest goniopholidid (Tykoski *et al.*, 2002; De Andrade *et al.*, 2011). As such, all the estimates obtained by this analysis (including the preferred tree set IV) emerge as too young — even the oldest estimate of 188.8 ± 7.6 is younger than the estimated age of *C. valliceps*, 199.3–190.8 mya (Table 3.5). Equally, previous author’s age estimates for the divergence of Goniopholididae range from 184–197 mya (De Andrade *et al.*, 2011; Turner *et al.*, 2017). Thus the group is certainly older than the estimates obtained in this analysis, and it is very likely
of early Early Jurassic origin.

'Derived' Goniopholididae

In contrast to Goniopholididae, the ages obtained in previous studies for the emergence of the most derived taxa within the clade (*Goniopholis, Amphi-cotylus, Anteophthalmosuchus*) lie within the estimates found here, ranging from 147–160 mya (De Andrade *et al.*, 2011; Turner *et al.*, 2017). The oldest known specimen that is thought to be referrable to *Goniopholis* has been dated to the late Bathonian (166–167 mya) although the identification is ambiguous and it might represent an immature specimen of *Nannosuchus* (Evans & Milner, 1994). All other specimens, which are clearly identified as belonging to one of the three above mentioned genera, are either of Late Jurassic age or younger (Alroy, 1998). The age estimate obtained here, especially that derived from the preferred tree set IV (156–171 mya), and those of other authors are likely correct and the most derived members of Goniopholididae originated during the Middle Jurassic.

Crocodylia

The estimates for the emergence of Crocodylia obtained here vary markedly from the Middle Jurassic to Late Cretaceous, both within and between the sets of results obtained from different divergence dating methods. Most ages previously obtained for the divergence of this clade fall in the Late Cretaceous, with emergence dates including 73 mya (De Andrade *et al.*, 2011; Turner *et al.*, 2017), over 80 mya (Martin *et al.*, 2010; Oaks, 2011), 90 mya (Salisbury *et al.*, 2006; Puértolas *et al.*, 2011) and 100 mya (Roos *et al.*, 2007; Oaks, 2011; Turner *et al.*, 2017; Lee & Yates, 2018). Only the cal3 analyses of tree sets II, IV and X fall within this range. The reason for the rather old dates estimates derived from tree set XII is the inclusion of the assumed Late Jurassic tethysuchian *Crocodiliaemus* as part of Crocodylia. The differences between the four meth-
ods are remarkable, as most cal3 estimates are much younger than the others. This is presumably due to differences in the nature of the various algorithms (see above) — sGLA and FBD are more vulnerable to the ages of the immediate sister taxa/clades to Crocodylia in the phylogenies obtained here, causing *Hylaeochampsia* and *Bernissartia* to push back the age estimates obtained.

Tree set IV gives estimates between 84–141 mya (84–134 mya if the usually too old estimates from Extended Hedman are disregarded). Given the age of oldest eusuchian taxon (*Hylaeochampsia vectiana*: 129–125 mya) it is unlikely that Crocodylia emerged before this date, giving more credence to the younger cal3 estimates. Taking the divergence ages calculated by other authors into account (73–100 mya) it is probable that Crocodylia originated towards the end of the Early Cretaceous. This would be in line with an observed burst in diversification that led to the high biodiversity of pseudosuchians in general that occurred in concert with the high temperatures of the mid-Cretaceous (Mannion *et al.*, 2015).

**Gavialoidea**

The estimates for the origin of Gavialoidea obtained from this study range over 70 Myr. The youngest ones (derived mostly from cal3 and with some using sGLA) all average around 80 mya for the emergence of Gavialoidea, which is close to previous author’s estimates of 68–89 mya (Martin *et al.*, 2010; Puértolas *et al.*, 2011; Turner *et al.*, 2017) and within the age ranges of the oldest specimen thought to belong to Gavialoidea, *Thoracosaurus neocesariensis* from the Campanian, which is dated to 84.9–70.6 mya (Schwimmer, 1986). The comparatively older estimates of tree set XII across all methods can be attributed to the clustering of Early to Late Cretaceous species of the tethysuchian *Elosuchus* with Gavialoidea. Although these very old estimates can probably be discarded, the estimates presented here confirm that Gavialoidea emerged before the K/Pg boundary in accordance with the suggestions of Brochu (2003).
and Brochu et al. (2012). As mentioned above, the sGLA age estimates for tree set IV yielded the curious result whereby the age estimates displayed a strong bimodal distribution, clustering around 80 mya and 110 mya, leading to a median of around 80 mya and a mean of over 90 mya.

The ages obtained from tree set IV range between 79–118 mya (79–93 mya without Extended Hedman). With high probability, Gavialoidea therefore emerged during the Late Cretaceous, between the Turonian and Campanian.

**Gavialinae**

The large variation of ages for Gavialinae seems to be entirely dependent on the method used, not the phylogeny. The oldest taxon, *Eogavialis africanum*, is from the Late Eocene, slightly younger than the youngest estimates obtained here of 38.9±2.7 mya. Only Extended Hedman provided ages older than the K/Pg boundary. Since Extended Hedman generally provides older estimates than the other dating methods and its obtained ages are pulled back in time by the early date for *Thoracosaurus* (an effect also observed by Lee & Yates (2018)), these estimates can be disregarded. Gavialinae probably emerged some time during the early Eocene, which coincides with the Paleocene-Eocene Thermal Maximum (PETM) or the early Eocene Climatic Optimum (EECO) (Lauretano et al., 2015).

**Brevirostres**

As with Gavialoidea and the other taxonomic groups discussed above, the divergence ages obtained here for Brevirostres encompass both estimates of previous studies at the lower scale and possible ages older than the oldest known brevirostran specimen. Previous authors have postulated that the emergence of Brevirostres occurred in the Late Cretaceous (75–99mya) (Turner et al., 2017), with a majority of estimates between 80–90 mya (Salisbury et al., 2006; Martin et al., 2010). The majority of the estimates obtained by the current study...
(except cal3) are older than 100 mya (the identification of *Elosuchus* as part of Tomistominae in analysis II and the discovery of older ages for Gavialoidea and Eusuchia in analysis XII lead to these analyses giving older estimates than expected).

Confident identification of the oldest possible specimen referable to Brevirostres (as well as Crocodyloidea, Crocodylidae and Crocodylinae) is difficult because of the ambiguous status of many fossils labelled as *Crocodylus*, since they do not all belong to Crocodylinae (Brochu, 2000; Oaks, 2011). In this case, the oldest specimen, an incomplete mandible from the Cenomanian, is dated to 100.5–93.9 mya and has been labelled as *Crocodylus selaslophensis* (Molnar & Willis, 2001), which was later shown to be a doubtful identification (Kear & Hamilton-Bruce, 2011).

In the light of this evidence it is difficult to evaluate the different divergence date estimates. Tree set IV gives divergence times between 82–120 mya. Taking into account the likely age of Crocodylia above (which, according to very short the branch lengths of the dated phylogenetic trees in this study, originated shortly before Brevirostres and Crocodyloidea), Brevirostres very likely emerged during the elevated temperatures of the late Early Cretaceous or close to the Early/Late Cretaceous boundary.

**Crocodyloidea**

As with Brevirostres, the age estimates for Crocodyloidea using tree set II are much older than those of the other tree sets obtained with the same dating method, due to the late Early Cretaceous tethysuchian *Elosuchus felixi* being resolved within Tomistominae. Most of the other estimates are in the Early Cretaceous. Other studies place the divergence date of Crocodyloidea between 73 mya (Salisbury *et al.*, 2006; Puértolas *et al.*, 2011) and 80 mya (Martin *et al.*, 2010; Lee & Yates, 2018). As a result of the above mentioned problem with the accurate identification of the oldest taxon it is difficult to establish a firm lower
boundary for any age estimates.

Tree set IV ages vary between 72–110 mya. Following the evidence from other dating studies, and the presumed emergence of Brevirostres and Crocodylia before or around the Early/Late Cretaceous boundary, Crocodyloidea emerged during the Late Cretaceous.

**Crocodileidae**

Apart from tree set II (for the reasons mentioned above) and Extended Hedgesman estimates, all of the emergence time dates for Crocodileidae in this study are located in the Late Cretaceous or close to the K/Pg boundary. There is evidence that crocodylids were present before the K/Pg boundary from some morphological studies (Brochu, 2003; Martin et al., 2010; Martin & Delfino, 2010; Brochu et al., 2012), whereas other morphological studies place their emergence in the early Paleocene around 60 mya (Salisbury et al., 2006; Puértolas et al., 2011) or later (Lee & Yates, 2018). Molecular studies either estimate their emergence to have happened 47–49 mya (Roos et al., 2007) or in a wider range of 39.85–69.91 mya (Oaks, 2011).

Divergence ages obtained by tree set IV range between 63–104 mya. This evidence, together with the morphological studies cited above, points to a likely emergence of Crocodileidae during the Late Cretaceous, before the K/Pg-boundary.

**Crocodylinae**

Estimates for the age of Crocodylinae are very similar to those for Crocodileidae, which stands in stark contrast to most of the emergence times obtained by other authors. Previous estimates range from 19–29 mya, for both molecular and morphological analyses (Salisbury et al., 2006; Roos et al., 2007; Oaks, 2011; Puértolas et al., 2011; Lee & Yates, 2018), whereas all of the estimates obtained here are in the Late Cretaceous or early Paleocene. The problem is the definition of the clade Crocodylinae and whether it should include the
early Oligocene (33.9–28.1 mya) *Crocodylus megarhinus*. According to Brochu (2000), *C. megarhinus* is a basal crocodylinid. The interpretation used here is similar to that used by Brochu (2000) and Gatesy *et al.* (2004): Crocodylinae encompasses all taxa that do not belong to Mekosuchinae (which is not included in this analysis) and are more closely related to extant taxa such as *C. niloticus* than to Tomistominae. The absence of taxa such as *C. megarhinus* in molecular analyses leads to much younger estimates. However, even with the inclusion of *C. megarhinus*, the estimates obtained here are still far older than those obtained by the other morphological studies (Table 3.1).

Tree set IV ages are generally on the younger side, ranging from 62–99 mya (with all estimates except cal3 before the K/Pg-boundary). This strongly implies that the crocodyline clade was present before the K/Pg-boundary. Sampling a larger proportion of Crocodylidae (especially Mekosuchinae) would help to clarify this issue.

**Tomistominae**

Ignoring the artificially too-old estimates of analysis II (due to the inclusion of *Elosuchus*), Tomistominae is estimated to have emerged either late in the Cretaceous or in the early Paleogene. The latter is in line with previous estimates from morphological studies that place the emergence around 57 mya (Salisbury *et al.*, 2006; Puértolas *et al.*, 2011). The oldest known tomistomine is *Thecachampsa antiqua* from the late Paleocene (59.2–56.0 mya).

The majority of tree set IV estimates place the emergence of Tomistominae after the K/Pg-boundary (with the exception of FBD), between 52–70 mya (50–61 mya if the FBD estimate is disregarded). Taken in conjunction with the age of *Thecachampsa* it seems likely that Tomistominae emerged in the Paleocene, immediately after the K/Pg-boundary.
Alligatoroidea

As observed for the estimates of the brevirostran ages above, the placement of Crocodiliaemus skews the ages of analysis XII towards older estimates than the other analyses. Most of the dates obtained here for Alligatoroidea fall within the 80–120 mya range, the lower end of which is congruent with previous author’s estimates of 82–93 mya (Salisbury et al., 2006; Puértolas et al., 2011; Lee & Yates, 2018) and the oldest identified alligatoroid taxon, the Late Cretaceous (83.6–72.1 mya) Albertochamps langstoni.

The oldest identified taxon, the above mentioned estimates for the emergence of Crocodylia and Brevirostres and the dates given by analyses on tree set IV here (82–111 mya) point to the emergence of Alligatoroidea around the Early/Late Cretaceous boundary during the high temperatures of the mid-Cretaceous and a definite existence of the group before the K/Pg boundary.

Diplocynodontinae with and without Leidyosuchus

The oldest known specimen of Leidyosuchus is L. canadensis from the Late Cretaceous (83.8–72.1 mya). The age of this taxon lies well within the lower boundaries of the estimates obtained here if this genus is referred to Diplocynodontinae. Most obtained divergence ages fall between 80–100 mya, with only the Extended Hedman dates being older. In contrast to the estimates obtained with the inclusion of Leidyosuchus in Diplocynodontinae, the vast majority of ages without Leidyosuchus (except the Extended Hedman dates) lie between 60–80 mya, equally distributed pre- and post the K/Pg boundary. The earliest known diplocynodont specimen (Diploxyonodon sp.) is Late Cretaceous (83.8–72.1 mya) in age (Grandstaff et al., 1992). However, the latter study does not provide any descriptions of the fossils nor is the specimen (NJSN 14363) described elsewhere in the literature, making it difficult to verify the claim that this is the only known Cretaceous diplocynodontine specimen.

Tree set IV ages place the emergence of Diplocynodontinae between 82–96
mya with *Leidyosuchus* and between 60–87 mya without (all estimates are in the Cretaceous with the exception of those obtained using cal3). As such it is highly probable that Diplocyondontinae was present before the K/Pg-boundary and emerged during the Late Cretaceous — either during the early Late Cretaceous if *Leidyosuchus* is included within it or late Late Cretaceous if it is excluded.

**Globidonta**

For Globidonta, there is a stark divide between the age estimates obtained by previous molecular and morphological studies. Molecular studies place its emergence around the K/Pg boundary, 62–71 mya (Roos *et al.*, 2007; Oaks, 2011). Morphological estimates, in contrast, are older, ranging from 80–83 mya (Salisbury *et al.*, 2006; Puértolas *et al.*, 2011; Lee & Yates, 2018). Although there are a few younger ages in this study, most of the estimates for Globidonta fall between 80–100 mya except for those obtained from Extended Hedman analyses, which are even older. The oldest definite globidontan taxa are the Late Cretaceous (72.1–66.0 mya) *Stangerochampsa mccabei* (Wu *et al.*, 1996) and *Albertochampsa langstoni* (83.6–72.1 mya) (Erickson, 1972). There are potential remains of *Brachychampsa* sp. that are apparently the same age (83.8–72.1 mya) (Storer, 1993; Nessov, 1995), but this cannot be verified from other publications at present.

Tree set IV estimates range between 79–104 mya (79–91 mya without Extended Hedman). In conjunction with the oldest known globidontan species and other authors’ age estimates, Globidonta evolved during the early Late Cretaceous (the same range as Gavialoidea). This is corroborated by the fact that its subclade Alligatoridae is thought to have been present before the K/Pg boundary also (Brochu *et al.*, 2012).

**Caimaninae**

The age estimates obtained for Caimaninae are uniform for tree sets ana-
ysed with the same dating method but show variation between dating methods, ranging from 44.2–63.9 mya. Most of these ages are below 60 mya, similar to the previously obtained divergence dates for this family based on morphological phylogenies (55–57 mya: Salisbury et al. (2006); Puértolas et al. (2011); Lee & Yates (2018)). Molecular studies place the emergence of Caimaninae as more recent, between 20–41 mya (Roos et al., 2007; Oaks, 2011). Dates obtained by molecular, as well as morphological, studies are incongruent with the age of the oldest known caimanin taxon, *Eocaiman palaeocenicus* from the Late Cretaceous and a number of species from the early Paleocene (Brochu, 2011; Pinheiro et al., 2013). Since these species were not included in the phylogenetic trees here the obtained estimates are probably too young and a reasonable assumption can be made that Caimaninae were present before the K/Pg boundary.

### 3.6 Conclusion

In order to assess the influence of both alternate phylogenetic hypotheses and different methods on node age estimates, four tip-dating techniques (cal3, Extended Hedman, sGLA and FBD) were applied to four tree sets selected from Chapter 2 based on their degree of stratigraphic congruence. Of these methods cal3 continuously gave the lowest divergence age estimates and Extended Hedman the highest. However, all four methods are limited by several factors, such as the accuracy of specimen dating, sampling bias and the completeness of sampling across the phylogenetic tree. Extended Hedman and sGLA are vulnerable to exclusion of the oldest known member of a clade, although phylogenetically unstable taxa can artifically inflate ages in all methods. Extended Hedman is also dependent on good coverage of taxon sampling.

The different methods show varying degrees of vulnerability to differences in topology. For example, cal3 is generally more robust to changes in phylogeny.
(unless they involve significantly older rogue taxa changing position), whereas minor changes in phylogeny have a particularly strong influence on the age estimates obtained by Extended Hedman, sGLA and FBD. Greater changes in topology particularly influence the age estimates obtained from Extended Hedman and sGLA. In this case, cal3 and FBD seem to provide the best age estimates. Future work should include the application of statistical tests to tease apart the exact amount by which phylogenetic and methodological differences influence node age estimations.

For all four methods, it is paramount to have detailed taxonomic knowledge of the clades under study in order to interpret and evaluate the obtained age estimates. Knowledge of the oldest known taxon of each phylogenetic group that is to be dated is of paramount importance when constructing phylogenetic trees in order to be dated and in evaluating the results, as is the ability to be able to identify 'rogue taxa' that might have been recovered in stratigraphically and morphologically unlikely positions within the dated phylogenies.

Despite the sensitivity of the various dating methods when different phylogenetic hypotheses are analysed it is likely that all three extant crocodylian clades (Crocodyloidea, Alligatoroidea and Gavialoidea), as well as Diplocynodontinae, diverged before the K/Pg boundary. In addition, the close divergence date estimates for Crocodylia, Brevirostres, Crocodyloidea and Alligatoridea and the origination of a large number of clades within the Cretaceous point to a potential diversification of crocodylian clades that occurred coincident with the high temperatures of the mid-Cretaceous. This was followed by the emergence of more deeply nested clades (Diplocynodontinae, Caimaninae and potentially Crocodylinae) during the latter part of the Late Cretaceous and Paleogene (Gavialinae, Tomistominae).
Chapter 4

The biogeographic history of Neosuchia

4.1 Abstract

Elucidating biogeographic patterns for neosuchians is important for understanding their evolution. While there are clear hypotheses for the palaeobiogeographic origins of some clades, such as Diplocynodontinae and Caimaninae, the ancestral areas for others are not as clear, for example Alligatoroidea and Eusuchia. An important factor complicating palaeobiogeographical analyses of Neosuchia is their saltwater tolerance and potential for transoceanic dispersal. While the extent of their saltwater tolerance is known for extant taxa, it cannot be assessed for extinct species. In order to simulate different degrees of transoceanic dispersal (ranging from no oceanic dispersal to there being no penalty for transmarine migration routes), four different methods of biogeographic reconstruction were selected using the newly dated neosuchian trees generated in Chapter 2. Application of these methods found some agreement in ancestral area reconstructions for some clades. Neosuchia most likely emerged somewhere in Laurasia, with subsequent dispersal within Laurasia to Europe...
and North America, as well as Africa. The three major eusuchian clades, Alligatoroidea, Crocodyloidea and Gavialoidea all radiated from North America. Gavialoidea and Crocodyloidea, along with the most ancient neosuchians, possessed a high degree of saltwater tolerance, with transoceanic dispersal playing an important role in their biogeography. Alligatoroidea, although less saltwater tolerant today, likely underwent at least one transoceanic dispersal event early in its evolutionary history, refuting the previous suggestion of a European origin.

4.2 Introduction

In order to understand the evolutionary history of a clade, and ultimately the processes leading to its diversification, knowledge of geographical ranges and dispersal routes through time are required. Ancestral areas are usually estimated on the basis of dated phylogenetic trees, coupled with geographic occurrence data. Most biogeographic methods employ an underlying model of palaeogeography changes over time (e.g. connectedness of land areas, positions of dispersal barriers, etc.). They are based either on parsimony (Ronquist, 1997), maximum likelihood (Ree, 2005; Ree & Smith, 2008) or Bayesian algorithms (Landis et al., 2013). Recently, newer methods have been developed that allow more flexibility in estimation and are not necessarily restricted by a single model of geographic evolution, including BioGeoBEARS (Matzke, 2013) and Bayesian area reconstruction in continuous space (O’Donovan et al., 2018). Similar to most biogeographic methods, these two enable analyses that are unconstrained by palaeogeographic processes and, in the case of BioGeoBEARS, manual control of the locations and strengths of potential dispersal limiting factors through time.

With their global distribution and long evolutionary history, Neosuchia represents an interesting clade for palaeobiogeographic analyses. Various studies have attempted to reconstruct the ancestral areas important in neosuchian evo-
lution. The majority of these studies, however, have not made use of statistical methods, but have relied on mapping fossil locations onto phylogenetic trees (e.g. Martin & Delfino (2010); Puértolas et al. (2011)). There have been a few analyses using statistical area reconstruction methods, including Turner (2004) and Hastings et al. (2014), but none using techniques such as BioGeoBEARS or Bayesian area reconstruction in continuous space in BayesTraits. The results obtained so far are inconclusive with respect to the origin of Neosuchia as its three major clades have different geographic distributions. It has been proposed that Crocodylia originated in Laurasia (Salisbury et al., 2006), potentially around the Tethys Sea (Holliday & Gardner, 2012), but there is no consensus regarding the Tethysuchia and Goniopholididae. Tethysuchia are proposed to have evolved either in Africa (Jouve et al., 2008b; Hastings et al., 2010, 2014; Young et al., 2016) or North America (De Andrade et al., 2011) and Goniopholididae either in North America or Central Asia (De Andrade et al., 2011; Halliday et al., 2013), respectively.

Perhaps the most challenging issue in neosuchian biogeography is determining possible marine dispersal routes, which is closely tied to the degree of saltwater tolerance in different taxa. Saltwater tolerance varies strongly between species. Some are relatively salt tolerant or even marine, such as dyrosaurids (Young et al., 2016), tomistomines (Piras, 2007; Jouve et al., 2015) or modern Crocodylus species (Brochu, 2003, 2007; Meredith et al., 2011; Oaks, 2011), and in others, such as extinct members of Gavialoidea, high salt water tolerance is considered likely (Brochu, 2003; Vélez-Juarbe et al., 2007). Extant members of Alligatoridae and Caimaninae, on the other hand, have very low salt water tolerance and it is unclear whether their direct ancestors could have crossed marine barriers (Brochu, 1999; Martin & Delfino, 2010; Hastings et al., 2013). This obscures the potential areas of origin for Alligatoroidea, for which Asia, North America and Europe have all been suggested (Martin & Buffetaut, 2008; Martin & Delfino, 2010; Puértolas et al., 2011).
In order to gain more insight into the ancestral areas and possible dispersal routes of the major neosuchian clades, this study employs cutting-edge biogeographical methods (BioGeoBEARS (Matzke, 2013, 2014) and the Bayesian approach proposed by O’Donovan et al. 2018) on the dated trees produced in Chapter 3. A variety of different dispersal models are used to simulate different scenarios of salt water tolerance and assess their effect on neosuchian ancestral area reconstructions.

### 4.3 Materials and Methods

**Dated trees**

Here, the FBD (Fossilised Birth-Death model) trees are used. As shown in Chapter 3, this analysis yielded one of the most accurate divergence date estimates. Although the cal3 analysis also provided accurate divergence time estimates, it is not used here since each node of every cal3 tree is assigned a random age from a previous distribution. Thus, no single cal3 tree provides average node age estimates (see Bapst (2013)). One of the main caveats of the dating study in the previous chapter was the absence of the oldest clade members in the phylogenetic datasets here, therefore, five taxa were added manually to the original preferred trees from analysis IV in Chapter 2 (see Table 4.1 for the exact taxa, their ages and positions). These five taxa represent the currently known oldest members of their respective clades and were chosen to increase the accuracy of the divergence age estimates in the FBD trees.

In addition, two taxa that caused problems during the divergence date estimations in Chapter 3 because of their inaccurate position in the phylogenetic tree were deleted: *Bernissartia fagesii* (incorrectly recovered as sister taxon to *Hylaeochampsa*) and *Steneosaurus bollensis* (a thalattosuchian incorrectly recovered with the tethysuchian taxa *Terminonaris* and *Hyposaurus*) (see Section 3.5.2 in Chapter 3). All five MPTs from analysis IV were dated again using FBD,
<table>
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<th>Taxon</th>
<th>Age</th>
<th>Position</th>
<th>Reference</th>
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</thead>
<tbody>
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<td><em>Albertochampsalangstoni</em></td>
<td>83.6-72.1</td>
<td>globidontan; between <em>Eoalligator</em> and <em>Brachychampsapuértoles et al. (2011)</em></td>
<td></td>
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<td><em>Calsoyasuchusvalliceps</em></td>
<td>199.3-190.3</td>
<td>basalmost goniopholidid</td>
<td>De Andrade et al. (2011)</td>
</tr>
<tr>
<td><em>Eocaimanpalaeocenicus</em></td>
<td>66.0-61.6</td>
<td>basalmost caimanin, sister taxon to <em>E. cavernensis</em></td>
<td>Pinheiro et al. (2013)</td>
</tr>
<tr>
<td><em>Meridiosaurusvallisparadisi</em></td>
<td>157.3-152.1</td>
<td>pholidosaurid, sister taxon to <em>Elosuchus</em></td>
<td>Fortier et al. (2011)</td>
</tr>
<tr>
<td><em>Thecachampsantiqua</em></td>
<td>59.2-56.0</td>
<td>tomistomine, between <em>Gavialosuchus</em> and <em>Kentisuchus</em></td>
<td>Jouve (2016)</td>
</tr>
</tbody>
</table>

Table 4.1: List of taxa added to the phylogenetic trees for the purposes of biogeographical analysis and the positions into which they were inserted. Ages are given in millions of years, based on the cited references and adjusted for the ICS chart (Cohen et al., 2013).

with the same specifications mentioned in Chapter 3, Section 3.3.3.4.

Biogeographic methods

The dated trees were analysed using two different methods for ancestral area reconstruction: BioGeoBEARS (BGB) (Matzke, 2013) and a new method based on O’Donovan et al. (2018), henceforth referred to as ‘Continuous Space Reconstruction’ (CSR).

BGB

BioGeoBEARS was developed by Matzke (2013) in order to provide a single framework in which different biogeographical models can be used for ancestral area reconstruction and their effectiveness be compared. The three main models used (with and without founder event speciation) are: DEC (Ree 2005; Ree & Smith 2008 and Matzke 2014 for added founder event speciation), DIVALIKE (based on Ronquist 1997) and BAYAREALIKE (based on Landis et al. 2013).
Dispersal-extinction-cladogenesis (DEC) allows for estimation of biogeographic maximum likelihood at every node of a dated tree, incorporating prior probabilities of potential changes in the ranges of ancestral areas at each node, as well as dispersal and extinction rates (Ree & Smith, 2008). This allows for the incorporation of changes in palaeogeography when estimating ancestral ranges, although is computationally intense since several possible geographic range combinations for each node are modelled. Dispersal-vicariance analysis (DIVA) reconstructs ancestral areas based on the lowest number of implied dispersal and extinction events. It considers widespread ancestral species distributions and relies mainly on vicariance as the mechanism for speciation (Ronquist, 1997).

In contrast to DEC, it allows for fewer scenarios of dividing widespread ancestral areas, especially outside vicariance scenarios. BayArea is a Bayesian approach that calculates the likelihood of a given biogeographical history for the given tree and chooses the scenario with the highest likelihood. It is based on the approach described in Ree (2005), but allows for a much larger number of areas to be used and different rates of colonisation. The whole set of areas present in an immediate ancestor can be inherited by its daughter species (Landis et al., 2013).

Since BGB cannot work with zero branch lengths as they are produced by FBD, all branches in the dated trees with lengths below 0.00001 were rescaled to a length of 0.0001. The capabilities of Neosuchia for transoceanic dispersal have long been debated without definite result (see e.g. Jouve et al. (2015) and Oaks (2011)) and three different approaches in BGB were chosen to reflect this: unconstrained, time-stratified, and distance-based (see below for details).

Several analyses were performed using the BioGeoBEARS package, which was implemented in R v. 3.4.2 (R Core Team, 2017). Five different trees (all MPTs of analysis IV in Chapter 2) were used, and seven different areas were defined: N (North America), S (South America), A (Asia), E (Europe), F (Africa), U (Australia) and I (India). Antarctica was excluded from the analysis due to the
absence of neosuchian taxa from this region. *Voay robustus*, a taxon from Madagascar, was designated as having been present in Africa. This is due to its very recent presence in the Holocene when Madagascar and India were fully separated and India had merged with Asia (Landis, 2017). In addition, it is probable that *V. robustus* dispersed from Africa to Madagascar (Brochu, 2007). See Table 4.3 for all fossil locations and Appendix C.6 for the full geography file. When 'unconstrained' (see below), this method does not place any limits on dispersal, allowing transoceanic dispersal to occur with the same probability as dispersal across land masses.

The first analysis was 'unconstrained', meaning that no further contraints were made on eventual dispersal routes besides the original areas of species occurrence. The second analysis performed was time-stratified, in which the time covered by the phylogenetic tree was divided into 18 different time slices. For each time slice the dispersal probabilities between the different geographical areas were defined. Mesozoic time slices were defined based on Hay et al. (1999), Csiki-Sava et al. (2015), Poropat et al. (2016 and refs therein) and the corrections to these presented in Xu et al. (2018) until the K/Pg-boundary (see Table 4.2 for a detailed description of all 18 time slices and their paleogeographic events). In addition to the 14 time slices before the K/Pg-boundary, the 4 time slices post K/Pg-boundary were based mainly on Bianchi & Morri (2000), Sanmartin et al. (2001) and Landis (2017). Time boundaries were mainly determined by the history of the Indian subcontinent and the formation of land bridges between various continents.

<table>
<thead>
<tr>
<th>Time slice</th>
<th>Age</th>
<th>Time period</th>
<th>Geography</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13.8–0</td>
<td>Serravallian to now</td>
<td>Beginning formation of Isthmus of Panama, Isthmus of Suez &amp; brief closure of Gibraltar, connecting North &amp; South America and Africa &amp; Asia/Europe respectively</td>
<td>Bianchi &amp; Morri (2000); O’Dea et al. (2016) and comments</td>
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<tr>
<td>Time slice</td>
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<td>Time period</td>
<td>Geography</td>
<td>References</td>
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<tr>
<td>2</td>
<td>25–13.8</td>
<td>Late Chattian to Langhian</td>
<td>Final disappearance of Tethys Sea; potential dispersal via Bering land bridge (dispersal multiplier=0.5)</td>
<td>Bianchi &amp; Morri (2000); Sanmartin et al. (2001)</td>
</tr>
<tr>
<td>3</td>
<td>35–25</td>
<td>Late Priabonian to Early Chattian</td>
<td>India joins with Tibet; Europe and Africa are close (dispersal multiplier=0.5)</td>
<td>Bianchi &amp; Morri (2000); Ali &amp; Aitchison (2008); Ali &amp; Krause (2011); Landis (2017)</td>
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<td>4</td>
<td>65.99–35</td>
<td>Danian to Early Priabonian</td>
<td>India starts to collide with Asia; potential dispersal via Bering land bridge (dispersal multiplier=0.5)</td>
<td>Bianchi &amp; Morri (2000); Sanmartin et al. (2001); Ali &amp; Aitchison (2008); Ali &amp; Krause (2011)</td>
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<td>5</td>
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<td>no dispersal between North America &amp; Europe; potential dispersal via Bering land bridge (dispersal multiplier=0.5), potential dispersal between Europe &amp; Africa and Europe &amp; Asia; potential dispersal between South America &amp; Australia</td>
<td>Hay et al. (1999); Sanmartin et al. (2001); Csiki-Sava et al. (2015); Poropat et al. (2016); Hay et al. (1999); Sanmartin et al. (2001)</td>
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<td>79–69</td>
<td>Late Campanian to Early Maastrichtian</td>
<td>no dispersal between Europe &amp; Asia; Bering land bridge dispersal between North America &amp; Asia, potential dispersal between Europe &amp; Africa, Europe &amp; Asia, South America &amp; Australia (dispersal multipliers=0.5)</td>
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<td>83.59–79</td>
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<td>Hay et al. (1999); Csiki-Sava et al. (2015); Poropat et al. (2016) and references therein</td>
</tr>
<tr>
<td>Time slice</td>
<td>Age</td>
<td>Time period</td>
<td>Geography</td>
<td>References</td>
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<td>8</td>
<td>100.49–83.59</td>
<td>Cenomanian to Santonian</td>
<td>no Bering land bridge; South America &amp; Africa split completely; Europe &amp; Asia connected; potential South America &amp; Australia dispersal (dispersal multiplier=0.5)</td>
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<td>107–100.49</td>
<td>Late Albian</td>
<td>Dispersal between Europe &amp; Asia; Bering land bridge; Indo-Madagascar separated from Australia/Antarctica; Africa separating from South America and potential South America &amp; Australia dispersal (dispersal multipliers=0.5); Beginning split Africa &amp; South America and potential South America &amp; Australia dispersal (dispersal multiplier=0.5)</td>
<td>Baraboshkin <em>et al.</em> (2003); Ali &amp; Aitchison (2008); Poropat <em>et al.</em> (2016) and references therein</td>
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<td>Early Albian</td>
<td>Dispersal between Europe &amp; Asia; Africa &amp; Europe dispersal interrupted; Indo-Madagascar beginning separated from Australia</td>
<td>Baraboshkin <em>et al.</em> (2003); Ali &amp; Krause (2011); Poropat <em>et al.</em> (2016) and references therein</td>
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<td>125–112.99</td>
<td>Aptian</td>
<td>Dispersal between Europe &amp; Asia; Africa &amp; Europe dispersal interrupted; Africa &amp; South America still connected; Indo-Madagascar beginning to split off from Antarctica; potential South America &amp; Australia dispersal (dispersal multiplier=0.5)</td>
<td>Baraboshkin <em>et al.</em> (2003); Torsvik <em>et al.</em> (2008); Poropat <em>et al.</em> (2016) and references therein</td>
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<tr>
<td>12</td>
<td>131.2–125</td>
<td>Late Hauterivian to Barremian</td>
<td>Dispersal between Europe &amp; Asia; no connection between North America &amp; Europe; India &amp; Australia still connected; Indo-Madagascar beginning to split off from Antarctica &amp; Africa; potential South America &amp; Australia dispersal (dispersal multiplier=0.5)</td>
<td>Baraboshkin <em>et al.</em> (2003); Torsvik <em>et al.</em> (2008); Poropat <em>et al.</em> (2016) and references therein</td>
</tr>
<tr>
<td>Time slice</td>
<td>Age</td>
<td>Time period</td>
<td>Geography</td>
<td>References</td>
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<td>142.2–131.2</td>
<td>Late Berriasian to</td>
<td>No dispersal between Europe &amp; Asia; potential dispersal between North</td>
<td>Baraboshkin et al. (2003); Poropat et al. (2016) and references therein</td>
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<td></td>
<td>Early Hauterivian</td>
<td>America &amp; Europe, Indo-Madagascar &amp; Africa and South America (dispersal</td>
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<td></td>
<td>multiplier=0.5)</td>
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<td></td>
<td>Dispersal between Asia &amp; Europe;</td>
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<td></td>
<td></td>
<td>Africa &amp; Australia separated; potential dispersal between North America &amp;</td>
<td>Baraboshkin et al. (2003); Poropat et al. (2016) and references therein</td>
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<td></td>
<td>144.99–142.2</td>
<td>Early Berriasian</td>
<td>Europe, Indo-Madagascar &amp; Africa and South America (dispersal multiplier=0.5)</td>
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<td></td>
<td>163.5–144.99</td>
<td>Oxfordian to Tithonian</td>
<td>Africa &amp; Indo-Madagascar beginning to separate; North America &amp; South</td>
<td>Poropat et al. (2016); Xu et al. (2018) and references therein</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>America separated; Europe &amp; North America connected; potential Europe &amp;</td>
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<td></td>
<td></td>
<td>Asia dispersal (dispersal multiplier=0.5)</td>
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<td>190.8–163.5</td>
<td>Pliensbachian to</td>
<td>North America &amp; Europe connected; Gondwana beginning to break away</td>
<td>Torsvik et al. (2008); Landis (2017) and references therein</td>
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<td>Callovian</td>
<td>(dispersal multipliers=0.5)</td>
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<td></td>
<td>201.3–190.8</td>
<td>Hettangian to</td>
<td>Asia beginning to separate; Europe &amp; Indo-Madagascar and Europe &amp;</td>
<td>Torsvik et al. (2008), Müller et al. (2016) maps</td>
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<td>Sinemurian</td>
<td>Australia dispersal unlikely</td>
<td>(Brune et al. (2016) model)</td>
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<td>260–201.3</td>
<td>Triassic</td>
<td>all landmasses more or less connected with each other, dispersal</td>
<td>Torsvik et al. (2008); Landis (2017) and Müller et al. (2016) maps</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>multipliers based on distances between landmasses</td>
<td>(Brune et al. (2016) model)</td>
</tr>
</tbody>
</table>

**Table 4.2:** All 18 time slices used in the classic time stratified analysis. Ages (in million years), time periods and descriptions of the applicable palaeogeography are given for each time slice.
Dispersal probabilities were slightly different to those included in Poropat et al. (2016) due to the nature of neosuchian ecology. A very large landmass between two continents (e.g. the presence of Africa and Madagascar between South America and India during the Triassic) leads to a dispersal probability of 0.5 since there are few purely terrestrial species in this dataset that could have crossed entire landmasses with ease, but dispersal is still possible using e.g. watersheds. If dispersal probability for continents with large landmasses in between was changed to 1.0 to allow unconstrained dispersal, there was little difference in the reconstructed ancestral areas. In addition, if only a small amount of water or potential land bridges were present between landmasses, dispersal was still set to 0.5 to allow for tentative crossing of these waterways. The presence of the de Geer landbridge between Greenland and North Scandinavia (Brikiatis, 2014) did not raise dispersal probabilities as its proposed position is at such high latitudes that it is beyond the known temperature limits occupied by neosuchians (Markwick, 1998). No 'areas allowed' file was specified since all land masses were present during the time period examined.

Several of the time slice durations were altered slightly in order for BGB to run smoothly because their ages coincided with several node ages of the tree. The following time slice ages were changed: 66 mya to 65.99 mya; 83.6 mya to 83.59 mya; 100.5 mya to 100.49 mya; 113 mya to 112.99 mya and 145 mya to 144.99 mya. 10,000 years was chosen as an acceptable difference in time slice length that would not influence results given the large overall time scale of the analysis (200 million years (Myr)) that 10,000 years lies within most error margins on taxon ages and relevant geographic events. The full dispersal multipliers matrix is available in Appendix C.6.

The third analysis was distance-based. Following a recent update, Bio-GeoBEARS allows the definition of dispersal probabilities based on physical distances between areas (Van Dam & Matzke, 2016). Using distances to inform dispersal probabilities instead of manual dispersal multipliers based on
the connectivity of land masses enables the incorporation of potential oceanic dispersal routes for Neosuchia. Therefore, instead of using the centroids of the seven geographical areas defined, the shortest possible distance between two land masses was measured. Eight time slices were defined of 30 Myr lengths each. For each time slice, the GPlates Portal (Müller et al., 2016) was used to simulate the approximate position of the land masses at the median point of each time slice (e.g. at 45 Myr for the time slice of 30–60 million Myr) using the Rift Velocity model from Brune et al. (2016). Distances were calculated based on the nearest points of the respective landmasses.

For the distance matrix used in the analysis, the distance set between connected areas was set to 1.0. It was decided to use the smallest distance in the matrix (170km) as a minimum distance beyond which dispersal probability would decrease (N. Matzke, pers. comm). This is close to the limit at which current salt-tolerant species such as Crocodylus porosus have been found from the coast in marine areas, 200 km (Bustard & Choudhury, 1980). Therefore, all distances were divided by 170 to obtain the dispersal factor. For example, in the earliest time slice, the minimum distance between North America and Asia is measured as 1,500km. To obtain the dispersal factor, 1,500 is divided by 170, leading to a factor of 8.8 in the distances matrix. The full distance matrix is available in Appendix C.6.

CSR

Continuous space reconstruction was introduced by O’Donovan et al. (2018) as a new method of ancestral area reconstruction. Unlike BGB, which assigns each species to a pre-defined area, CSR uses the taxon occurrence palaeo-coordinates as a basis for defining taxon distributions. Area reconstruction takes place in a three dimensional space using a Bayesian framework. The method has been implemented in BayesTraits v. 3.0.1 (Pagel et al., 2004). Palaeocoordinates for all neosuchian taxa in the analysis were obtained from
the Paleobiology Database (PBDB) via FossilWorks (Alroy, 1998). Since this dataset contains both extant taxa and a very small number of singletons (see Chapter 3), it was not feasible to turn every occurrence point into a tip of the phylogenetic tree as done in O’Donovan et al. (2018). Therefore, midpoints of all occurrences were calculated for each fossil taxon. For extant taxa, the geographical midpoint was calculated based on current and past distributions (adjusted so that the midpoint was located on land for non-marine taxa). The exact calculation method for midpoint calculation can be found under point A in http://geomidpoint.com/calculation.html. It constitutes conversion of the latitude/longitude coordinates into radians and then cartesian coordinates, taking into account both the curved surface of the earth and North/South- as well as East/West differences. Fossils of the taxon Gavialosuchus americanus have been found both in Europe and North America after their separation. Since a midpoint centered on the Atlantic Ocean would be unrealistic and more fossils were found in North America than in Europe, the midpoint of the North American occurrences was taken. The complete list of paleocoordinates is available in Table 4.3.

Since CSR in BayesTraits does not work with zero branch lengths, any branches in the FBD tree shorter than 0.00001 were rescaled to 0.0001. To check for convergence between the different MCMC chains each MPT was run 5 times, with 10,000,000 iterations each, sampled every 1000 iterations. The first 1,500,000 iterations were discarded as burnin.

Each iteration yielded reconstructed coordinates for each node of the phylogenetic tree, leading to 8,500 palaeocoordinate estimates for each node and run. Using R v. 3.4.2 (R Core Team, 2017), the means and standard deviations were calculated separately for the paleolatitude and paleolongitude of each node. The new divergence date estimates based on the re-dated FBD trees for each important neosuchian clade were extracted following the approach outlined in Chapter 3. Coordinates were matched to a model of the
Earth at the obtained divergence dates using the Rift Velocity model based on Brune et al. (2016) in the GPlates Portal (Müller et al., 2016).

<table>
<thead>
<tr>
<th>Species name</th>
<th>Area</th>
<th>Paleocoordinates</th>
<th>Singleton</th>
</tr>
</thead>
<tbody>
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<td>Albertochampsa langstoni</td>
<td>North America</td>
<td>N58.1 W76.0</td>
<td>x</td>
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<tr>
<td>Alligator mcgrewi</td>
<td>North America</td>
<td>N43.5 W98.1</td>
<td>x</td>
</tr>
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<td>Alligator mefferdi</td>
<td>North America</td>
<td>N43.2 W98.2</td>
<td>x</td>
</tr>
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<td>N46.2 W93.8</td>
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### Unconstrained analysis

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**Table 4.4:** Statistical values for unconstrained BGB analysis. Log Likelihood (LnL), Akaike scores (AIC), Akaike weights (AIC weight) and p-values comparing the models for each of the five MPTs (originally from analysis IV, dated with FBD).

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**Table 4.3:** Fossil locations and paleocoordinates for all taxa used in this study. Paleocoordinates represent the midpoint of known paleogeographical distributions. Locations and paleocoordinates taken from the PBDB. (Alroy, 1998).
4.4 Results

BGB model selection

Tables 4.4, 4.5 and 4.6 list the model statistics for all BGB analyses. Akaike Information Criteria (AIC) scores and corrected Akaike scores were almost the same for all analyses, with a maximum difference of 0.5.

The statistical patterns are similar across all five trees for each of the three BGB analysis types (Table 4.7).

Unconstrained analysis

For all three models, (DEC, DIVALIKE and BAYAREALIKE), there was a significant difference in performance for the data based on whether a variable incorporating founder event speciation (+J variant) was allowed or not (Table 4.4). The lowest log likelihood (and highest AIC score) was achieved for data analysis under the BAYAREALIKE+J model. Thus, the results of the +J models are preferred with respect to neosuchian ancestral area reconstruction.

Time-stratified analysis

The only model that shows a significant difference in likelihood with and without founder event speciation is BAYAREALIKE. Data analysed under BAYAREALIKE+J consistently yields higher log likelihood values and lower AIC scores (Table 4.5). Except for tree 4, all p-values for comparison between the DIVALIKE models are <0.05, with analyses carried out under DIVALIKE+J displaying the higher log likelihood values, lower AIC scores (except for tree 4) and very high AIC weights. There is no such pattern for the DEC and DEC+J models. None of the five MPTs showed a significant difference in model performance between the two. As such, BAYAREALIKE+J, DIVALIKE+J and both DEC and DEC+J were considered for further interpretation.
### Time-stratified analysis

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Table 4.5: Statistical values for time-stratified BGB analysis. Log Likelihood (LnL), Akaike scores (AIC), Akaike weights (AIC weight) and p-values comparing the models for each of the five MPTs (originally from analysis IV, dated with FBD).
### Distance-based analysis

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Table 4.6: Statistical values for distance-based BGB analysis. Log Likelihood (LnL), Akaike scores (AIC), Akaike weights (AIC weight) and p-values comparing the models for each of the five MPTs (originally from analysis IV, dated with FBD).
**Distance-based analysis**

Similarly to the unconstrained analysis, data analysed under +J models yielded significantly better results (p < 0.0001, higher log likelihood and Akaike scores less than 85 points of the analyses without +J) compared to analyses without founder event speciation. DEC+J yielded the highest log likelihood and lowest AIC scores (Table 4.6). For further results evaluation and discussion, DEC+J, DIVALIKE+J and BAYAREALIKE+J were chosen.

**CSR**

For all five MPTs the five different runs coalesced on the same mean coordinates for each MPT. In addition, there was no significant difference between the mean coordinates obtained for each comparable node in the different trees. However, the confidence interval on the coordinates for each node was substantial. Older nodes closer to the tree root generally showed larger confidence intervals (e.g. between N15 W30 and N11 W35 for the origin of Neosuchia) than younger nodes (e.g. S2 W54 and S5 W58 for Caimaninae).

**Ancestral area estimation**

Table 4.8 shows the degree of congruence in results between different methods of ancestral area reconstruction for the major neosuchian clades. Table 4.7 shows the reconstructed ancestral areas for each major neosuchian clade for all the relevant analyses.

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<td>Eusuchia</td>
<td>northern Europe</td>
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<tr>
<td>Tethysuchia</td>
<td>western Asia</td>
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<tr>
<td>Goniopholididae</td>
<td>middle North America</td>
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<td>Clade</td>
<td>Analysis</td>
</tr>
<tr>
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<td>----------------------------------------------</td>
</tr>
<tr>
<td>'derived' Goniopholididae</td>
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<tr>
<td>Crocodylia</td>
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<td>Gavialoidea</td>
<td>western border of Europe</td>
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<tr>
<td>Gavialinae</td>
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<td>Brevirostres</td>
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<tr>
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</tr>
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<td>Crocodylidae</td>
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</tr>
<tr>
<td>Crocodylinae</td>
<td>border of Europe &amp; Asia</td>
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</tr>
<tr>
<td>Globidonta</td>
<td>northern North America</td>
</tr>
<tr>
<td>Diplocynodontinae +</td>
<td>northern North America</td>
</tr>
<tr>
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</tr>
<tr>
<td>Diplocynodontinae</td>
<td>western Europe</td>
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<td>Caimaninae</td>
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**Unconstrained BioGeoBEARS**

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<td>Tethysuchia</td>
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<td>'derived' Goniopholididae</td>
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<td>North America</td>
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<tr>
<td>Diplocynodontinae +</td>
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<td>North America</td>
<td>North America</td>
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<tr>
<td><em>Leidyosuchus</em></td>
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<tr>
<td>Diplocynodontinae</td>
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<td>Europe</td>
<td>Europe</td>
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<tr>
<td>Alligatoroidea</td>
<td>North America</td>
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**Time-stratified BioGeoBEARS**

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**Distance-based BioGeoBEARS**

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<td>North America</td>
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<tr>
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<td>Africa</td>
<td>Africa</td>
</tr>
<tr>
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<td>North America</td>
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<td>Africa</td>
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</table>

Table 4.7: The geographical areas suggested as the origination areas for each of the major neosuchian clades. '/' between areas denotes different results yielded by MPTs. '&' denotes combined areas suggested by BGB as ancestral area.

**Neosuchia**

Estimates for the ancestral area of Neosuchia vary considerably between different reconstruction methods (Table 4.8). Whilst CSR indicates North America as the possible area of origin, unconstrained BGB suggests either Africa or Europe as the more likely ancestral area (depending on the source tree), which is also identified in the time-stratified (European area of origin) and distance-based (Africa/Europe or Europe) BGB analyses. All three BGB analyses, however, suggest a subsequent migration to Europe (if the origin point is in Africa) based on the ancestral area reconstructions of the subsequent nodes within Neosuchia. From Europe, dispersal occurred to North America and back into
Africa, with a large degree of interchange between the three of them until the emergence of Eusuchia.

**Eusuchia**

The results for eusuchian ancestral areas are limited to only two areas in contrast to the three for Neosuchia (Table 4.8). CRS and unconstrained BGB both suggest Europe as the ancestral area for this clade (northern Europe in the case of CRS). Time-stratified BGB suggests a joint origin in North America and Europe whereas distance-based BGB places the origin in North America. Even where Europe is suggested as the area of origin, taxa are postulated to have migrated to North America before subsequent radiation of the three major eusuchian families, based on the estimated ancestral areas for the other eusuchian nodes.

**Tethysuchia**

Here, Africa is most commonly suggested as the ancestral area for Tethysuchia (Table 4.7). The exceptions are CSR (western Asia), DIVALIKE+J and BAYARE-ALIKE+J in unconstrained BGB (North America) and DEC in unconstrained BGB (Europe).

**Goniopholididae**

All analyses estimated North America as the ancestral area for both Goniopholididae and 'derived' Goniopholididae (*Anteophthalmus*, *Amphicotylus* and *Goniopholis*). The most recent common ancestor of *Anteophthalmosuchus* and *Goniopholis* migrated to Europe where the remaining 'derived' Goniopholididae diversified.

**Crocodylia**

Results are congruent between CRS and BGB. CRS recovered the ancestral area of Crocodylia as the border between Europe and North America at
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<th>Clade</th>
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<th>Neosuchia</th>
<th>Eusuchia</th>
<th>Tethysuchia</th>
<th>Goniopholididae</th>
<th>'derived' Goniopholididae</th>
<th>Crocodylia</th>
<th>Gavialoidea</th>
<th>Gavialinae</th>
<th>Brevirostres</th>
<th>Crocodyloidea</th>
<th>Crocodylidae</th>
<th>Crocodylinae</th>
<th>Tomistominae</th>
<th>Globidonta</th>
<th>Diplocynodontinae +Leidyosuchus</th>
<th>Diplocynodontinae</th>
<th>Alligatoroidea</th>
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**Table 4.8:** Summary of the reconstructed ancestral areas for each of the major neosuchian clades, demonstrating the congruence between the different methods. CSR: continuous space reconstruction; uBGB: unconstrained BioGeoBEARS; tBGB: time-stratified BioGeoBEARS; dBGB: distance-based BioGeoBEARS
120mya. The BGB analyses estimated either North America (unconstrained, distance-based and DiVALIKE+J in time-stratified analysis) or North America and Europe (in all other time-stratified analyses) as the ancestral area for Crocodylia, with the subsequent spread of taxa across North America from which the other major clades evolved (Table 4.7).

**Gavialoidea**

Although the majority of analyses (all distance-based and unconstrained BGB analyses) place the origin of Gavialoidea in North America, CRS and the time-stratified BGB analyses identify different ancestral areas. CRS estimates the origin of Gavialoidea at the western border of Europe, whereas the time-stratified analysis suggests the broad area of Africa, Europe and North America. In contrast, Gavialinae is shown to have originated either in Africa (unconstrained and distance-based BGB) or in a combination of Africa and Europe or Asia (time-stratified BGB, CSR). Each ancestral area estimation postulates several different dispersal events into Asia for Gavialinae. However, they differ on whether the final dispersal of *Gavialis* into India took place via a mainland Asia route or via Africa and Madagascar.

**Crocodyloidea/Crocodylidae/Crocodylinae**

Reconstructing the ancestral area of Crocodyloidea and its constituent subclades yields vastly different results depending upon the method used (Table 4.8), although, despite the different ancestral area estimations, there is agreement that there were a number of migrations between Africa and Asia during the diversification of the different *Crocodylus* species.

CSR suggests an origin in the border area between North America and Europe and a subsequent expansion eastwards to Europe and Asia (with Crocodylidae originating in northern Europe and Crocodylinae at the border between Europe and Asia). Conversely, crocodyloid origins are generally placed
in North America (or North America + Asia, as well as North America + Europe + Asia in the time-stratified analysis). Crocodylidae are postulated to have emerged either from North America (DEC+J, unconstrained BGB), Europe (DIVALELIKE+J and BAYAREALIKE+J, unconstrained BGB, all distance-based BGB analyses) or a combination of Asia, Africa, Europe and North America (time-stratified BGB). After the divergence of Tomistominae (see below), the common ancestor of Crocodylinae was reconstructed as most likely in Africa (unconstrained and distance-based BGB), North America and Africa (BAYAREALIKE+J in time-stratified BGB) or Asia and Europe (all other time-stratified BGB analyses).

**Tomistominae**

Similarly to Crocodylidae, there is no clear consensus on the ancestral area reconstruction of Tomistominae. Suggested areas are all in the northern hemisphere and include a combination of, or the border of, Europe + North America (CSR, DEC+J in unconstrained BGB), Europe (remaining unconstrained BGB analyses, DIVALELIKE+J in time-stratified BGB, distance-based BGB), Asia + Europe (DEC and DEC+J in time-stratified BGB), and Europe, North America + Africa (BAYAREALIKE+J in time-stratified BGB) (Table 4.7). No consensus is reached in terms of the subsequent tomistomine dispersal routes, although most analyses suggest dispersal between Europe, Asia and Africa.

**Diplocynodontinae**

There is a marked difference in origination areas depending on whether *Leidyosuchus* is included as part of Diplocynodontinae as suggested by the trees used in this study (Table 4.8). Excluding *Leidyosuchus*, all analyses suggest Europe (western Europe in particular in the case of CSR) as the ancestral area for Diplocynodontinae. However, by adding *Leidyosuchus* there is less consensus between different reconstructions. Most analyses (CSR, unconstrained and
distance-based BGB) place the origin in North America. Time-stratified BGB yields slightly different results, indicating several combinations of North America, Asia, and Europe as areas of origin. In all cases, however, diplocynodont ancestors dispersed to Europe where the main diversification of the clade took place.

**Alligatoroidea**

All analyses suggest North America as the ancestral area for Alligatoroidea (Table 4.8), which likely seeded several groups into Asia, Europe and South America.

**Caimaninae**

All BGB analyses in this study estimate South America as the point of origin for Caimaninae, usually after an invasion from North America. CSR supports this finding as the ancestral area reconstruction yielded palaeocoordinates situated directly at the border between North America and South America (Table 4.8).

### 4.5 Discussion

Ancestral area estimations for Neosuchia using both BGB and CSR yielded a number of congruent results, however there were also differences, with several implications both regarding the choice of methodology and neosuchian dispersal patterns. With regards to BioGeoBEARS, analyses using the unconstrained and distance-based algorithms often yielded similar results, whereas the time-stratified model estimated different ancestral areas. In many instances the results of the distance-based analyses are mostly congruent with previously suggested hypotheses of neosuchian biogeography. These analyses allow for marine dispersal routes between land masses, with dispersal probability decreasing in correlation with increased marine distance. The unconstrained BGB analyses treat dispersal across marine and terrestrial habitats with the
same probability. This congruence between the unconstrained and distance-based BioGeoBEARS analyses, as well as with previous hypotheses, points to transoceanic dispersal playing a substantial role in neosuchian biogeography, unlike in the scenarios suggested by the regular time-stratified analysis.

Findings from the CSR analysis are congruent with some of the BGB results, especially the time-stratified BGB analysis (e.g. for Caimaninae, Crocodylia and Goniopholididae), but yield completely different ancestral areas for others (e.g. Tethysuchia). A problem with CSR is the absence of a method to incorporate temperature gradients and unsuitable habitats into ancestral area estimation, since the distribution of neosuchian taxa is known to be strongly influenced by temperature and climate (Markwick, 1998; Franca et al., 2014; Green et al., 2014; Hastings et al., 2014; Mannion et al., 2015). Whilst this is also true for BGB, temperature can at least be partially accounted for in analyses other than unconstrained, e.g. by disallowing dispersal routes in high latitudes.

Except for DEC and DEC+J under the time-stratified method, the models that account for founder events always proved significantly better in explaining the geographical patterns observed in the data. No previous studies in neosuchian biogeography have thus far placed great importance on founder event speciation, but have underlined the importance of vicariance instead (Turner, 2004; Puértolas et al., 2011).

The evidence for vicariance in neosuchian evolutions is less clear in the results of this study, as the data is explained equally well by DIVALIKE+J (allowing for a substantial degree of vicariance) and BAYAREALIKE+J (not taking vicariance into account) models. Substantial differences in the estimated ancestral areas under the two models, however, are observed only in the crocodyloid superfamily under the time-stratified BGB analyses. Therefore, whilst vicariance does play a role in neosuchian biogeography, it is less important than that of founder event speciation, especially when transoceanic dispersal is possible.
Figure 4.1: The most likely ancestral areas of Neosuchia, based on Table 4.7. Maps modelled using the Matthews et al. (2016) models in GPlates Portal Paleomap maker (Müller et al., 2016).
Neosuchia

There have been no studies that directly addressed the geographic origin of Neosuchia. The slightly different positions of basal neosuchian taxa between the MPTs complicate the analysis and lead to several areas of origin being reconstructed, ranging from North America to Africa to Europe. The ancestral area reconstruction is complicated further by the uncertain branching order of taxa at the base of Neosuchia in the trees obtained herein. Crocodylus depressifrons is resolved in various positions, as are several ‘rogue’ tethysuchian taxa such as Terminonaris and Hyposaurus (Fig. 2.3). Their positions and areas of origin greatly influence the ancestral area reconstructed for Neosuchia as a whole.

The dated trees used here place the emergence of Neosuchia at 220 mya, during the Late Triassic. At this time, all of the continents were connected in some form (Torsvik et al., 2008; Landis, 2017). This high level of interconnectedness seems to have facilitated numerous migrations in early neosuchian history as suggested by all analyses. Most of these dispersal events took place between Europe, Africa and North America, which remained connected until shortly before the suggested divergence date for Eusuchia, around 140 mya (Poropat et al., 2016; Landis, 2017).

Irrespective of the exact geographic point of origin, according to the ancestral areas reconstructed for the other neosuchian nodes, Neosuchia seem to have dispersed to Europe first and from there migrated to North America and back to Africa (around 200 mya) (Fig. 4.1). Africa is commonly reconstructed as the area of origin for Tethysuchia (see below and Young et al. 2016). The results also point to further dispersals within North America and then Europe in the latter part of early neosuchian history, 190–150 mya. The North American populations gave rise to Goniopholididae around 190 mya (see below) before the emergence of Eusuchia, 50 Myr later.
Eusuchia

The geographic origin of Eusuchia is generally regarded as unclear (Salisbury et al., 2006), however the findings of the current study all place the ancestral area of this group in either North America or Europe (Table 4.7). At the time of the proposed divergence date (140 mya according to the newly dated FBD tree), a potential connection between Europe and North America was still present and might have been especially relevant for those eusuchians able to cross open water (Taplin & Grigg, 1989). The warm Mesozoic climate provided an excellent and diverse habitat for eusuchians around the Tethyan Sea margins (Holliday & Gardner, 2012; Puértolas-Pascual et al., 2015) and made dispersal even at higher, now temperate, latitudes possible.

In addition to their origin in the region of North America and Europe, the results from this study support North America as the point of origin for most ancestral eusuchian taxa and nodes until 100 mya (Fig. 4.3). By then the three major eusuchian clades — Crocodyloidea, Alligatroidea and Gavialoidea — as well as clades closer to the eusuchian origin such as Borealosuchus (North American) and Planocraniiidae (North American and Asian) had diverged.

Tethysuchia

The majority of analyses in this study support the traditional view that Tethysuchia (especially Dyrosauridae) originated in Africa (Barbosa et al., 2008; Jouve et al., 2008a; Hastings et al., 2014; Young et al., 2016) where their diversification took place (Fig. 4.1). Although not included within the phylogenies here, there are a number of early Paleocene South American dyrosaurid taxa, such as Guarinisuchus munizi (Barbosa et al., 2008) and several species especially amongst the Pholidosauridae that have been found in Europe and North America (De Andrade et al., 2011), although these are unlikely to change to ancestral area estimations in the future due to the strong capabilities for transoceanic disper-
sal within Tethysuchia (see below). Their close relation to African dyrosaurids provides evidence for direct transoceanic dispersal between Africa and South America during the Cretaceous (Barbosa et al., 2008; Hastings et al., 2010), despite the hypothesis that more basal dyrosaurid forms likely preferred fresh or brackish water (Martin et al., 2016b; Young et al., 2016). However, a high number of tethysuchian and especially dyrosaurid specimens have been found in marine deposits (Khosla et al., 2009; Young et al., 2014), further supporting transoceanic dispersal routes for Tethysuchia during the latter part of their evolutionary history.

**Goniopholididae**

The findings of this study are in agreement with previous work that found that Goniopholididae originated in North America around 190 mya (De Andrade et al., 2011; Halliday et al., 2013; Martin et al., 2016a) where they subsequently diversified (Table 4.8). In addition, several dispersal events are postulated to have taken place between the then still closely connected continents of North America and Europe (Vectisuchus and Nannosuchus), as well as Asia (Sunosuchus), probably via a tenuous connection to Europe (Westermann, 2005; Landis, 2017) since most goniopholidid species are found in fresh- or brackish water deposits (Buffetaut & Ingavat, 1980; Buscalioni & Fregenal-Martinez, 2006; Ristevski et al., 2018).

Following the goniopholidid radiation in North America, dispersal occurred to Europe around 160 mya where the majority of the most ‘derived’ goniopholidids (Anteophthalmosuchus and Goniopholis) occurred (Fig. 4.1). This scenario concurs with previous studies (De Andrade et al., 2011; Martin et al., 2016a).

**Crocodylia**

Although there are slight differences between the findings in this study, all estimated ancestral areas for Crocodylia are located within either North America,
Europe, or both, at approximately 120 mya. This is congruent with Salisbury et al. (2006) who postulated a Laurasian origin for Crocodylia and Holliday & Gardner (2012) who placed their origin in the area around the Tethys Sea in Europe and northern Africa.

According to the analyses in this study, the dispersal events leading to the diversification of the three main crocodylian clades (Gavialoidea, Crocodyloidea and Alligatoroidea), 130–100 mya, had their origin in North America (Figs. 4.3 and 4.2), providing further support for potential trans-atlantic interchanges and an increased degree of saltwater tolerance in the earliest diverging eusuchian taxa and ancestors. This faunal exchange of Crocodylia between Europe and North America has been proposed previously (Martin & Delfino, 2010).

Gavialoidea

The biogeographic history of Gavialoidea has been regarded as complex (Vélez-Juarbe et al., 2007; Jouve et al., 2008b) and there is no definite consensus about their origin, as also reflected the results of this study. From 90 mya (the divergence date for Gavialoidea obtained here), possible connections between Europe, Africa and North America (or at least short distances in terms of sea-ways) did exist (Sanmartin et al., 2001; Csiki-Sava et al., 2015), making potential dispersal routes between the three areas possible as indicated by the results presented in this study. It is probable that Gavialoidea originated somewhere in the region of these three continents (Fig. 4.3).

There is evidence that older gavialoid taxa were saltwater tolerant and capable of transoceanic dispersal (Brochu, 2003; Delfino & Vos, 2010). This led to at least one dispersal event to South America from Africa (Vélez-Juarbe et al., 2007; Jouve et al., 2008b), although only one South American gavialoid, Piscogavialis, is represented in this study. It has been hypothesised that the Asian gavialoids resulted from a second transoceanic dispersal event from South America to Asia (Jouve et al., 2008b), although no evidence can be found for
Figure 4.2: The most likely ancestral areas of Crocodyloidea, based on Table 4.7. Maps modelled using the Matthews et al. (2016) models in GPlates Portal Paleomap maker (Müller et al., 2016).

In comparison with Gavialoidea, the potential ancestral areas of Gavialinae were probably located further west, with Africa, Europe and Asia being suggested here. The dated trees used in this study provide a divergence date of around 50 mya for Gavialinae, a time at which the Indian subcontinent was separate from Africa and had begun to join with Asia (Ali & Krause, 2011). The results show two hypotheses for the route by which *Gavialis* arrived in India: either via transoceanic dispersal from Africa and/or Madagascar or via mainland Asia (most likely via fluvial drainages as described in Martin et al. (2012)), which emerges as the more likely scenario due to the gavialine divergence age estimates.
Crocodyloidea/Crocodylidae/Crocodylinae

As with Gavialoidea, the findings reconstruct any combination of North America and Europe as potential ancestral areas for Crocodyloidea, with Asia added in several models (Table 4.7). All three areas were potentially connected until 100 mya (Sanmartin et al., 2001; Baraboshkin et al., 2003), the divergence date obtained for Crocodyloidea based on the trees herein, making an accurate ancestral area estimation more difficult.

Complications occur with Crocodylidae: the results of the analyses in this study cover almost every continent as the potential ancestral area for Crocodylidae, except South America, Australia and India. This is mirrored by the potential ancestral areas of Crocodylinae which are estimated as Africa, North America or Europe/Asia.

The findings of this study indicate multiple dispersal events, especially when transoceanic dispersal is allowed (Fig. 4.2). This differs from previous studies which find two completely separate Crocodylus groups for the Indopacific and the Americas Meganathan et al. (2010) or the clear Australasian origin for crocodylids as reported in Oaks (2011), which are likely due to differences in topology and the absence of fossil taxa in these molecular studies. There is a high probability that early crocodylids were saltwater tolerant (Brochu, 2003, 2007), making trans-marine dispersal very likely, as proposed here. Trans-Atlantic dispersal and a re-invasion of Africa from the neotropics for Crocodylus has been suggested several times, on the basis of both molecular and morphological studies (Brochu, 2007; Meredith et al., 2011; Oaks, 2011).

The ancestral area for Crocodylus is, however, still unclear. The position of Crocodylus depressifrons, an ambiguous crocodyline from Africa that may belong to Asiatosuchus (Delfino & Smith, 2009), causes most analyses that allow transoceanic dispersal to reconstruct Africa as one of the ancestral areas for the genus. By excluding C. depressifrons, a European/Asian origin around 80
mya is much more likely. The results here indicate that this origin was followed by *Crocodylus* colonising South America and Africa, around the K/Pg-boundary (Fig. 4.2).

**Tomistominae**

Although multiple ancestral areas for Tomistominae are suggested in this study, the majority of analyses (especially distance-based and unconstrained BGB that allowed transoceanic dispersal) reconstruct Europe as the area of origin sometime around the K/Pg-boundary (Table 4.8). Early tomistomines were probably highly saltwater tolerant (*Jouve et al.*, 2015) and thus capable of transmarine dispersal. The Tethys Sea has been suggested as the area of origin for Tomistominae by previous studies (*Piras, 2007; Jouve et al., 2015*). From this region, dispersal is suggested to have occurred into Africa, Asia and, potentially, South and North America (*Piras, 2007*) 80–30 mya until the ranges contracted again to the current Asian distribution of *Tomistoma* (Fig. 4.2).

**Diplocynodontinae**

Very little previous work has been conducted on diplocynodont origins. The results of this study concur with those of *Martin et al.* (2014) that Diplocynodontinae are probably of North American origin and dispersed from there to Europe. If *Leidyosuchus* is included within Diplocynodontinae, those analyses allowing for transoceanic dispersal (CSR, unconstrained and distance-based BGB) still postulate North America as the area of origin (Fig. 4.3). Asia and Europe also become potential ancestral areas if sea barriers played a more significant role (Table 4.7).

**Alligatoroidea**

The biogeographic origins of Alligatoroidea have been much debated (e.g. *Martin & Buffetaut 2008* and *Martin & Delfino 2010*). Most studies find the ancestral
Figure 4.3: The most likely ancestral areas of Eusuchia, based on Table 4.7. Maps modelled using the Matthews et al. (2016) models in GPlates Portal Paleomap maker (Müller et al., 2016).
area as either Europe (Martin, 2007) or North America (Martin & Delfino, 2010). However, all of the analyses here yielded the same result, estimating North America as the ancestral area for most Alligatoidea, with occasional dispersals to Europe and Asia (Table 4.8) during 100–60 mya (Fig. 4.3). This is similar to the scenario suggested by Puértolas-Pascual et al. (2016), although the early European alligatoroid Acynosodon iberoccticatus is not included in the phylogeny used here. There is no indication for multiple invasions of alligatoroids into South America from North America as postulated by Brochu (1999). However, this could also be due to the low number of South American alligatoroid species sampled outside Caimaninae and the non-monophyly of Alligatoridae that is consistently found in the MPTs obtained during this study.

The main problem in alligatoroid biogeography is the unknown degree of saltwater tolerance in extinct forms. Extant species of Alligator are much less tolerant than modern crocodyloids and therefore their distributions are more restricted, and they display higher degrees of endemism (Brochu, 1999, 2003). However, as with the saltwater tolerance of basal eusuchians, gavialoids and crocodyloids (see above), it can be assumed that the most basal alligatoroids were potentially capable of transmarine dispersal as well, making at least one dispersal event to Europe feasible.

Caimaninae

All the analyses in this study suggest South America as the area of origin for Caimaininae (Fig. 4.3), probably after their dispersal from North America via the potential North-South America connection that was present during the Late Cretaceous (see Hastings et al. (2013); Poropat et al. (2016); Xu et al. (2018) and references therein). In the case of CSR, the area of origin is reconstructed as the border between North and South America. According to the dated MPTs used here, the origination of the caimanin clade took place shortly before the K/Pg-boundary, as evidenced by the discovery of several old caimanin fossils
in South America (Brochu, 2011; Pinheiro et al., 2013). Although no North American caimain species were included in this phylogeny, there is evidence for their presence in North America before the Isthmus of Panama closed more than 10 mya (Brochu & Carbot-Chanona, 2015). This points either to a very early dispersal event via the North-South America land bridge, increased saltwater tolerance of extinct taxa or dispersal via an Eocene island chain (Hastings et al., 2013). Such potential dispersal routes led to a high diversity of Caimainae and other crocodylian species in the Miocene of South America (Scheyer et al., 2013; Salas-Gismondi et al., 2015; Tineo et al., 2015).

4.6 Conclusion

The four different biogeographical models applied here to the phylogenies obtained from Chapter 3 demonstrate that both transoceanic dispersal and founder event speciation were key mechanisms in neosuchian evolution. The main problem with the current analyses was caused by ancestral areas that included geographical regions with mean temperatures that are far below the tolerance levels of neosuchians, which would be biologically unrealistic. In addition, there is no way to incorporate differing degrees of saltwater tolerance into a single reconstruction analysis (e.g. by partitioning the phylogenetic tree for different modes of dispersal). Furthermore, increasing the sampling in the phylogenetic analyses to cover all known geographical areas for each clades would lead to greater accuracy in ancestral area estimations. Finally, incorrectly placed ‘rogue’ taxa might also have led to some erroneous ancestral area relationships.

Although there were differences in the estimated ancestral areas for several neosuchian clades, the results from these four models allow for a tentative synthesis of neosuchian biogeography. A Laurasian origin for Neosuchia is the most likely scenario, with subsequent colonisations of Africa (the area of origin for Tethysuchia), North America (the area of origin for Goniopholidi-
dae and Eusuchia) and Europe. North America subsequently served as the center of dispersal for the other major eusuchian clades. Gavialoidea radiated from Laurasia, whereas the crocodyloid ancestors dispersed from North America to Europe and from there into the rest of the world to achieve their current global distribution within their tolerable temperature range. Similarly, alligatoroids seemed to have dispersed from North America to Europe, South America and Asia.
Chapter 5

Conclusion & Prospectus

5.1 A synthesis of Neosuchian evolution

This study provides a new synthesis of neosuchian phylogeny based on the largest morphological dataset constructed to date, consisting of 569 completely revised and re-scored characters. The resulting phylogenetic trees were dated and used to investigate the biogeographic history of this major clade. A number of key findings of this study included: 1) in addition to the importance of transoceanic dispersal, founder event speciation also played an important role in neosuchian evolution; 2) it was found that Neosuchia evolved during the Late Triassic 200–220 mya in Laurasia; and 3) in addition to several smaller clades, three main clades comprise the majority of neosuchian taxa: Tethysuchia, Goniopholididae and Eusuchia (Fig. 4.1).

The exact phylogenetic relationships within Tethysuchia are still subject to debate, especially with respect to the monophyly of Pholidosauridae, Elosuchidae and Dyrosauridae. However, it is clear that this longirostrine clade is part of Neosuchia but outside Eusuchia and that it originated during the Early Jurassic, about 180 mya, on the African continent. Tethysuchia underwent a long history of evolution until its extinction in the Paleocene, with dispersal from its ancestral origin in Africa to other continents such as South America and the evolution of
several marine forms, especially among the Dyrosauridae.

Goniopholididae is the next clade to diverge from the lineage that ultimately leads to crown-group Crocodylia. In contrast to Tethysuchia, it is composed of mainly freshwater forms. The origins of this clade lie in the North American region during the Early Jurassic, around 190 mya. Until their disappearance in the ‘middle’ Cretaceous, goniopholidids dispersed to Europe and Asia via the land connections between the continents. The phylogenetic reconstruction here confirmed a ‘core’ group of the most ‘derived’/youngest goniopholidids formed by a European and North American cluster of species that originated around 160 mya: Amphicotylus, Anteophthalmosuchus and Goniopholis.

Several smaller neosuchian families, such as Susisuchidae, Bernissartiidae and Atoposauridae, were represented by only one taxon each in the phylogenies presented here, leading to uncertain placements in the phylogenetic trees, and more work is needed on these groups in the future.

Eusuchia, by far the largest neosuchian clade, which also contains all extant taxa, originated around 140 mya in the North American/European region. The results from the biogeographic analyses in this study show that the ancestors of the three major eusuchian clades (Crocodyloidea, Gavialoidea and Alligatoroidea) all dispersed from North America to the ancestral areas of these superfamilies. Two additional groups are resolved in the phylogenetic trees here as part of Eusuchia: Planocraniidae and Borealsuchus, which emerge as early diverging eusuchians (Fig. 4.3).

Gavialoidea is the sister clade to Brevirostres, which is composed of Alligatoroidea (Globidonta+Diplocynodontinae) and Crocodyloidea. As in the results of previous morphological analyses, Gavialoidea is resolved as its own superfamily that is separate from a second longirostrine eusuchian clade, Tomistominae, although basal tomistomines and gavialoids have been resolved as members of both groups depending on the tree reconstruction methods used here. Gavialoidea emerged in the early Late Cretaceous, about 100 mya in the ad-
jacent and tentatively connected region of Europe, Africa and North America. Due to the high degree of saltwater tolerance inferred for ancient gavialoids, a number of transoceanic dispersal events are likely, mainly to South America and Asia. Gavialinae, the subfamily containing the extant gharial, originated after the K/Pg-boundary, ca. 50 mya, either in Asia/Europe or Africa. *Gavialis* dispersed into its current habitat of India probably via mainland Asia after the collision of the Indian subcontinent and Pakistan.

The geographical origins of Crocodyloidea are less clearly defined, although it most likely took place in the region of North America and Europe, about 100 mya. A group of different taxa consistently emerged as the earliest diverging clade located in North America from around 80 mya onwards, separating Crocodylidae (Tomistominae+Crocodylinae) from Crocodyloidea (Fig. 2.3). This group is composed of several ancient *Crocodylus* species (*C. elliotti, C. cf. clavis* and *C. affinis*), *Prodiplocynodon* and *Brachyuranochampsia*. Crocodyloidea diversified rapidly, with only about 20 Myr between its emergence and that of Crocodylinae (Fig. 4.2).

The ancestral areas of Crocodylidae and Crocodylinae are equally difficult to reconstruct, complicated further by the phylogenies resolved for Crocodylinae that follow no geographic pattern in the evolution of extant crocodile species. Current crocodiles are highly saltwater tolerant, raising the probability of multiple transoceanic dispersal events throughout their 90 million year long history which led to their current global distribution today. Tomistominae, the third major neosuchian longirostrine clade that also contains the extant false gharial, originated potentially before the K/Pg-boundary, around 75 mya, in the region of Europe and the Tethys Ocean. Tomistomines used to be widespread, with species in Africa, Europe, Asia, and South and North America, although their distribution shrank during the last 10 Myr to the current Asian habitat of *T. schlegelii*.

Within Alligatoroidea, Diplocynodontinae is the sister clade of Globidonta (and the latter contains all extant alligator and caiman species). A number
of phylogenetic methods in this study resolved *Leidyosuchus gilmorei* and *L. canadensis* as sister taxa to Diplocynodontinae, changing both the clade’s emergence age (from 75 to 90 mya) and geographical area of origin (from Europe to North America). Although their common alligatoroid ancestor was likely located in North America, diplocynodonts evolved and diversified in Europe before the K/Pg-boundary.

The tree analyses in this study consistently fail to resolve Alligatoridae as the monophyletic sister group of Caimaninae. Instead, while Caimaninae remain monophyletic, all other globidontan species evolved sequentially, forming a pectinate grade of taxa according to the trees here (Figs. 2.3 and 4.3). Their origin lies in North America, about 100 mya, followed by a rapid sequence of branching events until the emergence of Caimaninae just before the K/Pg-boundary. Although extant alligatoroids exhibit very low saltwater tolerance, at least one transoceanic dispersal event between North America and Europe seems to have taken place during their early history in the Late Cretaceous, giving rise to genera such as *Acynodon*. Caimaninae emerged in South America 65–70 mya, with at least one dispersal event to North America before the contraction of their range to South America only.

Although multiple body shapes were acquired throughout neosuchian history, the longirostrine snout, which primarily serves as an adaptation to piscivory, is one of the most striking. Character tracing using the trees from this study revealed that longirostry evolved similarly in all three major neosuchian longirostrine clades (Tethysuchia, Gavialoidea, Tomistominae) through modification of the anterior part of the snout, mainly the elongation of premaxillae, maxillae and nasals. In contrast, each longirostrine clade (and other convergent longirostrine species such as *Mecistops cataphractus*) shows unique modifications of the posterior part of the skull in addition to general changes in the anterior snout region.
5.2 Notes on methodology

Phylogenetic methods

Neosuchia pose a difficult set of species to analyse with standard phylogenetic methods. The main problem lies in the longirostrine snout shape: because of the high superficial similarity in anatomy, longirostrine taxa from different clades often group together in morphological phylogenies. This leads to artificial species associations and low stratigraphic fit of the resulting trees. A number of different strategies were employed here to counteract this effect, including the use of 82 continuous characters, application of Bayesian and parsimony methods, deletion of longirostrine characters and the use of Extended Implied Weighting (EIW) during parsimony analyses.

Although analysing these data with Bayesian Methods yielded no change in the artificial clustering and trees of very low resolution, the combination of continuous characters and EIW with low k-values (k=3) successfully solved the longirostrine issue. In this study it was found that deleting those morphological characters associated with the longirostrine condition, in addition to the use of EIW and continuous characters, yielded the phylogenetic trees with the highest stratigraphic congruence. However, deleting characters associated with a homoplastic condition should be used only sparingly and in extreme cases in general phylogenetic analyses.

Divergence dating methods

Four different dating methods were compared in this study using the newly obtained phylogenetic trees: cal3, Extended Hedman, smoothed Ghost-Lineage-Analysis (sGLA) and the Fossilised Birth-Death-Model (FBD). There was large variation in the origination dates obtained for some neosuchian clades, between both different tree sets and dating methods. Extended Hedman usually deliv-
ered age estimates far older than those of the three other methods, whilst cal3 and FBD consistently yielded the youngest ones.

The different divergence dating methods used showed varying degrees of sensitivity to variations in tree topology. Cal3 is particularly reliant on the oldest known taxon of each clade being part of the tree, but is robust to minor differences to tree topology. Extended Hedman, on the other hand, is influenced more strongly by variations in tree topology and relies heavily on a very high taxon coverage of species analysed across the entire tree. Thus, it is best used for dating trees that contain all or a very high proportion of the known species within a clade. Similarly to Extended Hedman, sGLA is vulnerable to both minor and major differences in tree topology, as well as incomplete taxon sampling of clades. FBD, in contrast, is far less sensitive to major changes in tree topology, but more strongly impacted by minor differences. For Neosuchia, cal3 and FBD appear to yield the most realistic age estimates.

Biogeographic methods

The dated trees in this study were analysed using four different methods: continuous space reconstruction (CSR) and models based on DEC, DIVA and BAYAREA as implemented in BioGeoBEARS (thus called DEC, DIVALIKA and BAYAREALIKE), with added variants for founder-event speciation in all three models. CSR delivered different results than the other three methods in several cases, although all three BioGeoBEARS models agreed on the reconstruction of ancestral areas for the majority of neosuchian clades. In all cases but one, analysing the data in this study using the models incorporating founder event speciation yielded significantly better results.

Three additional modes of analysis were investigated in BioGeoBEARS in order to simulate different levels of saltwater tolerance in Neosuchia: unconstrained, time-stratified and distance-based. Ancestral area reconstruction was more influenced by these three analysis types than the different models, al-
though there was still a substantial overlap between the analytical results.

5.3 Future work

Several future research questions have emerged based on this study.

Firstly, more work can be done on the neosuchian phylogenetic tree itself. One of the most significant shortcomings of this study was the absence of several key taxa from the tree due to logistical reasons. There are several species that should be examined and added to the phylogenetic dataset:

- **Isisfordia duncani**: this Australian taxon is a member of the basal neosuchian or eusuchian family Suisuchidae along with *Susisuchus anatoceps* (Salisbury *et al.*, 2006; Turner & Pritchard, 2015; Leite & Fortier, 2018). In several of the phylogenetic trees presented herein, *Susisuchus* was resolved as the sister taxon of Goniopholididae. Adding *Isisfordia* would help to clarify the position of Suisuchidae within Neosuchia and, in particular, the branching order of basal neosuchian clades.

- **Additional hylaeochampsids**: in this study, long branch attraction likely caused *Hylaeochampsia* and *Bernissartia* to be resolved within the same clade, although the former is a basal eusuchian and the latter a non-eusuchian neosuchian. Adding more taxa from other hylaeochampsids, such as *Iharkutosuchus*, *Pietraroiasuchus* and *Pachycheilosuchus*, would lower the likelihood of long branch attraction occurring and resolve the positions of both Hylaeochampsidae and *Bernissartia* more accurately.

- **Additional species from smaller neosuchian/eusuchian families**: a number of minor families belonging to Neosuchia or Eusuchia were not included in this study. If members of the Atoposauridae (such as *Atoposaurus* or *Montsecosuchus*), Paralligatoridae (such as *Paralligator* or *Batrachomimus*) or Stomatsuchidae (*Laganosuchus*) were added, it would
help to clarify their positions in the neosuchian tree and provide assessment of previous studies’ phylogenies such as Tennant et al. (2016a).

- Mekosuchinae: fossils from this crocodyloid clade subfamily are found exclusively in Australia and the South Pacific (Yates, 2017). None of its members were available for examination during the scoring for this dataset. Adding Mekosuchinae to the dataset would allow for a more accurate assessment of crocodyloid phylogeny and biogeography.

- Alligatorinae: the paraphyly of Alligatorinae found repeatedly in this study is unique. A re-examination of scored alligatorines and addition of more alligatorine species will help to determine the cause and validity of said paraphyly.

In addition to adding more species to the current dataset, the findings regarding the implications of tree building method choices warrant further research. The longirostrine condition in Neosuchia poses an extreme case of homoplasy influencing phylogenetic reconstruction. The vast majority of organisms are less influenced in their phylogenies by such superficially similar homoplastic structures. Thus, it would be of interest to examine the effect that extended implied weighting has on the stratigraphic fit and total runtime of other phylogenies compared to traditional parsimony and Bayesian analyses. The examined datasets should be from a variety of different organisms with varying degrees of homoplasy in order to allow an accurate assessment of the influence of extended implied weighting on phylogenetic reconstruction. In addition, the effects of only three different k-values (k=3, k=6, k=12) on a single dataset were examined by this study. A higher number of different k-values, applied to several datasets with varying degrees of homoplasy, will bring more clarity when considering the influence of k-values on phylogenetic reconstruction.

The selected divergence dating methods have been compared more thoroughly in this study. However, despite a multitude of observational data and
conclusions, there were no statistical tests for objectively comparing the divergence dates obtained and examining whether they were significantly different from each other. In addition, Lee & Yates (2018) provided an intriguing case study of how Bayesian tip-dating coupled with phylogenetic analysis can lead to changes in the phylogeny obtained using Gavialoidea as a case study, a method that could be applied to the entire neosuchian tree.

A deeper comparison between the four different biogeographic methods would also be desirable. In this study, ancestral area reconstruction was applied to the MPTs from only a single tree set. Similarly to the dating study, the methods should be applied to different tree sets to investigate the influence of tree topology on biogeographic reconstructions and evaluate the vulnerability of the different methods to differences in phylogeny. In addition, the biogeographic methods can be more refined with regards to Neosuchia: by manipulating the time-stratified analyses, the importance of land bridges can be assessed and compared with the results of the analyses that allow more liberal transoceanic dispersal.

A final avenue that should be explored is the additional information that can be gleaned by incorporating molecular data into the study. Attempts to produce total evidence trees based on both molecular and morphological data in this study failed, both in Bayesian and parsimony analyses. The trees produced showed either low resolution (Bayesian analyses) and/or displayed strong clustering of longirostrine taxa regardless of their stratigraphic position. However, the molecular trees can still be used to investigate the phylogenetic signal in different areas of neosuchian morphology. Partitioning the character list into different body parts (e.g. anterior skull, braincase, vertebrae, etc.) and looking at the resulting phylogenies could identify those parts of neosuchian anatomy that possess signals that are closer to those recovered by molecular phylogenies. This work would give more of an insight into how homoplasy and the characters from different anatomical regions influence phylogeny and could help to
unravel the reasons for the strong divergences seen between molecular and morphological phylogenies of Neosuchia.
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Chapter 6

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Appendix A

Complete character list
CONTINUOUS CHARACTERS

C1. [Continuous] Premaxilla, width: ratio of maximum width of premaxilla in dorsal view to total skull length in dorsal view (NEW) [excluded in rediscretised version]

Figure 1: Alligator

\textit{sinensis} skull in dorsal view

C2. [Continuous] Premaxilla, width at external nares: ratio of width of premaxilla in dorsal view at anterior dorsal border of external nares to maximum width of premaxilla in dorsal view. [Discrete, excluded in rediscretised version because no cutoff ratio to be found] Premaxilla, width anterior to nares: narrow (0), or broad (1) (after Clark 1994, character 5)

Figure 2: Alligator

\textit{sinensis} snout in dorsal view

[Discrete] Thickness of anterior margin of external nares in relation to external nares: less than half anteroposterior length (0); greater than half anteroposterior length (1) (after Hastings et al 2010, character 3)

Figure 3: Alligator sinensis snout in dorsal view

C4. [Continuous] External nares, proportions: ratio of external naris maximum width in dorsal view to external naris maximum length in dorsal view.

[Discrete] External nares, proportions: circular or keyhole-shaped; shorter than long or equal (0), wider than long (1) (after Brochu 1999, character 161)

Figure 4: Alligator sinensis snout in dorsal view

C5. [Continuous] Incisive foramen, size in relation to premaxillae: ratio of maximum width of foramen in ventral view to maximum width of premaxillae in ventral view. [Discrete] Incisive foramen, size in relation to premaxillae small,
less than half the greatest width of premaxillae (0), large, more than half the greatest width of premaxillae (1) (after Brochu 1999, character 124)

Figure 5: Alligator
sinensis snout in ventral view

C6. [Continuous] Premaxillae, proportions: ratio of maximum width of premaxillae in dorsal view to maximum length of premaxillae in dorsal view. [Discrete] Premaxillae, proportions: less than three times longer than wide (0); three times longer than wide or more than three times longer than wide (1) (modified from Jouve et al. 2008, character 41; in Hastings et al 2010, character 22)

Figure 6: Alligator
sinensis snout in dorsal view

C7. [Continuous] Premaxilla, width: ratio of maximum width of premaxilla in dorsal view to snout width at premaxillary-maxillary suture in dorsal view. [Discrete, excluded in rediscrretised version since it reiterates ch133] Premaxillae, maximum width: less expended than the maximal width of the rostrum at the level of the 4 or 5 alveoli (0), or more expended than the maximal width of the rostrum at the level of the 4 or 5 alveoli (1) (after Jouve 2009, character 341)
C8. [Continuous] Rostrum dimensions at premaxillary-maxillary suture: ratio of height of rostrum at premaxillary-maxillary suture in lateral view to snout width at premaxillary-maxillary suture in dorsal view. [Discrete, Ordered] Rostrum dimensions at premaxillary-maxillary suture: higher than wide (0) (>1), nearly tubular (1), wider than high (2), more than twice as wide than high (3) (after Wu et al. 1997, character 3)

C9. [Continuous] Skull proportions, width of snout and nasals: ratio of maximum width of nasal bones in dorsal view to snout width at premaxillary-maxillary suture in dorsal view [Discrete] Nasal, width in relation to snout: less or nearly as wide as the minimal width of the snout (0), wider than the minimal width of the snout (1) (after Jouve 2009, character 311)
C10. [Continuous] Fourth premaxillary alveolus, relation in size to other alveoli: ratio of maximum diameter of fourth premaxillary alveolus to maximum diameter of the smallest alveolus of remaining premaxillary alveoli. [Discrete, excluded in rediscretised version because all character scores the same:] Fourth premaxillary alveolus, relation in size to other alveoli: enlarged or similar in size to first and second alveoli (0); reduced relative to all other premaxillary alveoli (1) (modified from Hastings 2010, character 17)

Figure 10: *Alligator sinensis* snout in ventral view

C11. [Continuous] Premaxilla and maxilla, proportion in comparison to skull: ratio of distance from maxilla-jugal suture, most ventral point in lateral view to posteriormost end of skull in lateral view to distance from most anterior point of rostrum contour to most ventral point of maxilla-jugal suture in lateral view. [Discrete] Premaxilla and maxilla, proportion in comparison to skull in lateral view: premaxilla-maxilla portion longer than remainder of skull (0) or shorter than remainder of skull (1) (after Wu et al. 1997, character 111)
Figure 11:

Alligator

sinensis skull

in left lateral view

C12. [Continuous] Maxilla, number of teeth per tooth row. [Discrete] Maxilla, number of teeth per tooth row: eight or more teeth (0), seven or fewer teeth (1) (after Wu & Sues, 1996, character 30)

C13. [Continuous] Largest maxillary alveolus, number of tooth. [Discrete] Largest maxillary alveolus, number of tooth: #3 (0), #4 (1), #5 (2), #4 and #5 are same size (3) (after Norell 1988, character 1, modified in Brochu 1999, character 89)

C14. [Continuous] Maxillary alveoli, size in relation to maxilla: ratio of maximum diameter of largest maxillary alveolus to maximum width of one maxillary bone on palatal surface in ventral view. [Discrete, excluded in rediscretised version because no reasonable cutoff ratio could be found] Maxillary tooth, size relative to maxillary palatal surface in palatal view: proportionally small teeth, occupying only marginal portion of ventral surface of maxilla (0), or proportionally well developed teeth, occupying large area of maxillary palatal surface (1) (after Andrade & Bertini 2008, in Montefeltro et al. 2013, character 373)
C15. [Continuous] Antorbital fenestra, size in relation to orbit: ratio of maximum antorbital fenestra length to maximum orbit length. [Discrete, Ordered] Antorbital fenestra, size in relation to orbit: as large as orbit (0), about half the diameter of the orbit (1), much smaller than the orbit (2) (after Clark 1994, character 67)

C16. [Continuous] Skull proportions, snout length: ratio of length of snout from most anterior point of orbit to most anterior point of rostrum in dorsal view to total skull length in dorsal view. [Discrete] Skull proportions, snout length: snout longer than remainder of skull (0), snout same length or shorter than remainder of skull (1) (after Wu & Sues 1996, character 195)
C17. [Continuous] Nasal, proportions: ratio of length of lacrimal-nasal contact to length of prefrontal-nasal contact. [Discrete] Nasal, proportions of length of lacrimal-nasal contact to length of prefrontal-nasal contact: less or equal (0); lacrimal-nasal contact longer (1) (after Jouve et al. 2005 & 2008, character 12, modified in Hastings et al. 2010, character 35)

C18. [Continuous] Lacrimal and prefrontal, dimensions: ratio of length of lacrimal to length of prefrontal. [Discrete, Ordered] Lacrimal and prefrontal, dimensions: Lacrimal longer than prefrontal (0), lacrimal and prefrontal both elongate and nearly the same length (1), prefrontal longer than lachrymal (2) (after Norell 1988, character 7, modified in Brochu 1999, character 117)

Figure 14:
Caiman latirostris
skull in dorsal view

C19. [Continuous] Lacrimal, length in relation to alveoli, maxillary alveolus count of posterior extension. [Discrete] Lacrimal, extension in relation to maxillary alveoli: only to posterior 1/3 maxillary alveoli (0); to anterior 2/3 alveoli (1) (after Hastings et al. 2010, character 34)
C20. [Continuous] Prefrontals, proportions anterior to orbits: maximum width of prefrontal anterior to orbits to prefrontal length anterior to orbits. [Discrete] Prefrontals, proportions anterior to orbitals: elongated (0), short and broad, width vs: length < 0.8 (1) (modified from Gomani 1997, character 4; in Pol & Norell 2004: character 111)

Figure 15:
*Caiman latirostris*
skull in dorsal view


Figure 16:
*Alligator sinensis*
skull in dorsal view

C22. [Continuous] Prefrontal and frontal, proportions: ratio of anterior process of frontal length to length of prefrontal [Discrete excluded in
rediscretised version because no reasonable cutoff ratio could be found]  
(NEW after Jouve et al. 2008)

**Figure 17:**
*Caiman latirostris*
skull in dorsal view

C23. [Continuous] Frontal, proportions of portion anterior to orbits: ratio of length of portion of frontal anterior to orbits to length of portion of lacrimal anterior to orbits. [Discrete] Frontal, proportions of portion anterior to orbits compared to lacrimal: frontal anterior to orbit much shorter than lacrimal (0) or longer than prefrontal, approaching the level of anterior tip of lacrimal anteriorly (1) (after Wu et al. 2001, character 129)

**Figure 18:**
*Caiman latirostris*
skull in dorsal view

C24. [Continuous] Interorbit distance in relation to nasals: ratio of minimum distance between orbits in dorsal view to maximum width of nasal bones in dorsal view. [Discrete] Nasal, width in relation to interorbital distance: narrow, as broad as nasals (0), broader, often twice as broad as nasals (1) (after Clark 1994, character 20)
Figure 19: 
Alligator 
*sinensis* skull 
in dorsal view

C25. [Continuous] Interorbit distance in relation to snout: ratio of minimum distance between orbits in dorsal view to snout width at premaxillary-maxillary suture in dorsal view. [Discrete] Interorbital distance in relation to snout narrow: less wide than the minimal width of snout (at the level of premaxillary-maxillary suture) (0), broad, same width or wider than minimal width of snout (1) (modified from Wu et al. 2001, character 20; in Jouve et al. 2006, character 83)

Figure 20: Alligator 
*sinensis* skull in 
dorsal view
C26. [Continuous] Interorbit distance in relation to skull table: ratio of minimum distance between orbits in dorsal view to maximum width of skull table in dorsal view. [Discrete excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW)

![Figure 21: Alligator *sinensis* skull in dorsal view](image)

C27. [Continuous] Orbit, proportions: ratio of minimum orbit width to maximum orbit length. [Discrete excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW)

![Figure 22: Alligator *sinensis* skull in dorsal view](image)

C28. [Continuous] Orbit, size in relation to skull: ratio of maximum orbit length to total skull length in dorsal view. [Discrete excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW)
C29. [Continuous] Jugal, antorbital vs infraorbital region height: ratio of maximum height of antorbital region of jugal to maximum height of infraorbital region of jugal. [Discrete] Jugal, relation of antorbital and infraorbital region height: equal or lower (0), antorbital region more expanded than infraorbital region of jugal (1) (after Pol 1999, character 144)

C30. [Continuous] Suborbit fenestrae, proportions: ratio of minimum suborbit fenestrae width to maximum suborbit fenestrae length. [Discrete excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW)
**Figure 25:** Alligator *sinensis* skull in ventral view

C31. [Continuous] Suborbit fenestrae, size in relation to orbits: ratio of maximum orbit length to maximum suborbit fenestrae length. [Discrete] Suborbital fenestrae, size in relation to orbits small (0), large, subequal or larger than orbit (1) (after Andrade et al. 2011; in Montefeltro et al. 2013, character 26)

**Figure 26:**

*Alligator sinensis* skull in ventral view

C32. [Continuous] Postorbital bar, position: ratio of distance from intersection of lacrimal-jugal suture with orbit to the middle point of the postorbital bar at the ventral edge of orbit to distance from intersection of lacrimal-jugal suture with orbit to intersection of jugal-quadratojugal with infratemporal fenestra.

[Discrete] Postorbital bar, position in relation to jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2) (after Pol 1999, character 157)
C33. [Continuous] Infratemporal fenestrae, proportions: ratio of medium infratemporal fenestra width to maximum infratemporal fenestra length. [Discrete] Infratemporal fenestrae, proportions: higher than wide or equal (0), anteroposteriorly elongated (1) (after Ortega et al. 2000, character 74)

C34. [Continuous] Supratemporal fenestrae in relation to orbits: ratio of maximum supratemporal fenestra length to maximum orbit length. [Discrete, excluded in rediscrretised version because no reasonable cutoff ratio could be found] Lateral border of orbits located lateral (0) or medial (1) to level of lateral margin of supratemporal fenestra (after Wu et al. 2001, character 130)
C35. [Continuous] Medial jugal foramen, size: ratio of maximum medial jugal foramen diameter to length of jugal margin below orbit & infratemporal fenestrae. [Discrete] Medial jugal foramen, size: small (0), very large, ratio > 0.1 (1) (after Brochu 1999, character 120)

C36. [Continuous] Quadratojugal, length of anterior process along infratemporal bar in dorsolateral view to length of infratemporal bar. [Discrete] Quadratojugal, length of anterior process along infratemporal bar in dorsolateral view: long (ratio > 0.1) (0), modest or absent (0) (after Brochu 1999, character 83)
C37. [Continuous] Skull, position of orbits: ratio of distance from anterior edge of orbits to posteriormost end of skull in dorsal view to total skull length in dorsal view. [Discrete] Skull, position of orbitals: distance from anterior orbital edge to anterior contour of rostrum equal or longer than remainder of skull (0); distance from anterior orbital edge to anterior contour of rostrum shorter than remainder of skull (1) (after Ortega et al. 2000, character 3, modified by Jouve et al. 2006, character 6)

**Figure 31:**

*Alligator sinensis* skull in dorsal view

C38. [Continuous] Skull proportions: ratio of minimum distance between suborbit fenestrae in ventral view to snout width at premaxillary-maxillary suture in dorsal view. [Discrete] Suborbital fenestrae, width between fenestrae compared to minimal width of snout at premaxilla-maxillary suture: width between suborbital fenestra narrower (0) or largely wider (1) (after Jouve 2004, character 106)
C39. [Continuous] Supratemporal fenestra, morphology: angle between medial and anterior margins of supratemporal fossa. [Discrete] Angle between medial and anterior margins of supratemporal fossa: ~90 degrees or greater (0), or ~45 degrees (1) (Gasparini et al. 2006, in Montefeltro et al. 2013, character 98)

C40. [Continuous] Skull table, postorbital and squamosal: ratio of maximum postorbital length in dorsal view to maximum squamosal length in dorsal view. [Discrete] Skull table, postorbital and squamosal: squamosal is longer (0); postorbital is longer or same length (1) (after Ortega et al. 2000, character 33)
C41. [Continuous] Skull table, proportions: ratio of maximum skull table length in dorsal view to maximum skull table width at lateral edge in dorsal view.
[Discrete] Skull table, proportions: wider than long (0), equal or longer than wide (1) (after Wu et al. 2001, character 131)

Figure 35: Alligator sinensis skull in dorsal view

C42. [Continuous] Lateral arches of supratemporal fenestrae, proportions: ratio of minimum lateral arches width to skull table length. [Discrete] Lateral arches of supratemporal fenestrae, proportions: thick (0), thin (1) (modified from Jouve et al. 2005, character 16 and Jouve et al. 2008, character 16; in Hastings et al. 2010, character 11)

Figure 36: Alligator sinensis skull in dorsal view
C43. [Continuous] Skull proportions, width: ratio of snout width at premaxillary-maxillary suture in dorsal view to maximum width of skull table in dorsal view. [Discrete, excluded from rediscretised version because all character scores same] Interorbital space narrow, less wide than the minimal width of snout (at the level of premaxillary-maxillary suture) (0), or broad, wider than minimal width of snout (1) (after Wu et al. 1997, character 20, modified by Jouve et al. 2006, character 83)

![Figure 37: Alligator sinensis skull in dorsal view](image)

C44. [Continuous] Skull proportions, dorsal and ventral surface: ratio of maximum width of skull table in dorsal view to maximum width of ventral skull surface in ventral view. [Discrete] Cranial table, proportions with respect to ventral surface: as wide as ventral portion of skull (0) or narrower than ventral portion (1) (after Wu et al. 1997, character 123)

![Figure 38: Alligator sinensis skull in dorsal and ventral view](image)
C45. [Continuous] Skull proportions, width: ratio of maximum width of skull table in dorsal view to maximum skull width in dorsal view. [Discrete, excluded from rediscretised version because all character scores same] Cranial table wider than long (0) or longer than wide (1). (after Wu et al. 2001, character 131)

Figure 39:
Alligator
sinensis skull in dorsal view

C46. [Continuous] Choanae opening, proportions: ratio of minimum choanae length to maximum choanae width. [Discrete] Choanae opening, proportions: of moderate size, wider than long (0), longer than wide, sometimes more than three times longer than wide (1) (after Wu et al. 1997, character 42 and Tykoski et al. 2002, character 42, modified in Jouve et al. 2006, character 18)

Figure 40:
Alligator sinensis skull in ventral view

C47. [Continuous] Choanae, relation with rest of skull: ratio of maximum choanae width to maximum skull width in dorsal view. [Discrete] Choanae, relation with rest of skull: of moderate size (0), nearly half of maximal skull width (1) (after

**Figure 41:**
*Alligator sinensis*

skull in ventral and dorsal view

C48. [Continuous] Foramen for the internal carotid artery, size: ratio of maximum diameter of foramen for internal carotid artery to maximum diameter of opening for cranial nerves IX-XI. [Discrete] Foramen for the internal carotid artery, size: reduced, similar in size to the openings for cranial nerves IX-XI (0), extremely enlarged (1) (after Jouve 2009, character 336)

C49. [Continuous] Exoccipital, proportion of participation in occipital condyle: ratio of length of exoccipital participating in occipital condyle to length of occipital condyle. [Discrete] Exoccipital, proportion of participation in occipital condyle: slightly (0) or largely (ratio > 0.3) (after Jouve 2004, character 96)

C50. [Continuous] Lateral Eustachian foramina, size in relation to medial one: ratio of maximum diameter of lateral eustachian foramina to maximum diameter of medial eustachian foramina. [Discrete] Lateral Eustachian foramina, size in relation to medial one: smaller (0), same size or larger (1) (after Montefeltro et al. 2011, in Montefeltro et al. 2013 character 275)
C51. [Continuous] Ventrally exposed part of basisphenoid, proportions: ratio of maximum length of ventrally exposed part of basisphenoid to minimum width of ventrally exposed part of basisphenoid. [Discrete] Ventrally exposed part of basisphenoid, proportions wider than long (0), longer than wide (1) (after Jouve 2009, character 325)

C52. [Continuous] Skull proportions: ratio of maximum skull width in dorsal view: ratio of maximum skull length in dorsal view. [Discrete, excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW)

**Figure 42:**

*Alligator sinensis* skull in dorsal view

MANDIBULAR CHARACTERS

[Ch. 53a - EXCLUDED – see main text for details] Anterior portion of mandible, proportions: ratio of mandible width at anterior end in dorsal
view to mandible width close to posterior end of symphysis in dorsal view.

[Discrete] Anterior portion of mandible, proportions: typically exhibits expansion (0); exhibits straight margins without significant lateral expansion (ratio > 0.8) (1) (after Sereno et al. 2001, character 72, modified in Hastings et al. 2010, character 70)

[Ch. 54a - EXCLUDED – see main text for details] Mandibular symphysis, proportions: ratio of maximum height of mandibular symphysis to maximum length of mandibular symphysis. [Discrete, excluded because all character scores the same] Symphysis wider than high (0) or about as wide as high (1) (after Jouve et al. 2005 & 2008, character 17)

C53. [Continuous] Dentary, proportions: ratio of dentary height below fourth alveolus to dentary height in between eleventh and twelfth alveoli in lateral view. [Discrete, excluded in rediscretised version because no reasonable cutoff ratio could be found] (NEW after Pinheiro et al. 2013)

Figure 43: Alligator sinensis mandible in left lateral view

C54. [Continuous] Dentary, proportions between fourth and tenth alveolus: ratio of minimum height of dentary between fourth and tenth alveolus to maximum height of dentary between fourth and tenth alveolus. [Discrete] Dentary, proportions between fourth and tenth alveolus: gently curved (ratio > 0.8) (0), deeply curved (1), linear (2) (after Brochu 1999, character 68)
C55. [Continuous] External mandibular fenestra, orientation: angle of main axis to horizontal plane in lateral view. [Discrete] External mandibular fenestra, orientation of main axis: horizontal (0), main axis inclined, directed anteroventrally-posterodorsally (1) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 305)

C56. [Continuous] External mandibular fenestra, proportions: ratio of minimum width to maximum length. [Discrete] External mandibular fenestra, proportions: anteroposterior axis less than three times long than dorso-ventral axis (0), anteroposterior axis three times long or longer than dorso-ventral axis (1) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 306)

C57. [Continuous] Coronoid, proportions of projections: ratio of length of dorsal anterior projection in medial view to length of ventral projection in medial view.
Coronoid, proportions of projections: dorsal projection longer than ventral (0),
ventral projection longer than dorsal (1) (after Brochu 1999, character 63)

Figure 47: *Alligator sinensis* coronoid in right medial view

POSTCRANIAL CHARACTERS

C58. [Continuous] Proatlas, ventral tubercle size: ratio of width of ventral tubercle of proatlas to width of dorsal crest of proatlas. [Discrete] Proatlas, ventral tubercle size: one-half the width of the dorsal crest (0) or less than one half the width of the dorsal crest (1) (after Brochu 1999, character 1)

C59. [Continuous] Atlas intercentrum, proportions: ratio of maximum width of intercentrum to maximum length of intercentrum. [Discrete] Atlas intercentrum, proportions: broader than long (0), or as long as broad (1) (after Clark 1994, character 89)

C60. [Continuous] Axial hypapophysis, location: ratio of distance from anterior end of axial hypapophysis to anterior end of centrum to distance from posterior end of axial hypapophysis to posterior end of centrum. [Discrete] Axial hypapophysis, location: toward the center of centrum (0), toward the anterior end of centrum (1) (after Brochu 1999, character 6)
C61. [Continuous] Axial neural spine, proportions: ratio of maximum height of axis neural spine to maximum height of axis centrum. [Discrete] Axial neural spine, height: high, subequal to centrum height (0), low, less than half centrum height and nearly horizontal (1) (after Larsson & Sues 2007; in Montefeltro et al. 2013 character 384)


C63. [Continuous] Prezygapophyses of axis, length in relation to anterior edge of neural arch: ratio of maximum length of prezygapophyses of axis to maximum length of anterior edge of neural arch. [Discrete] Prezygapophyses of axis, length in relation to anterior edge of neural arch: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of neural arch (1) (after Pol 1999, character 169)

C64. [Continuous] First postaxial cervical, neural spine proportions: ratio of maximum neural spine height of first postaxial cervical to maximum length of centrum of first postaxial cervical. [Discrete] First postaxial cervical, neural spine proportions: wide, dorsal tip at least half the length of the centrum without the cotyle (0) or narrow, dorsal tip acute and less than half the length of the centrum without the cotyle (1) (after Brochu 1999, character 9)

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C66. [Continuous] Caudal vertebrae, neural arch dimensions: ratio of length of longest centrum of caudals to maximum height of tallest neural arch of caudals. [Discrete] Caudal vertebrae, neural arch dimensions: less than two times the length of centrum (0), or more than two time length of centrum (1) (after Jouve 2009, character 303)

C67. [Continuous] Scapulocoracoid facet anterior to glenoid fossa, proportions: ratio of width at posterior end of scapulocoracoid facet anterior to glenoid fossa to width at anterior end of scapulocoracoid facet anterior to glenoid fossa. [Discrete] Scapulacoracoid facet anterior to glenoid fossa, proportions: uniformly narrow (0) or broad immediately anterior to glenoid fossa (1) (after Brochu 1999, character 25)

C68. [Continuous] Coracoid, length in relation to scapular: ratio of maximum length of coracoid to maximum length of scapular. [Discrete] Coracoid, length in relation to scapular: up to two-thirds of the scapular length (0), or subequal in length to scapula (1) (modified from Clark 1994 and Pol & Norell 2004, character 83)
C69. [Continuous] Ulna, length in relation to humerus: ratio of maximum length of ulna from proximal to distal end to maximum length of humerus from proximal to distal end. [Discrete] Ulna, length in relation to humerus: nearly as long as humerus (0), or more than one-quarter shorter than humerus (1) (after Jouve 2009, character 330)

C70. [Continuous] Ulna, proportions: ratio of maximum width of distal end of ulna to maximum width of proximal end of ulna. [Discrete] Ulna, proportions: distal extremity of the ulna expanded transversely with respect to the long axis of the bone; maximum width equivalent to that of the proximal extremity (0) or proximal extremity of the ulna considerably wider than the distal extremity (1) (after Salisbury et al. 2006, character 173)

C71. [Continuous] Radiale, proportions: ratio of maximum width of radiale at proximal end to maximum length of radiale from proximal to distal end. [Discrete] Radiale, proportions: longer than wide (0); as long as wide (considering its proximal width as reference) (1) (after Ortega et al. 2000, character 127)

Figure 48: right forelimb on Crocodylus cf. clavis
C72. [Continuous] Radiale, proportions: ratio of maximum width of radiale at proximal end to maximum width of radiale at distal end. [Discrete] Radiale: proportions of proximal and distal ends: almost equally expanded (0); proximal head wider than distal one (1) (after Ortega et al. 2000, character 150)

\[ \text{Figure 49:} \]
right forelimb on *Crocodylus cf. clavis*

C73. [Continuous] Radiale, articular surface for the ulna, proportions: ratio of maximum length of articular surface of radiale for ulna from proximal to distal end to maximum length of radiale from proximal to distal end. [Discrete] Radiale, articular surface for the ulna, proportions: short and wide, being up to than 30% of the total length of the radiale (0), or proximodistally elongated, being more than 40% of the total length of the radiale (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 429)

\[ \text{Figure 50:} \]
right forelimb on *Crocodylus cf. clavis*
C74. [Continuous] Ulnare, proportions: ratio of minimum width of ulnare bone shaft to maximum length of ulnare from proximal to distal end. [Discrete, excluded in rediscretised version because no reasonable cutoff ratio could be found] Radiale and ulnare short and massive (0) or elongated (1) (after Wu & Sues, 1996, character 40)

![Figure 51: Right forelimb on Crocodylus cf. clavis](image)

C75. [Continuous] Metacarpals, proportions: ratio of maximum width of shaft of metacarpal I to maximum width of widest metacarpal except I. [Discrete] Metacarpals, proportions of shaft of metacarpal I: as broad as the shaft of other metacarpals (0), or broader than other metacarpals, being the digit I the most robust element of the metacarpus (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 436)

![Figure 52: Right forelimb on Crocodylus cf. clavis](image)
C76. [Continuous] Ilium, anterior process dimensions: ratio of maximum anterior process of ilium length to maximum ilium length. [Discrete] Ilium, anterior process dimensions: prominent (0), virtually absent (1) (adapted from Benton and Clark 1988 and Clark 1994, character 84; in Brochu 1999, character 34)

C77. [Continuous] Supraacetabular crest, proportions: ratio of maximum supraacetabular crest width to maximum supraacetabular crest height. [Discrete] Supraacetabular crest, proportions: narrow (0), broad (1) (after Brochu 1999, character 32)

C78. [Continuous] Postacetabular process of the ilium: ratio of maximum length of postacetabular process from anterior to posterior end to maximum length of acetabulum on ilium. [Discrete] Postacetabular process of the ilium, development: well developed as a distinct process that extends anteroposteriorly at least 60% of the acetabular length (0), or extremely reduced or absent, extending anteroposteriorly not more than 50% of the acetabular length (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 439)

Figure 53: pelvic girdle on Crocodylus sp. in right lateral view
C79. [Continuous] Femur, proportions: ratio of maximum length from proximal articular facet of femur to distal end of fourth trochanter to maximum length of femur. [Discrete] Femur, proportions of maximum length from proximal articular facet of femur to distal end of fourth trochanter to maximum to total length of femur: more than one-third of total femoral length (0); one-third or less of total femoral length (1) (after Ortega et al. 2000, character 161)

C80. [Continuous] Femur, length in proportion to humerus: ratio of maximum length of femur to maximum length of humerus. [Discrete] Humerus, length in proportion to femur: more than two-third (0), nearly two-third (1), or nearly one-third (2) the length of the femur (after Jouve 2009, character 328)

C81. [Continuous] Dorsal osteoderms, proportions: ratio of minimum width of dorsal osteoderms to maximum length of dorsal osteoderms. [Discrete] Dorsal osteoderms, proportions: broader than long (0), equal or longer than broad (1) (Clark 1994, character 95)

C82. [Continuous] Limb bones, length: ratio of maximum length for forelimb to maximum length of hind limb. [Discrete] Limb bones, length: hindlimb much longer than forelimb at maturity (0) forelimb and hindlimb more equal in length at maturity (1) (after Brochu 1999, character 33)
DISCRETE CHARACTERS

Overall skull morphology

C83. Skull, external surface of dorsal cranial bones, structure: smooth or slightly grooved (0), heavily ornamented with deep pits and grooves (1) (after Clark 1994, character 1)

C84. First notch for mandibular occlusion, size in relation to adjacent occlusal spacing: same diameter (0); larger in diameter (1) (after Hastings et al 2010, character 18)

C85. Rostrum, dorsal surface, medial dorsal boss: absent (0); present (1) (after Brochu 1999, character 101)

Figure 54: Medial dorsal boss on Crocodylus rhombifer, left lateral view, (character 85, state 1)

C86. Rostrum, morphology of dorsal contour in lateral view: convex (0); straight (1); concave (2) (after Jouve et al. 2006, character 4) [ORDERED]

C87. Skull, preorbit ridges on dorsal surface: absent (0), reduced (1), very prominent at maturity (2) (after Brochu 1999, character 144) [ORDERED]

C88. Skull, extent of expansion at orbits: gradually (0); abruptly (1) (Clark 1994, character 2)
C89. Skull table surface, slope at maturity: ventrally from sagittal axis (0); planar (1) (after Brochu 1999, character 123)

C90. Posterodorsal margin of the skull roof, morphology in posterior view: dorsally convex (0); almost horizontal (1) (after Jouve et al. 2006, character 110 and Jouve 2009, character 323)

Figure 55: Dorsally convex posterodorsal margin on *Dyrosaurus phosphaticus*, occipital view (character 90, state 0)

C91. Paired foramina located at anterior region of palatal ventral surface (not homologous to maxillo-palatine fenestrae and palate canals): absent (0); present (1) (Montefeltro et al. 2013, character 479)

**Premaxilla**

C92. Premaxillae anterior to nares, morphology: strongly sutured (0), loosely sutured (1), or not in contact (2) (Andrade et al. 2011, in Montefeltro et al. 2013, character 36) [ORDERED]

C93. Premaxillae, extent of participation in dorsal border of external nares: absent (0), present (1) (after Pol & Norell 2004, character 124)

C94. Premaxillae, dorsal projection at anterodorsal margin of external nares at level of suture between right and left premaxillae: absent (0); present (1) (after Jouve 2004, character 3)
Figure 56: Anterodorsal margin of external nares in dorsal view on *Crocodylus rhombifer* (left, character 94, state 0) and *Alligator sinensis* (right, character 94, state 1)

C95. Premaxillae, external nares, orientation: laterally (0), dorsolaterally (1), dorsally (2), anteriorly (3) (after Clark et al. 1994 and Wu et al. 1997, character 6) [UNORDERED]

C96. Premaxillae, external nares, position in dorsal view relative to anterior rostral contour: concealed (0), premaxillary bar separating external nares and anterior rostral contour (1) (after Clark et al. 1994, character 6 and Ortega et al. 2000, character 17)

C97. Premaxillae, external nares, division: by a septum (0), confluent (1) (after Clark 1994, character 66)

C98. Premaxillae, notch at two-thirds the height of the lateral vertical margin of the external nares: absent (0); present (1) (modified from Jouve et al 2006 character 24 (from Pol, 1999, 2003 (135 and 123, respectively) and Brochu 1999, character 142)
C99. Premaxillae, external nares, medial tubercles on posterior margin: absent (0); present (1) (after Hastings et al. 2010, character 2)

C100. Premaxillae, external nares, medial tubercles on posterior margin: dorsal (0); ventral (1) (after Hastings et al. 2010, character 2)

C101. Premaxillae, extent of participation in internarial bar: forming at least the ventral half (0), with less participation (1) (after Clark 1994, character 4)

C102. Premaxillae, perinarial fossa: absent (0); present (1) (after Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 127)

C103. Premaxillae, perinarial fossa, extension: restricted (0), reaching alveolar margin of premaxillae (1) (after Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 128)
C104. Premaxillae, perinarial fossa, extent of posterior margin: not reaching the level of the posterior margin of external nares (0), reaching to or beyond the level of posterior margin of external nares (1) (after Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 129)

C105. Premaxillae, perinarial crests: absent (0), present as well-defined and distinct ridges, cornering the lateral to posterior borders of the naris (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 42)

**Figure 59**: Perinarial crests on *Amphicotylus lucasii*, dorsal view (character 105, state 1)

C106. Postnarial fossa: absent (0); present (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 43)

**Figure 60**: Perinarial crests on *Amphicotylus lucasii*, dorsal view (character 106, state 1)

C107. Premaxillae, small pit posterior to external nares: absent (0); present (1) (NEW)
C108. Premaxillae, dorsal process length: reaches proximal or anterior to second maxillary alveolus (0), further than second but not beyond third maxillary alveolus (1); long, extending beyond third maxillary alveolus (2) (combination of Brochu 1999, character 145 & Hastings et al 2010, character 13)

[ORDERED]

C109. Premaxillae, anteroventral expansion: present (0); absent (1) (after Hastings et al. 2010, character 21)

C110. Premaxillary palate, circular paramedian depressions: absent (0); present (1) (Sereno et al. 2001, character 67)

C111. Premaxillo-maxillary suture, orientation in lateral view: vertical (0); posterodorsally directed (1) (after Jouve et al. 2006, character 32)
C112. Premaxilla-maxilla contact, ventral edge position of premaxilla in relation to ventral edge of maxilla in lateral view: placed almost at same height (0); deeper and anterior dorsal contour of dentary is also strongly concave (1) (after Ortega et al. 2000, character 10)

C113. Premaxilla-maxilla contact, constriction of snout at contact: absent (0), present (1) (after Wu et al. 1997, character 9)

C114. Premaxilla-maxilla, lateral fossa excavating alveolus of last premaxillary tooth: absent (0); present (1) (Larsson & Sues 2007, in Montefeltro et al. 2013, character 205)

**Figure 63:** Lateral fossa at premaxillary-maxillary suture on *Amphicotylus lucasii*, dorsal view (character 114, state 1)

C115. Premaxilla-maxilla contact, lateral opening between maxilla and premaxilla, morphology: laterally open notch (0), narrow slit (1), broad, laterally directed concavity (2), lateral fenestra (3) (after Wu et al. 1997, character 9)

[UNORDERED]

C116. Premaxilla-maxilla contact, two parallel ridges creating recess on lateral wall of premaxillary notch: absent (0), present (1) (NEW)
C117. Premaxillo-maxillary contact, small foramen located on lateral surface of suture (not for largemandibular teeth): absent (0); present (1) (after Pol 1999, character 149 and Ortega et al. 2000, character 13; in Pol & Norell 2004: character 135)

C118. Premaxillo-maxillary contact, ventral opening on ventral edge: absent (0), present (1) (modified from Clark 1994 after Pol & Norell 2004 character 9)

Figure 64: Recess on premaxillary-maxillary suture on *Araripesuchus gomesii*, left dorso-lateral view (character 116, state 1)

Figure 65: Opening on Premaxilla-maxillary contact in dorsal view on *Alligator sinensis* (right, character 118, state 0) and *Crocodylus rhombifer* (left, character 118, state 1)
C119. Premaxillo-maxillary contact, ventral opening on ventral edge, morphology: 
notch (0), large fenestra (1) (modified from Clark 1994 after Pol & Norell 2004 
character 9)

Figure 66: Large fenestra

on premaxillary-maxillary

suture on *Amphicotylus lusci*, dorsal view

(character 119, state 1)

C120. Premaxilla-maxilla suture, morphology in palatal view: projected markedly 
forward (0), projected slightly anteriorly (1), projected posteriorly (2) (Pol 
1999, character 139 and Ortega et al. 2000, character 9 Pol & Norell 2004: 
character 126) [ORDERED]

C121. Premaxillae and maxillae, orientation of external surface: with single plane 
face laterally 90 degrees (0); with ventral region facing laterally and dorsal 
region facing dorsolaterally (1) (Pol & Norell 2004, character 139)

C122. Premaxillo-maxillary contact, morphology of ventral part: straight (0), bowed 
or with one median projection of premaxillae (1), with two or more 
curves/projections of premaxillae (2) (NEW) [ORDERED]
**Figure 67**: Premaxillo-maxillary contact in ventral view on ‘Crocodylus’ affinis (left, character 122, state 0), ‘Crocodylus’ cf. clavis (middle, character 122, state 1) and Leidyosuchus canadiensis (right, character 122, state 2)

C123. Premaxillo-maxillary contact, morphology of premaxillary ventral projections: rounded (0); with sharp tips (1) (NEW)

**Figure 68**: Premaxillo-maxillary contact in ventral view on Leidyosuchus canadiensis (left, character 123, state 0) and Osteolaemus tetrapsis (right, character 123, state 1)

C124. Premaxillae and maxillae: neurovascular foramina, overall distance to the alveolar margin and teeth: ventralmost foramina clearly apart from the alveolar margin, distant to the teeth (0), ventralmost foramina reach area next to the alveolar margin, close to teeth (1) (Andrade & Bertini 2008, in Montefeltro et al. 2013, character 130)

**Maxilla**

C125. Maxillae, inner antero-posterior margins bordering nasal and lacrimal on dorsal surface in dorsal view: not linear (0); linear for anterior 2/3 or less (1); linear for over the anterior 2/3 (2) (after Hastings et al 2010, character 23)

[ORDERED]
Figure 69: Nasal bones in dorsal view on *Theriosuchus pusillus* (left, character 125, state 0), *Goniopholis simus* (middle, character 125, state 1) and *Alligator sinensis* (right, character 125, state 2)

C126. Maxillae, canthi rostrallii: absent or very modest (0); very prominent, significant height difference to remainder of rostrum surface (1) at maturity (Brochu 1999, character 143)

Figure 70: Canthi rostrallii on *Caiman latirostris*, right dorso-lateral view (character 126, state 1)

C127. Maxillae, lateral expansion in dorsal view: absent, lateral margins linear (0); present, lateral margins 'festooned' (1) (modified from Jouve et al. 2008, character 40; in Hastings et al. 2010, character 24)
C128. Maxillae, ventral edge in lateral view: straight or convex (0); sinusoidal (1) (after Ortega et al. 2000, in Montefeltro et al. 2013, character 133)

C129. Maxillae, line of neurovascular foramina, morphology: line of foramina following overall outline of margin (0), strongly-arched line mid-rostrum, ample area of smooth margin ventral to the arched line of foramina (1) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 131)

C130. Maxillae, antero-posteriorly directed longitudinal groove directed along entire length of lateral surface: absent (0), present (1) (NEW)

C131. Maxillae, height of alveolar walls in lateral view: raised relative to ventral surface of the maxillae (0); walls level with ventral surface (1) (after Hastings et al 2010, character 25)
C132. Maxillae, unsculpted region along alveolar margin on lateral surface: absent (0); present (1) (modified from Wu and Sues 1996, character 29; in Pol & Norell 2004, character 106)

C133. Maxillae, large and aligned neurovascular foramina on lateral surface: absent (0); present (1) (after Pol 1999, character 152)

\[\text{Figure 73}: \text{Large and aligned neurovascular foramina on } Araripesuchus gomesii, left dorso-lateral view (character 133, state 1}\]

C134. Maxillae, depression on posterolateral surface: absent (0); present (1) (after Wu et al. 1997, character 127)

\[\text{Figure 74}: \text{Posterolateral maxillary depression on } Amphicotylus lucasii, dorsal view (character 134, state 1}\]

C135. Maxillae, neurovascular foramina on posterior part, distribution on the alveolar margin: posterior ventralmost foramina not high on the maxillary margin, either close or next to the alveoli (0), posterior ventralmost foramina high on the maxilla (up to twice the distance compared to anterior foramina), very distant to the alveoli (1) (after Andrade & Bertini 2008, in Montefeltro et al. 2013, character 132)
C136. Maxillae, foramen for palatine ramus of CN-V: absent (0); present (1)
(modified from Brochu 1999, character 111)

C137. Maxillae, foramen for palatine ramus of CN-V, size: small (less than adjacent
alveoli length) (0), very large (at least 50% or more of adjacent alveoli length)
(1) (modified from Brochu 1999, character 111)

C138. Maxillae, single enlarged foramen medial to row of small foramina along
alveolar margin on palatal surface: absent (0); present (1) (NEW)

C139. Maxillae, participation in anterior edge of suborbit fenestrae: present (0),
absent (1) (after Andrade & Bertini 2008, in Montefeltro et al. 2013, character
211)

C140. Maxillae, palatal process, next to the anterior border of suborbit fenestrae:
absent (0); present (1) (after Andrade & Bertini 2008, in Montefeltro et al.
2013, character 218)

C141. Maxillae, posterior extension: anterior or close to level of postorbital bar (0)
projects posterior to the level of postorbital bar (usually level with the
anteroposterior midlength of supratemporal fenestrae) (1) (after Hastings et al
2010, character 29 and Wu et al. 1997, character 114)
C142. Maxillae, participation in orbit: absent (0); present (1) (Andrade et al 2011, in Montefeltro et al. 2013, character 51)

C143. Maxillae: posterior extension in a process devoid of teeth on ventral surface: absent (0); present (1) (NEW after Buscalioni et al. 2011).

Figure 76: Maxillae posterior process on *Eosuchus lerichei*, ventral view (character 143, state 1)

C144. Maxilla, posterior process on dorsal surface: absent (0), present (1) (after Brochu 1999, character 93).

Figure 77: Maxillae posterior process on *Caiman latirostris*, dorsal view (character 144, state 1)

C145. Maxilla, posterior process on dorsal surface, position: process between lacrimal and prefrontal (0), process within lacrimal (1) (after Brochu 1999, character 93).

Figure 78: Maxillae posterior process within lacrimal on *Caiman latirostris*, dorsal view (character 145, state 1)
C146. Maxillae, posteromost lateral contact of the maxillary and lacrimal bones in dorsal view: closer to posterolateral corner of orbits (0); closer to anterolateral corner of orbits (1) (after Hastings et al. 2010, character 36)

**Nasal**

C147. Nasal-premaxilla contact: present (0), absent (1) (Clark 1994, character 14, Wu et al. 1997 character 14)

C148. Nares, projection of the internarial bar relative to the main body of premaxilla and narial opening: does not project anterior to the main body of premaxilla (0), strongly projected anteriorly from narial opening, anterior to main body of premaxilla (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 39)

![Figure 79: Projected internarial bar](image)

*Araripesuchus gomesii*, left dorso-lateral view (character 148, state 1)

C149. Nasal, contact with external nares: absent (0), present (1) (adapted from Norell 1988, character 3; Clark, 1994, characters 13 and 14; in Brochu 1999, character 95)

C150. Nasals, participation in dorsal border of external nares: absent (0), present (1) (after Pol & Norell 2004, character 124)

C151. Nasal, participation in internarial bar, bisecting external nares: absent (0), present (1) (adapted from Norell 1988, character 3; Clark, 1994, characters 13 and 14; in Brochu 1999, character 95)
C152. Nasal, anteromost extension relative to level of first maxillary tooth: posterior (0); on the same level (1); anterior (2); (modified from Jouve et al. 2008, character 42; in Hastings et al. 2010, character 33) [ORDERED]

C153. Nasal, sagittal bar elevated above dorsal surface of maxillae: absent (0); present (1) (after Montefeltro et al. 2011; in Montefeltro et al. 2013, character 53)

C154. Nasals, morphology of lateral border posterior to external nares: laterally concave (0); straight (1) (Pol 1999; in Pol & Norell 2004, character 127)

\[\text{Figure 80: Laterally concave borders of nasals on \textit{Theriosuchus pusillus}, dorsal view (character 154, state 0)}\]

C155. Nasal, lateral edges: nearly parallel (0), parallel but the anterior end oblique to each other (1); entirely oblique to each other (2) (Pol 1999, character 141) [ORDERED]

\[\text{Figure 81: Nasal bones in dorsal view on \textit{Alligatori sinensis} (left, character 255)}\]
155, state 0), *Goniopholis simus* (middle, character 155, state 1) and *Theriosuchus pusillus* (right, character 155, state 2)

C156. Nasals, morphology of posterolateral region: flat surface facing dorsally (0), lateral region deflected ventrally, forming part of the lateral surface of the snout (1) (Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 56)

C157. Nasal, posterior tip: converge at sagittal plane (0); separated by anterior sagittal projection of frontals (1) (after Ortega et al. 2000; in Montefeltro et al. 2013, character 61)

C158. Nasal-frontal contact, anterior tip of frontal forms a broad, complex sutural contact with nasals: absent (0), present (1) (NEW after Brochu 2011; in Skutschas et al. 2014 character 131)

*Figure 82*: Complex sutural nasal-frontal contact on *Caiman latirostris*, dorsal view

(character 158, state 1)

C159. Antorbital fenestra: absent (0); present (1) (after Norell & Clark 1990, character 2)

**Lacrimal**

C160. Lacrimals, contact with nasal at medial edge: absent (0), present (1) (after Jouve et al. 2006, character 50)

C161. Lacrimal, visibility in dorsal view: present (0), absent (1) (after Jouve 2009, character 315)
C162. Lacrimal orbit contour, orientation: facing laterally (0); facing laterodorsally (1) 
(after Ortega et al. 2000, character 172)

C163. Lacrimal, lateral extension almost reaching the medial border of the orbit 
edge: absent (0); present (1) (NEW after Buscalioni et al. 2011)

Figure 83: Lateral extension of 
lacrimal on Hylaeochamps montana, dorsal view 
(character 163, state 1)

C164. Lacrimal, length in relation to antorbital fenestra: does not exceed (0); 
exceeds the anterior margin (1) (after Jouve 2009, character 314)

C165. Orbits, lateral margin comprised dominantly by: lacrimal (0); jugal (1) 
(Hastings et al 2010, character 5)

C166. Orbits, orientation of lateral border relative to lateral margin of supratemporal 
fenestra: lateral (0); level or medial (1) (after Wu et al. 2001, character 130)

C167. Lacrimal, posterior extent and relationship with jugal: extending 
posteroventrally, widely contacting jugal (0); tapering posteroventrally, does 
not contact jugal or contacts the jugal only slightly (1) (Zaher et al. 2006, in 
Montefeltro et al. 2013, character 142)

Prefrontal

C168. Prefrontal-lacrimal, crest dorsal to orbit: absent (0); present (1) (Andrade et al. 
2011, in Montefeltro et al. 2013, character 70)
C169. Prefrontals, support for the anterior palpebral bone: marked depression forming a barely noticeable lateral projection (0), marked depression forming a great lateral projection, large enough to support the anterior palpebral (1) (Sereno & Larsson 2009, in Montefeltro et al. 2013, character 65)

C170. Prefrontals, general morphology of facet for palpebral articulation: borders not marked forming an anteroposterior elongated area (0), well marked borders forming a shallow hemispherical surface (1) (Pol et al. 2009, in Montefeltro et al. 2013, character 66)
C171. Prefrontals, anterior process, morphology: split into two processes (0), single anterior process (1) (modified from Gomani 1997, character 4; in Jouve et al. 2006, character 52)

C172. Prefrontals, orientation anterior to orbits: oriented parallel to anteroposterior axis of the skull (0); oriented postero-medially-anteroanterolaterally (1) (modified from Gomani 1997, character 4; in Pol & Norell 2004: character 111)

C173. Prefrontals, extent of prefrontal pillars: do not reach palate (0); solidly integrated with palate (1) (modified from Wu et al. 1997, character 15; Ortega et al. 2000, character 29; Clark 1994, character 15)

C174. Prefrontals, morphology of dorsal half of prefrontal pillar: narrow, edges of dorsal half parallel when viewed in lateral view (0); expanded anterioposteriorly, edges of dorsal half flaring when viewed in lateral view (1) (adapted from Norell 1988, character 41; in Brochu 1999, character 137)

C175. Prefrontals, prefrontal pillar, direction of medial process expansion: dorsoventrally (0); anteroposteriorly (1) (after Brochu 1999, character 136)

C176. Prefrontals, prefrontal pillar, medial process morphology at base: wide, not constricted (0); constricted (1) (after Brochu 1999, character 138)
C177. Prefrontals, morphology of prefrontal pillar: solid (0); with large pneumatic sinus (prefrontal recess of Witmer 1997) (1) (Brochu 1999, character 99)

C178. Orbits, morphology of margin: flush with skull surface (0); dorsal edges of orbits upturned (1); orbit margin telescoped (strongly upturned and elongated) (2) (after Brochu 1999, character 103) [ORDERED]

**Figure 87:**
Telescoped orbit margins on *Gavialis gangeticus*, left dorso-lateral view (character 178, state 1)

C179. Orbits, orientation: dorsally or laterodorsally (0); fully laterally (1) (Wilkinson et al. 2008; in Montefeltro et al. 2013, character 11)

C180. Orbits, position: medially (midpoint of orbit closer to median axis than lateral edge) (0); laterally (midpoint of orbit closer to lateral edge than median axis) (1) (modified from Hastings et al. 2010, character 4)

**Figure 88:** Laterally positioned orbits on *Araripesuchus gomesii*, left dorso-lateral view (character 180, state 1)
Frontal

C181. Frontals, anterior extension position: posteriorly located, level with or slightly (not more than 5mm) anterior to the prefrontal (0); very anterior (more than 5mm) to prefrontal (1) (modified from Hastings et al. 2010, character 38)

C182. Frontals, morphology of anteriormost border of anterior process: truncated (0), wedge-like (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 76)

C183. Frontals, extension of anterior margin: long, extends anterior to the orbits (0); short, does not extend anterior to the orbits (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 79)

C184. Orbits, medial margin of the orbit in dorsal view, extent of frontal participation: formed mostly by the frontal (same as or more than 50% frontal participation) (0); formed mostly by the prefrontal (less than 50% frontal participation) (1) (Jouve 2009, character 326)

C185. Orbits, number of palpebrals: one (0), two (1) (after Clark 1994, character 65)

C186. Frontals, suture with palpebrals: separated from (or weakly sutured to) lateral edge of frontals (0), extensively sutured to each other and to lateral margin of frontals (1) (Pol & Norell 2004b, in Montefeltro et al. 2013, character 107)

**Figure 89**: Extensively sutured palpebrals on *Araripesuchus gomesii*, left dorso-lateral view (character 186, state 1)
C187. Frontals, midline suture: fused (0); unfused (1) (after Clark 1994, character 21)

C188. Frontals, participation in the primary medial border of orbit, at dorsal skull roof, not considering palpebrals: extensive participation in the orbit, more than prefrontal (0), reduced participation in orbit, less than prefrontal (1) excluded from the orbit by prefrontal-postorbit contact (2) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 87) [ORDERED]

C189. Frontals, dorsal surface posterior to orbits, morphology: flat or slightly concave (0); markedly concave transversally (not considering the elevated orbit rim when it occurs) (1) (after Riff & Kellner 2011, in Montefeltro et al. 2013, character 81)

C190. Frontals, dorsal longitudinal ridge, placement: restricted to the posterior portion (0), restricted to central portion (1); restricted to anterior portion (2) (Montefeltro et al. 2011, in Montefeltro et al. 2013, character 78) [ORDERED]

C191. Frontals, transverse ridge: absent (0); present (1) (after Jouve 2009, character 319, same as Pol et a. 2009; in Montefeltro et al. 2013, character 80)

C192. Frontals, wide plate in the anteromedial corner of supratemporal fenestra: absent (0); present (1) (after Jouve 2009, character 320)

C193. Frontoparietal suture, placement: deeply within supratemporal fenestra; frontal prevents broad contact between postorbit and parietal (0); suture makes modest entry into supratemporal fenestra at maturity; postorbit and parietal in broad contact (1); suture on skull table entirely (2) (Brochu 1999, character 81) [ORDERED]
C194. Frontoparietal suture, morphology: concavoconvex (0); linear (1) (after Brochu 1999, character 86)

Figure 90: Frontoparietal suture on *Caiman crocodilus* (left, character 194, state 0) and *Goniopholis simus* (right, character 194, state 1)

C195. Frontoparietal suture on interfenestral bar, morphology: straight/smooth (0), zigzag (1) (after Hastings et al. 2010, character 40)

Figure 91: Frontoparietal suture on *Goniopholis simus* (left, character 195, state 0) and *Pholidosaurus purbeckensis* (right, character 195, state 1)

C196. Frontal, narrow median ridge on dorsal surface: absent (0); present (1) (after Jouve et al. 2006, character 85)
Figure 92: Narrow median ridge on frontal on *Theriosuchus pusillus*, dorsal view (character 196, state 1)

C197. Frontal and parietal, midline ridge across dorsal surface of both: absent (0); present (1) (after Clark 1994, character 22)

C198. Postorbital & Frontal, bar between orbit and supratemporal fenestra, morphology: broad and solid (0); narrow (a third or less than supratemporal fenestra diameter) (1) (after Clark 1994, character 31)

C199. Postorbit and frontal, bar between orbit and supratemporal fenestra, extent of surface sculpting: broadly sculpted (0); sculpting restricted to anterior surface (1) (after Clark 1994, character 31)

Postorbit

C200. Postorbits, anterolateral process: absent or poorly developed (0); well developed, long and acute (1) (modified from Clark 1994 after Pol & Norell 2004, character 28)

Figure 93: Anterolateral postorbit process on *Dyrosaurus phosphaticus*, left lateral view (character 200, state 1)
C201. Postorbits, medial contact with quadrate at dorsal angle of infratemporal fenestra: absent (0), present (1) (after Brochu 1999, character 76)

C202. Postorbit, morphology of descending flange lateral surface: flat (0); concave (1) (Montefeltro et al. 2011, in Montefeltro et al. 2013, character 175)

C203. Postorbits, medial contact with quadratojugal at dorsal angle of infratemporal fenestra: absent (0), present (1) (after Brochu 1999, character 76)

C204. Postorbit-ectopterygoid contact: present (0); absent (1) (Pol 1999 character 158 and Ortega et al. 2000, character 36 modified in Pol & Norell 2004: character 144)

C205. Postorbits, orientation of edges of dorsal part: anteriorly and laterally (0); anterolaterally (1) (after Clark 1994, character 29)

C206. Postorbit, posteroventral process: absent or extremely reduced (i.e. tip of laterotemporal fenestrae appears close to dorsal edge of skull) (0), present (i.e. tip of laterotemporal fenestrae appears firmly separated from the dorsal edge of skull) (1) (after Larsson & Sues 2007, in Montefeltro et al. 2013, character 173)

*Figure 94*: Postorbit posteroventral process on *Araripesuchus gomesii*, left lateral view (character 206, state 1)
C207. Postorbital and squamosal, upper temporal bars, outline of lateral margins in dorsal view: margin mostly straight or slightly convex (0), margin strongly sinusoidal (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 102)

C208. Postorbital and squamosal, supratemporal roof, dorsal surface: complex, no clearly distinct flat skull table developed (0); dorsally flat "skull table" developed, with postorbital and squamosal with flat shelves extending laterally, beyond quadrate contact (1) (after Clark 1994, character 24)

![Figure 95: Skull table in dorsal view on *Dyrosaurus phosphaticus* (left, character 208, state 0) and *Alligator sinensis* (right, character 208, state 1)]

**Postorbital Bar**

C209. Postorbital bar, ornamentation: sculpted (0); unsculpted (1) (after Clark 1994, character 25)

C210. Postorbital bar, morphology: transversely flattened (0); cylindrical (1) (after Clark 1994, character 26)
C211. Postorbital bar, orientation: nearly vertical (0); slightly (20 or less degrees) anterodorsally inclined (1); strongly anterodorsally (more than 20 degrees) inclined (2) (after Hastings et al. 2010, character 50) [ORDERED]

![Figure 96: Postorbital bar in left lateral view on Alligator mefferdi (left, character 211, state 0), Thoracosaurus macrorhynchus (middle, character 211, state 1) and Tomistoma schlegelii (right, character 211, state 2)]

C212. Postorbital bar, morphology of dorsal end: broadens dorsally, continuous with dorsal part of postorbit (0), constricted, distinct from the dorsal part of the postorbit (1) (after Clark 1994, character 30)

![Figure 97: Postorbital bar on Gracilisuchus stipanicicorum, left lateral view (character 212, state 1)]

C213. Postorbital bar, morphology: weak (width less than half of bar height) (0); robust (width half or more than bar height) (1) (Jouve et al. 2006, character 60)
C214. Postorbital bar, vascular opening in dorsal surface: absent (0); present (1)  
(Clark 1994, character 27)

C215. Postorbital bar, participation of jugal in lateral surface: present (0), absent (1)  
(after Gasparini et al. 2006, in Montefeltro et al. 2013, character 162)

![Figure 98: Postorbital bar on *Alligator mefferdi*, left lateral view](image)

(character 215, state 1)

C216. Postorbital bar, number of projections: two prominent projections (0); single projection, generally not prominent (1) (after Brochu 1999, character 134)

C217. Postorbital bar, position of ventral portion in relation to jugal: flush with lateral surface of jugal (0), slightly medially displaced (1), medially displaced and a ridge separating postorbital bar from lateral surface of jugal (2) (modified from Ortega et al. 2000, character 34; in Jouve et al. 2006, character 72)

[ORDERED]

Squamosal

C218. Supratemporal fenestra, position of parietal and squamosal: widely separated by quadrate on posterior wall, distance between parietal and squamosal at least $1/16^{th}$ of the supratemporal fenestra circumference (0); parietal and squamosal approach each other on posterior wall without actually making contact (1); parietal and squamosal meet along posterior wall (2) (Brochu 1999, character 131) [UNORDERED]
C219. Supratemporal fenestra, morphology of rims: raised and hypertrophied: absent (0), present (1) (Montefeltro et al. 2011, in Montefeltro et al. 2013, character 96)

Figure 99: Supratemporal fenestrae rims on *Crocodylus rhombifer*, left lateral view (character 219, state 1)

C220. Supratemporal fenestrae, morphology in dorsal view: square-shaped to subrectangular (0), circular to elliptical (1), triangle shaped, converging medially (2) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 16) [UNORDERED]

C221. Supratemporal fenestrae: open dorsally in adults (0), close during ontogeny (1) (adapted from Norell 1988, character 9; in Brochu 1999, character 87)

C222. Supratemporal fenestrae, morphology of rim at maturity: dermal bones of skull roof do not overhang rim (0); overhang fenestrae (1) (adapted from Norell 1988, character 9; in Brochu 1999, character 87)

C223. Supratemporal fenestrae, foramina on the medial parietal wall: absent (0); present (1) (after Norell 1988, character 51)

C224. Supratemporal fenestrae, extension relative to skull roof: relatively large, covering more than 50% of surface of skull roof (0); relatively small, fenestrae surrounded by a flat and extended skull roof (1) (modified from Clark 1994, after Ortega et al. 2000, character 41 and Pol & Norell 2004 character 68)
C225. Supratemporal fenestrae, visibility of posterior walls: barely visible in dorsal view (0); largely visible in dorsal view (1) (modified from Hastings et al 2010, character 10)

C226. Temporal canal, exposure of anterior opening: exposed in dorsal view (0); hidden in dorsal view and overlapped by squamosal rim of supratemporal fossa (1) (Ortega et al. 2000, character 75)

C227. Squamosals, extent of anterior process in lateral view: not extending to orbit margin (0), extending to orbit margin and thus overlapping postorbit (1) (after Turner & Buckley 2008, in Montefeltro et al. 2013, character 183)

C228. Squamosals, extent of laterodorsal orientation of outer surface: extensive (0), minimal (1) (after Ortega et al. 2000, character 42)

C229. Squamosal, position of dorsal and ventral edges of groove for upper ear lid: ventral edge is lateral to dorsal (0), ventral edge is directly beneath dorsal (1) (Clark & Sues 2002, in Montefeltro et al. 2013, character 110)

C230. Squamosal, morphology of dorsal and ventral rims of groove for external ear valve musculature: parallel (0); flaring anteriorly (1) (after Brochu 1999, character 84)

Figure 100: Groove for external ear valve musculature on *Gavialis lewisi*, right lateral view (character 230, state 1)
C231. Squamosal, longitudinal groove for attachment of the upper ear lid at lateral surface: absent (0); present (1) (Clark & Sues 2002, in Montefeltro et al. 2013, character 109)

C232. Squamosals, ventrolateral extension to lateral extent of quadrate: absent (0), present (1) (modified from Brochu 1999, character 150)

C233. Squamosal, size of prongs [processes that attach to the paroccipital process]: short, covering little to no area of paroccipital process (0), long, covering large part of paroccipital process, at least 10% (1) (after Brochu 1999, character 140)

Figure 101: Squamosal prongs in left lateral and dorsal view on Comahuesuchus brachybuccalis (left, character 233, state 0) and Alligator sinensis (right, character 233, state 1)

C234. Squamosal, position of posterolateral process in relation to skull table: level with skull table (0); depressed from skull table (1) (Sereno & Larsson 2009, in Montefeltro et al. 2013, character 117)
**Figure 102:** Posterolateral process of squamosal on *Comahuesuchus brachybucale*, left lateral view (character 234, state 1)

C235. Squamosal, descending ornamented process at posterolateral edge: absent (0); present (1) (after Pol & Norell 2004, character 163)

**Figure 103:** Descending ornamented process of squamosal on *Araripesuchus gomesii*, left dorso-lateral view (character 235, state 1)

C236. Squamosal, morphology of posterior posterolateral process: tapered (0); broad, with almost parallel sides (1) (Larsson & Sues 2007, in Montefeltro et al. 2013, character 119)

**Figure 104:** Posterior posterolateral process of squamosal on *Amphicotyulus lucasi*, dorsal view (character 236, state 1)

C237. Squamosals, elongated and posteriorly directed process at posterior edge: absent (0); present (1) (after Clark 1994, character 36)
C238. Squamosal-quadrate, extension: dorsally along posterior margin of external auditory meatus (0); only to posteroventral corner of external auditory meatus (1) (Brochu 1999, character 132)

![Figure 105](image.png)

*Figure 105*: External auditory meatus in left lateral view on *Araripesuchus gomesii* (left, character 238, state 0) and *Alligator sinensis* (right, character 238, state 1)

C239. Anterior opening of temporo-orbit canal, in dorsal view: present (0), absent (1) (Ortega et al. 2000, in Montefeltro et al. 2013, character 113)

C240. Otic aperture, participation of squamosal in dorsal margin, externally: absent, formed by the quadrate (0); present (1) (after Jouve et al. 2006, character 131)

C241. Cranioquadrate passage, composition with quadrate, squamosal and otocipital: do not meet to enclose cranioquadrate passage (0), enclose passage near lateral edge of skull (1), meet broadly lateral to the passage (2) (Clark 1994, character 49) [ORDERED]

C242. Squamosal, morphology of posterior margin lateral to occipital tuberosity: straight (0); anteriorly concave (1) (Hastings et al. 2010, character 48)
C243. Skull roof, posterior lamina of posterior margin above posttemporal fenestrae and the occipital tuberosities which overhangs, hiding part of the occipital tuberosity from dorsal view: absent (0); present (1) (Hastings et al. 2010, character 46)

**Figure 107:** Overhanging posterior lamina of squamosal in dorsal view on *Rhabdognathus keiniensis* (character 243, state 1)

**Parietal**

C244. Parieto-postorbit suture, presence on dorsal skull roof: absent (0), present (1) (after Clark 1994, character 23)

C245. Parieto-postorbit suture, within supratemporal fossa: absent (0), present (1): (after Clark 1994, character 23)

C246. Parietal, morphology of dorsal surface: flat (0), depressed (1) (after Hill et al 2008, character 35)
C247. Parietal, ornamentation of dorsal surface: strongly ornamented with deep pits (0); slightly ornamented (1); smooth (2) (modified from: Jouve et al. 2005, character 27; Jouve et al. 2008, character 27; in Hastings et al. 2010, character 45) [ORDERED]


C249. Parietal, posterior region of dorsal surface, anteroposteriorly oriented medial dorsal ridge: absent (0); present (1) (after Montefeltro et al. 2013 ch. 478)

Figure 108: Depressed dorsal surface of parietal in left dorso-lateral view on Sarcosuchus imperator (character 246, state 1)

Figure 109: Medial dorsal ridge on parietal in dorsal view on Shamosuchus djadochtaensis (character 249, state 1)
**Jugal**

C250. Jugal and lacrimal, anterior margins: confluent with no notch at anterior contact (0), jugal edge convex producing an anterior notch at contact (filled by maxilla) (1) (Larsson & Sues 2007, in Montefeltro et al. 2013, character 143)

C251. Jugal, large foramen on the lateral surface (not the same as medial jugal foramen) near the anterior margin: absent (0); present (1) (after Zaher et al. 2006, in Montefeltro et al. 2013, character 150)

C252. Jugal, participation in antorbital fenestra: present (0); absent (1) (Ortega et al. 2000, character 71)

C253. Jugal, extension in relation to orbit: does not exceed the anterior margin (0); exceeds margin (1) (after Pol 1999, character 134)

C254. Jugal, position of postorbit process: anteriorly placed (0), in the middle (1); posteriorly positioned (2) (Pol & Norell 2004, character 143) [ORDERED]

C255. Jugal, direction of base of postorbit process: posterodorsally (0); dorsally (1) (after Pol 1999, character 156)

C256. Orbits, morphology of ventral margin: gently circular (0); with prominent notch (1) (Brochu 1999, character 139)

*Figure 110:* Prominent notch in ventral margin of orbits in left dorso-lateral view on *Gavialis gangeticus* (character 256, state 1)
C257. Jugal, morphology of region beneath infratemporal fenestra: transversely flattened (0); rod-like (1) (after Clark 1994, character 18)

C258. Jugal, lateral surface in ventral view: exposed lateral to maxilla, jugal outwardly bowed (0), not visible in ventral view, jugal thus straight (1) (after Ortega et al. 2000, character 174; Wu et al. 1997, character 101; in Jouve et al 2006, character 69)

C259. Jugal, longitudinal ridge on lateral surface below infratemporal fenestrae: absent (0), present (1) (Pol & Norell 2004b, in Montefeltro et al. 2013, character 164)

C260. Jugal, posterior process, length: longer than infratemporal fenestrae posteriorly (0); shorter or same length as infratemporal fenestrae posteriorly (1) (after Pol 1999, character 150)

C261. Jugal, posterior ramus, orientation: laterally bowed (0), straight (1) (NEW after Buscalioni et al. 2011)

Figure 111: Laterally bowed jugal in ventral view on Hylaeochamps vectiana (character 261, state 1)
C262. Jugal, extension of ventral lamina in relation to ventral surface of ectopterygoid: far anterior (0); ends level with ventral surface of ectopterygoid (1) (after Jouve et al. 2006, character 75)

Quadratojugal

C263. Infratemporal fenestrae, morphology: clearly triangular (0), elliptic to subpolygonal (1) (Andrade et al. 2011; in Montefeltro et al. 2013, character 20)

C264. Infratemporal fenestrae, orientation: facing laterally (0); facing laterodorsally (1) (after Ortega et al. 2000, character 46)

C265. Infratemporal fenestrae, composition of posterior angle: quadratojugal forms posterior angle of infratemporal fenestra (0); quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (1); jugal forms posterior angle of infratemporal fenestra (2) (adapted from Norell 1989, character 10; in Brochu 1999, character 75) [ORDERED]

C266. Quadratojugals, ornamentation at base: absent (0); present (1) (Pol 1999; in Montefeltro et al. 2013, character 176)

C267. Quadratojugal, extension to superior angle of infratemporal fenestra: absent (0); present (1) (after Brochu 1999, character 80)

C268. Quadratojugal, dorsal process, contact with postorbit: small, contact simple (0), extensive, contact complex (1) (after Clark 1994, character 19)
Figure 112: Complex quadratojugal-postorbit contact in left lateral view on *Simosuchus clarki* (character 268, state 1)

C269. Quadratojugal, size of spina quadratojugalis at maturity: prominent, more than 10% of infratemporal fenestrae length (0); greatly reduced or absent in maturity, less than 10% of infratemporal fenestrae length (1) (Adapted from Norell 1989, character 1; in Brochu 1999, character 69)

C270. Quadratojugal, position of spina quadratojugalis: low, near posterior angle of infratemporal fenestra (0); high, between posterior and superior angles of infratemporal fenestra (1) (Brochu 1999, character 114)

C271. Quadratojugal, extent of posteroventral corner: reaching the quadrate condyles (0); not reaching the quadrate condyles (1) (from Pol 1999 & 2003 (155 and 141 respectively) in Jouve et al. 2006 character 79)

Figure 113: Posteroventral extent of quadratojugal in left lateral view on *Simosuchus clarki* (character 271, state 1)
C272. Quadratojugal, extent: reaches but does not participate in quadrate condyles (0), forms lateral extension to the quadrate condyles and participates in mandibular joint (1) (Pol 1999, in Montefeltro et al. 2013, character 168)

**Quadrate**

C273. Quadrate, direction of major axis: posteroventrally (0); ventrally (1) (after Pol 1999; in Pol & Norell 2004, character 150)

![Figure 114](image)

**Figure 114**: Quadrate in left lateral/latero-dorsal view on *Alligator sinensis* (left, character 273, state 0) and *Araripesuchus gomesii* (right, character 273, state 1)

C274. Quadrate, number of fenestrae: none (0), one (1); two or more fenestrae on dorsal and posteromedial surfaces (2) (after Clark 1994, character 45)

[ORDERED]

C275. Quadrate, position of foramen aerum in relation to quadrate: on mediodorsal angle (0); on dorsal surface (1) (after Brochu 1999, character 121)

C276. Quadrate, deep groove along ventral edge of pterygoid ramus: absent (0), present (1) (after Clark 1994, character 50)
C277. Quadrate, orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0); ventrolaterally (1) (Pol & Norell 2004: character 181)

![Figure 115: Orientation of quadrate in left lateral view on Simosuchus clarki (character 277, state 0)](image)

C278. Quadrate, morphology of intercondylar groove between condyles: poorly developed, condyles form flat continuous surface with slight indentation (0); deep (1) (modified from Ortega et al. 2000, in Montefeltro et al. 2013, character 280)

![Figure 116: Intercondylar groove in right dorso-lateral view on Comahuesuchus brachybacalis (character 278, state 0)](image)

C279. Quadrate, with small, ventrally-reflected medial hemicondyle (0); with small medial hemicondyle; dorsal notch for foramen aerum (1); with prominent dorsal projection between hemicondyles (2); with expanded medial hemicondyle (3) (Brochu 1999, character 112) [UNORDERED]
Figure 117: Hemicondyle in dorsal view on Comahuesuchus brachybuccalis (top left, character 279, state 0) and Alligator sinensis (top right, character 279, state 1), in ventral view on Boverisuchus vorax (bottom left, character 279, state 2) and in occipital view on Crocodylus cf. clavis (bottom right, character 279, state 1)

C280. Quadrate, morphology of distal end in cross section: mediolaterally wide and anterioposteriorly thin (0); subquadrangular (1) (after Pol & Norell 2014 character 164)
C281. Quadrate, morphology of distal end: with only one plane facing posteriorly (0); with two distinct faces in posterior view, a posterior one and a medial one bearing the foramen aereum (1) (Pol 1999, character 167)

C282. Quadrate, morphology of dorsal surface of posterior branch: concave or flat and smooth (0); with longitudinal ridge from base of paraoccipital process to articular end (1) (Ortega et al. 2000, character 55)

C283. Quadrate, morphology of posterior edge in dorsal view: gently concave (0); strongly concave (1) (modified from Clark 1994, character 46)

C284. Significant ventral quadrate process on lateral braincase wall (0); quadrate-pterygoid suture linear from basisphenoid exposure to foramen ovale (1) (Brochu 1999, character 127)

C285. Jaw joint, location: placed at level with basioccipital condyle (0), below basioccipital condyle, but about or above level of lowest point of toothrow (1); below level of lowest point of toothrow (2) (after Pol & Norell, character 104)

[ORDERED]
Supraoccipital

C286. Supraoccipital, dorsal exposure: absent (0), present (1) (after Ortega et al. 2000, character 62)

C287. Supraoccipital, extent of dorsal exposure: exposed in the midline portion of posterior region of skull table (0), restricted to a thin surface attached to posteriormost portion of parietal and squamosal (1) (Montefeltro et al. 2011; in Montefeltro et al. 2013, character 121)

C288. Supraoccipital, position of dorsal margin in relation to dorsal margin of squamosal in posterior view: higher (0); same height (1); lower (2) (after Jouve 2009, character 323) [UNORDERED]

Exoccipital

C289. Exoccipital, position of dorsal margin of paroccipital process in relation to quadrate condyle: at the same level or posterior (0); anterior (1) (after Jouve 2004, character 91)

C290. Exoccipital, orientation of paroccipital process in occipital view: dorsally-laterally directed at a 45° angle (0); medial edge horizontal, then terminal third sharply inclined dorsal laterally at a 45° angle (1); horizontal (2), curves downwards strongly (3) (Young & Andrade 2009, in Montefeltro et al. 2013, character 290) [ORDERED]
Figure 119: Hemicondyle in occipital view on *Crocodylus megarhinus* (top left, character 290, state 0), in occipital view on *Gavialis hysudricus* (top right, character 290, state 1), in left lateral view on *Alligator sinensis* (bottom left, character 290, state 2) and in left dorso-lateral view on *Araripesuchus gomesii* (bottom right, character 290, state 3)

C291. Exoccipital, dorsoventral expansion of paroccipital process at lateral termination: absent (0); present (1) (NEW after Wu et al. 2001)

C292. Exoccipital, position of medioventral projection: remains far (0); nearly reaches (1) the ventral projection of the basioccipital (after Jouve 2009, character 340)
C293. Exoccipital, position of cranial nerves IX-XI: pass through common large foramen vagi in otoccipital (0); cranial nerve IX passes medial to nerves X and XI in separate passage (1) (Clark 1994, character 59)

C294. Exoccipital, large ventrolateral part of otoccipital ventral to paroccipital process: absent (0); present, exoccipital area width below paroccipital process 50% or more of total skull width below paroccipital process in posterior view (1) (Clark 1994, character 60)

C295. Exoccipital, small but clear tuberosity dorsolateral to foramen magnum on occipital surface: absent (0); present (1) (NEW after Wu et al. 2001)

Figure 120: Exoccipital in occipital view on *Dyrosaurus phosphaticus* (character 292, state 1)

Figure 121: Exoccipital tuberosity in left dorso-occipital view on *Terminonaris robusta* (character 295, state 1)
C296. Exoccipital & supraoccipital, morphology of posterior surface: nearly flat (0); with bilateral posterior prominences (1) (after Clark 1994 character 64)

Figure 122: Bilateral posterior prominences in dorsal view on Dyrosaurus phosphaticus (character 296, state 1)

C297. Exoccipital, orientation of occipital surface ventral to basioccipital condyle: slopes anteroventrally (0); is roughly parallel to transverse plane (1) (adapted from Hua & Jouve 2004, character 167; in Salisbury et al 2006, character 174)

C298. Exoccipital, boss on paroccipital process, posterior surface, dorsally directed: prominent (0), absent or strongly reduced (1) (after Brochu 1999, character 141)

Figure 123: Paroccipital process boss in occipital view on Hylaeochampsia vectiana (character 298, state 0)

C299. Exoccipital, length of paroccipital process lateral to cranioquadrate opening: short, barely posteriorly extended in dorsal view (0); long, 20% or more of
skull width without paroccipital process (1) (after Brochu 1999, character 141)

**Figure 124:** Paroccipital process in occipital view on *Hylaeochampsa vectiana* (character 299, state 0)

C300. Exoccipital, orientation of occipital condyle: posteriorly directed (0), ventroposteriorly directed (1) (after Ortega et al. 2000, character 176)

C301. Otoccipitals, participation in basioccipital tubera: absent (0), present (1) (after Brochu 1999, character 151)

**Figure 125:** Basioccipital tubera in occipital view on *Alligator sinensis* (left, character 219, state 0) and *Crocodylus rhombifer* (right, character 301, state 1)

C302. Otoccipitals, process ventral to basioccipital tubera, morphology: robust, 25% or more of basioccipital width (0), slender, less than 25% of basioccipital width (1) (after Brochu 1999, character 151)
Basioccipital

C303. Basioccipital, orientation of proximal surface: condyle surface gradually slopes onto occipital surface (0), distinct clearing marking a neck separating occipital condyle and surrounding occipital surface (1) (Montefeltro et al. 2013, character 483)

C304. Basioccipital, midline crest on basioccipital plate below occipital condyle: absent (0), present (1) (Turner & Sertich 2010, in Montefeltro et al. 2013, character 271)

C305. Basioccipital, large bilateral pendulous tubera: absent (0); present (1) (after Clark 1994, character 57)

C306. Basioccipital, ventral projection from exoccipital in occipital view: present, ventrally distinct (0); absent, indistinct (1) (Jouve 2004, character 142)

C307. Basioccipital, paired grooves along ventral surface, extending from base of occipital condyle to basioccipital tubera: absent (0), present (1) (Hastings et al. 2010, character 57)

C308. Basioccipital and ventral part of otoccipital, orientation: facing posteriorly (0); posterovertrally (1) (modified from Gomani 1997, character 32; in Pol & Norell 2004, character 112)

Figure 126: Basioccipital in ventral view on Sebecus icaeorhinus (character 308, state 1)
C309. Basioccipital, ventral part, visibility in occipital view: main parts of posterior surface visible (0); few or no parts of posterior surface visible (1) (after Hastings et al. 2010, character 59)

C310. Basioccipital, orientation of median Eustachian foramen: ventral (0), lateral (1), posterior (2) (Montefeltro et al. 2013, character 480) [UNORDERED]

C311. Basioccipital, position of lateral eustachian canals in relation to medial eustachian canal: open dorsal (0); lateral (1) (adapted from Norell 1988, character 46; in Brochu 1999, character 147)

**Basisphenoid**

C312. Basisphenoid, visibility below basioccipital in occipital view: posterior surface not (or only slightly) visible (0); posterior surface widely exposed (1) (Jouve 2009, character 331)

![Figure 127: Basisphenoid in occipital view on Alligator sinensis (character 312, state 1)](image)

C313. Basisphenoid, length in relation to basioccipital in ventral view: basisphenoid shorter or equal to basioccipital (0); basisphenoid anteroposteriorly longer than basioccipital (1) (modified after Jouve et al. 2006, character 147)
C314. Basisphenoid, exposure ventral to basioccipital at maturity in occipital view:
not broadly exposed ventral to basioccipital at maturity; pterygoid thus short
ventral to median eustachian opening (0); basisphenoid exposed as broad
sheet ventral to basioccipital at maturity; pterygoid tall ventral to median
eustachian opening (1) (after Brochu 1999, character 119)

C315. Basisphenoid, sulcus on anterior braincase wall lateral to basisphenoid
rostrum: present (0); absent (1) (after Brochu 1999, character 122)

C316. Basisphenoid, strong anteroposterior medial crest: absent (0) present (1)
(after Jouve 2004, character 139)

C317. Basisphenoid, lateral exposure on braincase: absent (0); present (1) (after Pol
1999, character 163)

C318. Basisphenoid, position of lateral carotid foramen: opens lateral (0); dorsal (1)
to basisphenoid lateral exposure at maturity (Brochu 1999, character 127)

C319. Basisphenoid, median Eustachian foramen posterior wall: present (0), absent
(1) (Montefeltro et al. 2013, character 481)

**Laterosphenoid**

C320. Laterosphenoid, orientation of suture with parietal: parallel to skull table (0);
descends posteriorly relative to skull table (1) (Hastings et al. 2010, character
63)

C321. Laterosphenoid bridge, participation of palatine via ascending process: absent
(0), present (1) (after Brochu 1999, character 115)
C322. Prootic bone, extent of exposure on external braincase wall: extensive (0); prootic largely obscured by quadrate and laterosphenoid externally (1) (Brochu 1999, character 74)

C323. Otic aperture, general morphology (including otic aperture of cranio-quadrate passage but not preotic siphonal foramen nor quadrate fenestrae when present): closed posteriorly and subpolygonal to elliptic (0), closed posteriorly and triangular, with apex directed dorsally (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 30)

Figure 128: Otic aperture in left lateral view on Alligator sinensis (character 323, state 1)

C324. Otic aperture, morphology of posterior margin: straight (0); invaginate (1) (Brochu 1999, character 102)

Figure 129: Otic aperture in left lateral view on Alligator sinensis (character 324, state 1)
C325. Laterosphenoid, orientation of capitate process towards midline: oriented laterally (0); anteroposteriorly (1) (Brochu 1999, character 130)

**Ectopterygoid**

C326. Ectopterygoid, contact with posterior part of palatine: absent (0); present, pterygoid is excluded from participating in posterior edge of the fenestra palatina (1) (after Martinelli 2003, character 35)

C327. Ectopterygoid, extent of contact with maxillary toothrow: abuts maxillary toothrow (0); maxilla broadly separates ectopterygoid from maxillary toothrow (1) (Norell 1988, character 19)

C328. Ectopterygoid, length in relation to posterior tip of pterygoid flange at maturity: extends along entire pterygoid length to tip (0); does not extend towards tip (1) (adapted from Norell 1988, character 32; in Brochu 1999, character 149)

C329. Ectopterygoid, length in relation to postorbital bar: extends along medial face of postorbital bar (0); stops abruptly ventral to postorbital bar (1) (after Brochu 1999, character 133)

C330. Ectopterygoid, contact with maxilla at palatal branch of maxilla: absent (0); present (1) (after Ortega et al. 2000, character 61)

C331. Ectopterygoid, morphology of the distal ramus: laminar, extending as a flattened sheet over the pterygoid wing (0); robust, extending as a rod over most of the pterygoid wing, with subcircular cross-section through most of its length (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 261)

C332. Ectopterygoid-pterygoid flexure, existence during ontogeny: disappears during ontogeny (0); remains throughout ontogeny (1) (Brochu 1999, character 116)
C333. Ectopterygoid, extent of medial projection on the ventral surface of pterygoid flanges: barely extended (0); widely extended, covering approximately lateral half of ventral surface of pterygoid flanges (1) (Zaher et al. 2006, in Montefeltro et al. 2013, character 254)

C334. Ectopterygoid, posterior process: present (0); absent (1) (Pol 1999, character 148)

C335. Pterygoid-ectopterygoid fenestra: absent (0); present (1) (Jouve 2009, character 324)

Pterygoid

C336. Pterygoids, ornamentation of palatal surface: smooth (0); sculpted (1) (Clark 1994, character 40)

C337. Pterygoids, long anterior process that contact the maxillae anteromedial to primary choanae: absent (0); present (1) (Tykoski et al. 2002, character 119)

C338. Pterygoids, morphology of flanges: thin & laminar (0); dorsoventrally thick with pneumatic spaces (1) (Wu et al. 1997, character 106)

C339. Pterygoids, position of anteromost point of posterior margin of pterygoidean wing: anterior to medial eustachian foramen (0); level with medial eustachian...

C340. Pterygoids, size of pterygoid flanges: large, reaches laterally beyond medial extent of quadrate condyle (0); relatively small, does not reach laterally to level of quadrate medial condyle (1) (Ösi et al. 2007, character 166)

C341. Pterygoid, posteriorly facing notch between the base of pterygoid wings: absent (0); present (1) (Pol & Norell 2004, character 148)

C342. Pterygoids, depression on primary pterygoidean palate posterior to choana: absent or moderate in size in being narrower than palatine bar (0); similar length or wider then palatine bar (1) (modified from Clark 1994 after Pol & Norell 2004, character 42 and Ortega et al. 2000, character 139)

C343. Pterygoids, morphology posterior to choana: unfused (0); fused (1) (Wu et al. 1997, character 41)

C344. Pterygoid, transverse ridge on ventral surface of pterygoid rami, proximal end: absent (0), present (1) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 239)

C345. Pterygoids, presence of posterolateral pterygoid-basisphenoid wing: absent (0); present (1) (after Jouve 2004, character 117)

C346. Pterygoids, size of posterior pterygoid processes: small, elevation above pterygoid surface same or less than basisphenoid length (0); tall, with prominent elevation above pterygoid surface (1) (after Brochu 1999, character 98)
C347. Pterygoids, orientation of posterior pterygoid processes: projects posteroventrally (0); projects posteriorly (1) (after Brochu 1999, character 98)

C348. Pterygoids, morphology of quadrate ramus in ventral view: narrow, less than 25% of quadrate (0); broad, more than or equal to 25% of quadrate (1) (modified from Wu et al. 1997, character 119; in Pol & Norell 2004, character 173)

C349. Pterygoids, quadrate process: present (0); absent (1) (after Pol 1999, character 165)

**Choanae**

C350. Vomer, exposure on palate: obscured (0), exposed on palate at premaxillary-maxillary suture (1); exposed on palate between palatines (2) (modified from Brochu 1999, after characters 125 & 126) [UNORDERED]

C351. Choanae, orientation of opening: ventrally from palate (0) posteriorly into midline depression (1) (after Clark 1994, character 39)

C352. Choanae, position of anterior edge: closer to posterior edge of suborbit fenestrae (or anteriorly) than pterygoid flanges (0); closer to posterior edge of pterygoid flanges than suborbit fenestrae (1) (modified from Clark 1994, after Pol & Norell character 44)
Figure 131: Choanae in ventral view on *Dyrosaurus phosphaticus* (character 352, state 0)

C353. Internal choanae, septation: absent (0); present (1) (after Brochu 1999, character 152)

C354. Choanae, participation of maxillae in anterior margin: absent (0); present (1)
(modified from Wu et al. 1997, character 44; in Jouve et al 2006 character 19)

C355. Choanae, participation of palatines in anterior margin: absent (0); present (1)
(modified from Wu et al. 1997, character 44; in Jouve et al 2006 character 19)

C356. Choanae, participation of pterygoids in anterior margin: absent (0); present (1)
(modified from Wu et al. 1997, character 44; in Jouve et al 2006 character 19)

C357. Choanae and pterygoids, orientation of pterygoid surface lateral and anterior to internal choana: flush with choanal margin (0); pushed inward to form "neck" (1) (Brochu 1999, character 73)

C358. Choanae, morphology of posterior rim of internal choana: not deeply notched (0); deeply notched (1) (after Brochu 1999, character 107)
C359. Choanae, position of opening: opened posteriorly and continuous with pterygoid surface (0); closed posteriorly by an elevated wall formed by the pterygoids (1) (Pol & Norell, character 183)

C360. Choanae, morphology in palatal view: subcircular, elliptic or lanceolated (0), triangular (1), rectangular (2) (Andrade & Bertini 2008, in Montefeltro et al. 2013, character 22) [UNORDERED]

**Palatine**

C361. Palatines, anterior palatal fenestra: absent (0); present (1) (Wu et al. 1997, character 128)

C362. Palatine-maxilla suture: foramina at posteromost end: absent (0); present (1) (NEW)

C363. Palatines, morphology ventral to narial passage: do not meet on palate below the narial passage (0), form palatal shelves that do not meet (1); meet ventrally to the narial passage, forming part of secondary palate (2) (Clark 1994, character 37) [ORDERED]

C364. Palatines, morphology along anteroposterior axis: run parasagittally along midline (0), diverge laterally, becoming rod-like and forming palatine bars posteriorly (1) (Martinelli 2003, in Montefeltro et al. 2013, character 228)
C365. Palatines, row of foramina flanking the midline contact of palatine bones:
absent (0), present (1) (after Montefeltro et al. 2011, in Montefeltro et al. 2013, character 223)

C366. Palatines, morphology of lateral edges in anterior half of interfenestral bar
between suborbit fenestrae: parallel to subparallel (0); flared anteriorly (1)
(after Pol et al. 2009, in Montefeltro et al. 2013, character 224)

C367. Palatines, morphology of lateral edges in posterior half of interfenestral bar
between suborbit fenestrae: parallel to subparallel (0); flared posteriorly (1)
(after Pol et al. 2009, in Montefeltro et al. 2013, character 225)

C368. Palatines, lateral process projecting into suborbit fenestra on anterior lateral
edges: absent (0); present (1) (after Brochu 1999, character 94)

C369. Palatine, morphology of anterior face of anterior median process into maxilla:
rounded or pointed anteriorly (0); invaginate (1) (after Brochu 1999, character 108)

Figure 133: Anterior palatine face in ventral view on Hylaeochampsia vectiana (left, character 369, state 0) and Eosuchus lerichei (right, character 369, state 1)
C370. Palatines, length of anterior median palatine process into maxilla in relation to anterior end of suborbit fenestra: extends beyond it (0); does not extend beyond it or terminates at same level (1) (after Brochu 1999, character 110)

C371. Palatines, morphology of anterior median palatine process into maxilla: generally broadly curved anteriorly (0); in form of thin wedge (1) (after Brochu 1999, character 118)

C372. Palatines, anterior length of suborbit fenestra in relation to alveoli: posterior to the anterior 2/3 of the maxillary alveoli (0); anterior or level with the anterior 2/3 (1) (after Hastings et al 2010, character 12)

C373. Palatines, posterior notch of suborbit fenestra: absent (0); present (1) (after Brochu 1999, character 88)

C374. Palatines, morphology of ventral face of palatine bar: flat and wide (0), ventral surface restricted and dorsal portion cylindrical (1) (Montefeltro et al. 2011, in Montefeltro et al. 2013, character 226)

C375. Palatines, position of anterior foramen for palatine ramus of cranial nerve VII relative to basisphenoid rostrum: ventrolateral (0); ventral (1) (Brochu 1999, character 164)

C376. Palatine-pterygoid suture, distance to posterior angle of suborbit fenestra: close, almost at angle (0), far, distinctly separate from angle (1) (after Brochu 1999, character 85)
Dentition (Skull)

C377. Premaxillae, number of teeth: five (0), four (1) (modified from Wu and Sues 1996, character 27 and Ortega et al. 2000, character 133; in Pol & Norell 2004: character 105)

C378. Premaxillae, space between left and right first premaxillary alveoli: similar or large than adjacent spacing to second alveolus (0); first premaxillary teeth closely spaced, smaller than spacing to second alveolus (1) (after Hastings et al 2010, character 19)

C379. Premaxillae, orientation of anterior alveolar margin and teeth: vertical (0); inturned (1) (Sereno et al 2001, character 68)

C380. Premaxillae, position of teeth 1 and 2: separated like adjacent teeth (0); nearly confluent (1) (modified from Sereno et al. 2001, character 56; in Jouve et al 2006, character 192)

C381. Premaxillae, separation of alveoli 2 and 3: absent (alveoli confluent) (0); present (1) (NEW)

Figure 134: Premaxillary alveoli in ventral view on *Euthedodon arambourgi* (character 381, state 0)

C382. Premaxillae, position of last tooth relative to first maxillary tooth: anterior (0); anteromedial (1) (after Sereno et al. 2001, character 70)
C383. Premaxillae, size of last premaxillary alveolus compared to rest of premaxillary toothrow: same size or smaller (0); larger (1) (from Ortega et al. 2000, character 15 and Wu et al. 1997, character 77; in Jouve et al 2006, character 184)

C384. Premaxillae and maxillae: presence of flat depressions the size of small alveoli between alveoli: absent (0); present (1) (NEW)

Figure 135: Flat depressions between alveoli in ventral view on *Tomistoma dowsoni* (character 384, state 1)

C385. Maxillary teeth, orientation of compressed crown in ventral view: oriented parallel to the longitudinal axis of skull (0); obliquely disposed (1) (after Pol 1999; in Pol & Norell 2004, character 137)

Figure 136: Compressed maxillary teeth in ventral view on *Notosuchus terrestris* (character 385, state 1)
C386. Maxillae, size of teeth: all maxillary teeth similar in size or with the largest alveolus placed at middle of maxillary row (0), tooth row with waves of size variation (1) (from Ortega et al. 2000, character 20 and Wu et al. 1997, character 78; in Jouve et al. 2006, character 186)

C387. Maxillae, dental implantion: teeth in isolated alveoli (0); located in dental groove (1) (Ortega et al. 2000, in Montefeltro et al. 2013, character 375)

C388. Maxillae, spacing between teeth: increasing between 7th and 11th teeth (0); relatively constant (1) (Hill et al. 2008, character 39)

C389. Maxillae, anterior portion of tooth row, position relative to dentary toothrow: adjacent (0); offset labially and ventrally (1) (after Sereno et al. 2003, character 75)

C390. Maxillae, morphology of alveoli & teeth: homodont (0), heterodont (1) (after Ortega et al. 2000, character 132)

Figure 137: Morphology of teeth in right lateral view on *Planocrania datangensis* (character 390, state 1)

C391. Maxillae, third alveoli, size in relation to second alveoli: larger in diameter than second alveolus (0), same size (1) (modified from Hastings 2010, character 16)
C392. Maxillae, third alveoli, size in relation to fourth alveoli: larger in diameter than fourth alveolus (0), same size (1) (modified from Hastings 2010, character 16)

C393. Maxillae, diastema at 7th and 8th tooth positions: absent, 7th and 8th teeth regularly spaced (0), present, 7th and 8th teeth apart from each other and closer to 6th and 9th (1) (Montefeltro et al. 2013, character 484)

C394. Maxillae, position of posteriormost alveolus in relation to orbit: closer to level of anterior margin than posterior margin (0); closer to posterior margin than anterior margin (1); close to or posterior to anteroposterior midlength of supratemporal fenestrae (2) (Hastings et al. 2010, character 30) [ORDERED]

**Dentition (All)**

C395. Teeth, morphology: Serrated (0); not serrated (1) (modified from Gasparini et al. 1993, character 31; in Jouve et al. 2006, character 200)

C396. Maxillary and dentary teeth, outline in horizontal section: labiolingually compressed (0), subcircular (1) (after Ortega et al. 2000, character 104)

![Figure 138: Labiolingually compressed maxillary teeth in ventral view on Notosuchus terrestris (character 396, state 1)]

C397. Teeth, morphology: robust with very wide alveoli (0); thin and long teeth, at least three times longer than wide (1) (Jouve 2005, character 11)
C398. Teeth, accessory ridges on labial-lingual surfaces of mid to posterior teeth:
absent (0), present (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 363)

C399. Posterior maxillary and dentary teeth, morphology: not constricted at base of
crown (0); constricted (1) (Ortega et al. 1996; in Pol & Norell 2004, character 157)

Dentary

C400. Dentary, extent of symphysis: extends to fourth or fifth alveolus (0); to sixth
through eighth dentary alveoli (1); beyond eight dentary alveolus (2)
[ORDERED] (adapted from Brochu 2004, character 166; in Salisbury et al. 2006, character 166)

C401. Dentary, morphology of symphysis in ventral view: tapering anteriorly forming
an angle (0), U-shaped, smoothly curving anteriorly (1); lateral edges
longitudinally oriented, convex anterolateral corner, and extensive
transversally oriented anterior edge (2) (modified from Pol 1999, character 212; in Pol & Norell 2004, character 155) [UNORDERED]
**C402.** Dentary, morphology of dorsal edge: slightly concave or straight and subparallel to longitudinal axis of skull (0); straight with abrupt dorsal expansion, being straight posteriorly (1), with single dorsal expansion and concave posteriorly (2); sinusoidal, with two concave waves (3) (Ortega et al. 1996, in Montefeltro et al. 2013, character 317) [UNORDERED]

![Figure 140](image)

**Figure 140:** Dentary in left lateral view on *Gavialis gangeticus* (top left, character 402, state 0), on *Araripesuchus gomesii* (top right, character 402, state 1), on *Baurusuchus sp.* (bottom left, character 402, state 2) and on *Alligator sinensis* (bottom right, character 402, state 3)

C403. Dentary, unsculpted region below the toothrow: absent (0); present (1) (Pol 1999, character 213)

C404. Dentary, size of occlusal pits for maxillary occlusion: minimal (0); several large indentations, size close to that of alveoli (1) (modified from Hastings et al. 2010, character 72)

C405. Dentary, morphology of lateroventral surface anterior to external mandibular fenestra: flat (0); convex (1) (after Ortega et al. 1996, in Montefeltro et al. 2013, character 315)
Figure 141: Dentary anterior to mandibular fenestra in left lateral view on *Sebecus icaeorhynus* (reconstructed) (character 405, state 0)

C406. Dentary, orientation of lateral surface below alveolar margin, at mid posterior region of tooth row: vertically oriented, continuous with the rest of the lateral surface of dentary (0); flat surface exposed dorsolaterally, divided by ridge from rest of lateral surface of dentary (1) (Pol & Apesteguía 2005, in Montefeltro et al. 2013, character 313)

C407. Dentary, large occlusional pit lateral to seventh alveolus: absent (0); present (1) (after Jouve et al. 2006, character 163)

C408. Dentary, length in relation to external mandibular fenestra: extends posteriorly beneath mandibular fenestra (0), does not extend beneath fenestra (1) (after Clark 1994, character 70)

C409. External mandibular fenestra: present (0), absent (1) (Clark 1994, character 75)

C410. Mandibular fenestra, placement of intersection of surangular-dentary suture: anterior to posterodorsal corner (0); at posterodorsal corner (1) (Brochu 1999, character 65)

C411. External mandibular fenestra, size: small, so that foramen intermandibularis caudalis is not visible laterally (0); external mandibular fenestra large so that
foramen intermandibularis caudalis visible laterally (1) (adapted from Norell 1988, character 14; in Brochu 1999, character 64)

C412. External mandibular fenestra, morphology: circular/elliptic (0), slit-like (1), tear-drop like (2), triangular (3) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 306) [UNORDERED]

![Diagram of external mandibular fenestra in Alligator sinensis, Borealosuchus wilsoni, Araripesuchus gomesii, and Protosuchus richardsoni.]

**Figure 142**: External mandibular fenestra in left lateral view on *Alligator sinensis* (top left, character 412, state 0), on *Borealosuchus wilsoni* (top right, character 412, state 1), on *Araripesuchus gomesii* (bottom left, character 412, state 2) and on *Protosuchus richardsoni* (bottom right, character 412, state 3)

**Dentition (Mandibles)**

C413. Dentary teeth, morphology of posterior part of tooth row: forms waves in dorsal view (0); nearly straight, oriented posterolaterally, each tooth being
more lateral than the immediately anterior one (1) (after Jouve 2009, character 342)

C414. Dentary teeth, morphology: subcircular (0), strongly compressed labiolingually (alveolus length at least 125% or more of alveolus width) (1) (NEW)

Figure 143: Dentary teeth in dorsal view on *Sebecus icaeorhynus (reconstructed)*

(character 414, state 1)

C415. Dentary, size of second alveolus relative to first alveolus: smaller (0), similar (between 90% and 110% of first alveolus diameter) (1), larger (2) (modified from Hastings et al. 2010, character 64) [ORDERED]

C416. Dentary, size of second alveolus relative to third alveolus: smaller (0), similar (between 90% and 110% of third alveolus diameter) (1), larger (2) (modified from Hastings et al. 2010, character 64) [ORDERED]

C417. Dentary, size of interalveolar space between second and third dentary alveoli relative to that of first and second: roughly equal in proportion (between 90% and 110% of space between first and second alveolus) (0), greater (1) (after Hastings et al. 2010, character 65)

C418. Dentary, placement of third alveoli in relation to fourth: interalveolar space is roughly equal to that between second and third dentary alveoli (between 90% and 110% of space between second and third alveolus) (0); interalveolar
space is smaller between dentary third and fourth than between second and third (1) (after Hastings et al. 2010, character 66)

C419. Dentary, position of fourth alveolar wall: level with adjacent alveoli (0); raised relative to adjacent alveoli (1) (after Hastings et al. 2010, character 68)

C420. Dentary, placement of alveoli for teeth 3 and 4: confluent (0); separate (1) (after Brochu 1999, character 52)

C421. Dentary, size of alveoli for teeth 3 and 4, size: same size, ratio 1:1 (0); fourth alveolus diameter larger than third (1) (after Brochu 1999, character 52)

C422. Dentary, size of seventh tooth: alveolus same size as other alveoli (between 90% and 110% of alveoli immediately closest to it) (0); alveolus smaller than the others (1) (after Jouve 2004, character 153)

C423. Dentary, 7th and 8th teeth spaced more closely together than other teeth: absent (0), present (1) (NEW)

**Figure 144**: Dentary teeth in dorsal view on *Dyrosaurus phosphaticus* (character 423, state 1)

C424. Dentary, largest alveolus immediately posterior to fourth is: 13 or 14 (0), 13 or 14 and a series behind it (1), 10, 11 or 12 (2); all alveoli are of a uniform size (3) (adapted from Brochu 2004, character 167; in Salisbury et al 2006, character 167) [UNORDERED]
C425. Dentary, position of teeth: occlude lingually to maxillary teeth (0); occlusion pit between the 7th and 8th maxillary teeth; all other dentary teeth occlude lingually (1); dentary teeth occlude in line with maxillary toothrow (2) (adapted from Norell 1988, character 5 and Willis 1993, character 1; in Brochu 1999, character 78) [ORDERED]

**Splenial**

C426. Splenial, outer surface sculpture: absent (0); present (1) (after Montefeltro et al 2011, in Montefeltro et al. 2013, character 301)

C427. Splenial, anterior extent: reaches 5th dentary tooth (0); does not reach 5th dentary tooth (1) (after Hill et al. 2008, character 32)

C428. Splenial, extent of involvement in symphysis in ventral view: not involved (0), involved slightly in symphysis, no more than the distance between two alveoli (1), extensively involved (2) (modified from Clark 1994 after Pol & Norell 2004, character 77) [ORDERED]

C429. Splenial, morphology of medial surface posterior to symphysis: flat or slightly convex (0), markedly concave (1) (Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 329)

C430. Splenial, morphology posterior to symphysis: thin (0); robust dorsally, more than a third of mandible width (1) (Ortega et al. 1996, in Montefeltro et al. 2013, character 334)
C431. Splenial, anterior perforation on mandibular ramus of cranial nerve V: present (0); absent (1) (adapted from Norell, 1988, character 15 and Norell 1989, character 8; in Brochu 1999, character 41)

C432. Splenial, perforation for mandibular ramus of cranial nerve V: single (0), double (posteriorly) (1) (after Brochu 1999, character 42)

C433. Splenial, position of first perforation for mandibular ramus of cranial nerve V: anteriorly (0), posteriorly (1) (after Brochu 1999, character 42)

C434. Splenial, process separating angular and coronoid: present (0); absent (1) (after Brochu 1999, character 59)

Angular

C435. Angular, dorsal extension in relation to foramen intermandibularis caudalis: extends toward or beyond anterior end with acute anterior tip (0); does not
extend beyond anterior end and has blunt anterior tip (1) (Brochu 1999, character 66)

C436. Angular, sharp ridge on lateral surface: absent (0); present (1) (Pol & Norell 2004b, in Montefeltro et al. 2013, character 346)

C437. Angular, placement of sharp ridge on surface: at ventral-most margin (0); along lateral surface (1) (Pol & Norell 2004b, in Montefeltro et al. 2013, character 347)

C438. Angular, extension of ventral face in lateral view in relation to orbits: doesn't extend beyond posterior margin of orbits (0), extends beyond posterior margin of orbits (1) (Wilkinson et al. 2008, in Montefeltro et al. 2013, character 337)

C439. Angular, extension of insertion area for M. pterygoideus posterior: does not extend onto lateral surface of angular (0); extends onto lateral surface of angular (1) (Clark 1994, character 76)

Figure 147: M. pterygoideus posterior in left lateral view on Alligator sinensis (character 439, state 1)

C440. Angular, strongly pitted pattern on lateral surface and posterior surangular: absent (0); present (1) (after Andrade et al. 2011, in Montefeltro et al. 2013, character 302)
C441. Angular-surangular suture, position: contacts external mandibular fenestra at posterior angle at maturity (0); passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1) (Brochu 1999, character 47)

C442. Angular, morphology of posteroverentral margin: straight or gently arched dorsally, less than 60 degree angle between horizontal line and posteroverentral margin (0); strongly arched dorsally, more than 60 degree angle (1) (after Pol et al. 2009, in Montefeltro et al. 2013, character 344)

**Figure 148**: Mandible in left lateral view on *Alligator sinensis* (left, character 442, state 0) and *Gavialis gangeticus* (right, character 442, state 1)

**Surangular**

C443. Surangular, position of lingual foramen for articular artery and alveolar nerve: on surangular entirely (0); on surangular-articular suture (1); on articular entirely (2) (Brochu 1999, character 45) [ORDERED]

**Figure 149**: Dentary in right medial view on *Alligator sinensis* (middle, character 443, state 1)
C444. Surangular, morphology of anterior projection in lateral view: single and acute (0); forked (1) (after Ortega et al. 2000, character 96)

C445. Surangular, morphology of dorsal anterior forked process onto dentary: unequal, one side of forked process shorter than the other (0); equal, both sides of forked process same length, ratio exactly 1:1 (1) (Brochu 1999, character 48)

Figure 150: Mandible in right and left lateral view, respectively, on *Alligator sinensis* (left, character 445, state 0) and *Maroccosuchus zennaroi* (right, character 445, state 1)

C446. Surangular, morphology of dorsal edge: flat (0); arched dorsally (1) (Clark 1994, character 74)

C447. Surangular, dorsal extension at lateral wall of glenoid fossa: continues to dorsal tip of lateral wall of glenoid fossa (0); truncated and not continuing dorsally, thus not reaching dorsal tip of lateral wall of glenoid fossa (1) (Brochu 1999, character 106)

Figure 151: Mandible in right lateral view on *Crocodylus rhombifer* (character 447, state 1)
C448. Surangular-angular suture, placement of contact with articular: medially at ventral tip (0); dorsal to ventral tip (1) (after Brochu 1999, character 67)

**Figure 152:** Mandible in right medial view on *Alligator mississippiensis* (character 448, state 0)

C449. Surangular-articular suture, orientation within glenoid fossa: anteroposteriorly (0); bowed strongly laterally (1) (modified from Gomani 1997, character 46 and Buckley et al. 2000, character 113; in Brochu 1999, character 162)

C450. Surangular, extension: to posterior end of retroarticular process (0); pinched off anterior to tip of retroarticular process (1) (adapted from Norell 1988, character 42; in Brochu 1999, character 51)

C451. Craniomandibular joint, participation of surangular and quadratojugal: absent (0); present (1) (after Ortega et al. 2000, character 99)

**Prearticular**

C452. Prearticular: present (0); absent (1) (Clark 1994, character 72)

**Articular**

C453. Articular-surangular suture, anterior process dorsal to lingual foramen ("crocodyline process" of Aoki 1994): absent (0), present (1) (after Brochu 1999, character 44)
C454. Articular, sulcus between articular and surangular: present (0); absent (1)  
(after Brochu 1999, character 60)

C455. Articular, morphology of posterior ridge on glenoid fossa: posterior margin well  
developed, evidently high (0), posterior margin poorly delimited, crest absent  
(1) (Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 350)

C456. Articular, location of foramen aerum in relation to retroarticular process: at  
extreme lingual margin (0); set in from margin (1) (adapted from Norell 1988,  
character 16; in Brochu 1999, character 49)

C457. Articular, orientation of retroarticular process: projects posteriorly (0); projects  
posterodorsally (1) (Adapted from Benton and Clark 1988; Clark 1994,  
character 71 and Norell and Clark 1990, character 7; in Brochu, 1999,  
character 50)
C458. Articular, length of retroarticular process: short, does not ascend to the articular glenoid cavity (0); ascends surpassing the articular glenoid cavity (1) (Jouve et al. 2006, character 174)

C459. Articular, position of medial wing of retroarticular process: dorsal to mandible in position (0); deflected ventrally (1) (Jouve et al. 2006, character 178)

C460. Articular, posteromedial wing of retroarticular process: absent (0), present (1) (after Jouve et al. 2006, character 179)

C461. Articular & quadrate, size of articular facet for quadrate condyle: equal in length to the quadrate condyles (0), longer than quadrate condyle, but quadrate condyle:facet articulation ratio lower than 1:3 (1); longer than quadrate condyle, with quadrate condyle:facet articulation ratio 1:3 or higher (2) (modified from Wu & Sues 1996; in Pol & Norell 2004, character 103)

[ORDERED]

Coronoid

C462. Coronoid: present (0), absent (1) (Jouve et al 2006, character 181)

C463. Coronoid, orientation of dorsal edge: slopes strongly anteriorly (0); horizontal (1) (Brochu 1999, character 54)

C464. Coronoid, position of ventral process: laps strongly over inner surface of Meckelian fossa (0); remains on medial surface of mandible (1) (Brochu 1999, character 55)

C465. Coronoid, perforation posterior to foramen intermandibularis medius: absent (0); present (1) (after Brochu 1999, character 56)

Mandible in general
C466. Mandibular symphysis, morphology in transverse cross section: flat or slightly concave (0); strongly concave and narrow, trough shaped (1) (after Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 328)

Figure 155: Symphysis on *Araripesuchus buitreraensis* (character 466, state 1)

C467. Symphysis, posterior peg: absent (0), present (1) (Pol & Apesteguia 2005, in Montefeltro et al. 2013, character 322)

C468. Mandible, morphology of distal rami in dorsal/ventral views: distal rami mostly straight or slightly curved (0), distal rami strongly curved medially at mid-mandible, giving the mandible a broad Y-shape (1) (Andrade et al. 2011, in Montefeltro et al. 2013, character 307)

**POSTCRANIAL CHARACTERS**

**Atlas & Axis**

C469. Proatlas, morphology: boomerang-shaped (0), strap-shaped (1); massive and block-shaped (2) (Brochu 1999, character 2) [UNORDERED]

C470. Proatlas, tall dorsal keel: present (0); absent (1) (after Brochu 1999, character 17)

C471. Proatlas, prominent anterior process: present (0); absent (1) (after Brochu 1999, character 10)
C472. Atlas, morphology of intercentrum in lateral view: wedge-shaped, with insignificant parapophyseal processes (0); plate-shaped, with prominent parapophyseal processes at maturity (1) (Brochu 1999, character 5)

C473. Atlantal ribs, morphology of dorsal margin: generally smooth with modest dorsal process, less than a quarter of rib height (0); with prominent process, more than or equal to a quarter of rib height (1) (after Brochu 1999, character 14)

![Figure 156: Atlantal rib in left lateral view on *Caiman crocodilus* (character 473, state 1)](image)

C474. Atlantal ribs, very thin medial laminae at anterior end: absent (0); present (1) (after Brochu 1999, character 16)

C475. Axial rib, morphology of tuberculum: wide, with broad dorsal tip (0); narrow, with acute dorsal tip (1) (Brochu 1999, character 20)

![Figure 157: Axial rib in left lateral view on *Gavialis gangeticus* (character 472, state 1)](image)

C476. Axial rib, position of rib tuberculum: contacts diapophysis during maturity, if at all (0); contacts diapophysis early in ontogeny (1) (Brochu 1999, character 21)
C477. Axis, orientation of anterior part of dorsal surface of neural spine: horizontally
   (0); slopes anteriorly (1) (after Brochu 1999, character 11)

   Figure 158: Atlas & axis in
   right lateral view on
   Crocodylus cf. affinis
   (character 477, state 1)

C478. Axis, neural arch, diapophysis: absent (0); present (1) (adapted from Norell
   1989, character 7; in Brochu 1999, character 4)

C479. Axis, deep fork in hypapophysis: present (0), absent (1) (Brochu 1999,
   character 19)

C480. Axis, crest on dorsal surface of neural spine: present (0), absent (1) (after
   Brochu 1999, character 12)

C481. Axis, anteroposterior development of neural spine: well developed covering all
   the neural arch length (0); poorly developed, located over the posterior half of
   the neural arch (1) (Pol 1999, character 168)

C482. Axis, morphology of postzygapophyses: well developed, curved laterally (0);
   poorly developed, no lateral curvature (1) (Pol 1999, character 170)

**Post-axial cervical Vertebrae**

C483. Cervicals, presence of hypapophyseal keels until: tenth vertebrae behind atlas
   (0), eleventh vertebrae behind atlas (1), twelfth vertebra behind atlas (2);
(Brochu 1999, character 7, but see also Clark 1994, character 91)

[ORDERED]

C484. Cervicals, prominent hypapophysis on first postaxial vertebra: present (0); absent (1) (adapted from Norell 1989, character 12; Norell and Clark 1990, character 11 and Clark 1994, character 91; in Brochu 1999, character 8)

C485. Cervicals, morphology of prezygapophysis on third cervical vertebra (CIII): poorly developed, slightly projecting anterior to the vertebral centrum (0), well developed, clearly projecting anteriorly, beyond the vertebral centrum (1) (Andrade et al. 2011; in Montefeltro et al. 2013, character 397)

C486. Cervicals, morphology of prezygapophyseal process of anterior to middle vertebrae in lateral view: anterior margin straight or evenly convex (0); anterior margin bearing a distinct bulge at the midpoint of the prezygapophyseal process (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 394)

C487. Cervicals, morphology of medial surface of prezygapophyseal process of anterior to middle vertebrae: flat or slightly convex (0); with an ovoid or triangular depression close to the neural canal (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 403)

C488. Cervicals, morphology of neural spine base in anterior vertebrae: gracile base, with neural spine clearly distinct from the neural arch (0), robust base, with the development of spinozygapophyseal ridges (1) (after Andrade & Bertini 2008; in Montefeltro et al. 2013, character 392)
C489. Posterior cervicals and anterior dorsals, morphology of the articular surface of the parapophysis in the posterior cervicals and anterior dorsals:
subcircular/ovoid with the major axis oriented anteroposteriorly (0);
subtriangular/ovoid with major axis oriented dorsoventrally (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 395)

C490. Cervicals, morphology: all amphicoelus (0); some amphicoelus and some procoelus (1); all procoelus (2) (Norell & Clark 1990, in Salisbury et al. 2006, character 170) [ORDERED]

C491. Cervical ribs, posterodorsally projecting spine at the junction with the tubercular process on posterior process of shaft: absent (0); present (1)
(Turner 2006; in Montefeltro et al. 2013, character 412)

Thoracic Vertebrae

C492. Thoracic vertebrae, morphology: amphicoelus or amphiplatyan (0), procoelus (1) (modified from Clark 1994, character 93, after Jouve et al. 2006, character 223)

C493. Thoracic vertebrae, spinopostzygapophyseal lamina: absent (0); present as a high and sharp lamina (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 404)
C494. Thoracic vertebrae, distinct rounded depression on the dorsal surface of the neural arches of the anterior to middle dorsal vertebrae, located between the base of the neural spine and the postzygapophyseal process: absent (0); present (1) (Pol et al. 2012; in Montelfeltro et al. 2013, character 405)

C495. Thoracic vertebrae, relative positions of the transverse process and the postzygapophysis in middle dorsal vertebrae: postzygapophysis located dorsal to the transverse process (0); postzygapophysis level with the transverse process (1) (Pol et al. 2012; in Montelfeltro et al. 2013, character 406)

C496. Thoracic vertebrae, dorsal migration of parapophysis on the neural arch on middle dorsals: dorsal vertebrae 4 to 9 showing a gradual dorsal migration of parapophysis, with at least two vertebrae bearing the parapophysis on the neural arch pedicles, well below the diapophysis (0); abrupt change in position of parapophysis, with dorsal 4 bearing the parapophysis at the neurocentral suture and dorsal 5 with parapophysis level with diapophysis forming a transverse process (1) (Pol et al. 2012; in Montelfeltro et al. 2013, character 402)

C497. Thoracic vertebrae, position of transverse process of posterior dorsal vertebrae: dorsoventrally low on posterior dorsal vertebrate surface (on lower 50% of surface) & laminar in shape (0); dorsoventrally high on posterior dorsal vertebrate surface (on higher 50% of surface) (1) (modified from Buscalioni and Sanz 1988, character 39; in Pol & Norell 2004, character 114)

### Sacral Vertebrae
C498. Sacral vertebrae, number: two (0); three (1) (Buscalioni and Sanz 1988 character 44)

C499. Sacral vertebrae, anterior capitulum, extension: projects far anteriorly of tuberculum and is broadly visible in dorsal view (0); far anterior margins of tuberculum and capitulum nearly in same plane and capitulum largely obscured dorsally (1) (Brochu 1999, character 13)

C500. Sacral ribs, position of dorsolateral end of first sacral rib: located at the level of the neural canal (0); dorsoventrally expanded, projecting dorsally above the level of the neural canal (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 409)

Caudal vertebrae


C503. Caudals, morphology of centrum from second vertebra on: amphicoelus (0), procoelus (1) (after Norell & Clark 1990, in Salisbury et al. 2006, character 171)

Pectoral Girdle

C504. Scapula, morphology of deltid crest: with sharp margin, very thin, no more than 2mm in width (0); with broad margin, very wide (1) (Brochu 1999, character 23)
C505. Scapula, morphology of blade: flares dorsally at maturity (0); sides of scapular blade subparallel; minimal dorsal flare at maturity, ratio of distal width to blade width near base 1:1 (1) (Benton & Clark 1988; in Brochu 1999, character 22)

C506. Coracoid, extension of glenoid surface: extended on a vertical plane (0), extended on an oblique plane and the glenoid lip faces outwards and posterovertrally (1) (Jouve et al. 2006, character 207)

C507. Clavicle, morphology of anterior end: flat (0); rod-like (1) (Brochu 1999, character 31)

C508. Interclavicle, morphology: flat along length, without dorsoventral flexure (0); with moderate dorsoventral flexure, tip to tip length more than 80% of interclavicle length along curvature (1); with strong dorsoventral flexure, tip to tip length 80% or less than interclavicle length along curvature (2) (after Brochu 1999, character 30) [ORDERED]

**Forelimbs**

C509. Humerus, position of proximal edge of deltopectoral crest: emerges smoothly from proximal end of humerus and is not obviously concave (0); emerges abruptly from proximal end of humerus and is obviously concave (1) (Brochu 1999, character 26)

C510. Humerus, anterior projection and profile of deltopectoral crest: well-developed crest bearing a pointed tubercle for the insertion of the supracoracoideus complex (sensu Meers, 2003) (0); low and anteriorly convex in lateral view, lacking a well-developed tubercle (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 422)
C511. Humerus, orientation and extension of the distal half of the deltopectoral crest: extending along the lateral edge of the humerus or slightly deflected medially reaching, at the most, the lateromedial midpoint of the humeral shaft (0); strongly deflected medially, surpassing the lateromedial midpoint of the anterior surface of the humeral shaft (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 424)

C512. Humerus, position of proximal one-third of the deltopectoral crest: originating at the proximolateral corner of the humerus and extending distally along the proximal region of the lateral margin of the humerus (0); proximal origin medially displaced from the proximolateral corner of the humerus and extending distally, leaving an anteriorly facing concave surface between the crest and the lateral margin of the anterior surface of the humerus (which probably corresponds to the insertion area of the M. coracobrachialis brevis dorsalis) (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 423)

C513. Humerus, circular depression on the posterior surface of the proximal end, related to the insertion of the M. scapulohumeralis caudalis: absent (0); present (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 425)

C514. Humerus, morphology of lateral and medial surface of distal end: flat and anteroposteriorly broad, similar in anteroposterior length to the lateromedial width of the distal end of humerus (0); convex and reduced in comparison with the lateromedial width of the distal humerus (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 426)
C515. Humerus, morphology of shaft: straight (0), sigmoidal with a pronounced posterior curvature of shaft on proximal area of humerus (1) (Ortega et al. 2000, character 180)

C516. Humerus, placement of insertion of M. teres major and M. dorsalis scapulae: insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0); insert with common tendon; single insertion scar (1) (Brochu 1999, character 29)

C517. Humerus, orientation of the area of insertion of M. subscapularis above the internal tuberosity of the humerus: obliquely oriented in anterior view, with the area of insertion facing proximomedially (0); vertically oriented in anterior view, with the area of insertion facing medially (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 421)

C518. Ulna, morphology of olecranon process: narrow and subangular (0); wide and rounded (1) (Brochu 1999, character 27)

Figure 160: Ulna and radius in right lateral view on *Crocodylus* cf. *clavis* (character 518, state 1)

C519. Radiale, extent of proximal end expansion: expanded symmetrically, similarly to the distal end (0); more expanded proximomedially than proximolaterally (1) (Buscalioni and Sanz 1988, character 54)
C520. Radiale, morphology of anterior surface: smoothly convex (0); bearing a proximodistal crest that extends along the shaft dividing the anterior surface of the radiale (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 434)

C521. Radiale, morphology of distal region of articular surface for the ulnare: merging gradually with the posterolateral surface of the radiale shaft (0); separated from the shaft of the radiale by a distinct step, usually triangular (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 432)

**Pelvic Girdle**

C522. Ilium, morphology of dorsal margin of iliac blade: rounded with smooth border (0); rounded, with modest dorsal indentation, less than 1/10th of total blade height (1); rounded, with strong dorsal indentation ("wasp-waisted"), indentation at least 1/10th of total blade height (2); (modified from Brochu 1999, character 28) [ORDERED]

*Figure 161: Ilium in right lateral view on Crocodylus acutus* (character 522, state 2)

C523. Ilium, morphology of posterior tip of iliac blade: posterior tip of blade not deep, at least twice as long as it is high (0), posterior tip of blade very deep, less than twice as long as it is high (1) (modified from Brochu 1999, character 28)

C524. Ilium, length of anterior process in relation to posterior process: more than half of the length of posterior process (usually of similar length) (0); less than half
the length of the posterior process (usually one-quarter or less) (1) (Clark 1994, character 84)

C525. Ilium, height of posterior lamina of iliac blade in relation to anterior lamina: of same height (0); higher (1) (after Jouve et al. 2006, character 209)

C526. Ilium, supraacetabular crest: present (0); absent (1) (Buscalioni and Sanz 1988, character 49)

C527. Ilium, orientation of the rugose surface for the insertion of the M. iliotibialis that forms the supracetabular crest: dorsal (0), dorsolateral (1), lateral (2) (after Buscallioni & Sans 1988; in Montefeltro et al. 2013, character 443)

[ORDERED]

C528. Ilium, morphology of the rugose surface for the insertion of the M. iliotibialis that forms the supracetabular crest: lateromedially narrow (0), lateromedially broad (1) (Buscallioni & Sans 1988; in Montefeltro et al. 2013, character 438)

C529. Ilium, dorsoventral position of the ventral margin of the postacetabular process (along its posterior-most third): located at the same height as or dorsal to the acetabular roof (0); located ventral to acetabular roof (usually located at or below the dorsoventral midpoint of acetabular height) (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 442)

C530. Ilium, orientation of postacetabular process: directed posteroventrally (0); directed posteriorly (1); directed posterodorsally (much higher in position than preacetabular process) (2) (after Pol & Norell 2004, character 110)

[ORDERED]
C531. Ilium, morphology of posterior end of the postacetabular process: tapering posteriorly and ending in an acute tip (0); subrectangular with the posterior end vertically oriented, with its dorsoventral height being at least 60% of the height at the origin of the postacetabular process (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 440)

C532. Pubis, morphology: rod-like without expanded distal end (0); with expanded distal end (1) (Clark 1994, character 85)

**Hindlimbs**

C533. Femur, morphology of lateral supracondylar ridge on anterior surface of distal part: prominent and broad lateral supracondylar ridge separating the anterior concave surface of femur from the lateral surface (0); absence of well developed lateral supracondylar ridge, anterior surface of femur flat or slightly concave and continuous with the lateral surface of the distal femur (1). (Pol et al. 2012; in Montefeltro et al. 2013, character 449)

C534. Tibia, morphology of distal articular surface: medial region of distal articular surface extends further distally than the lateral region, forming a strongly oblique distal margin (0); medial and lateral regions subequally extended, with distal margin subhorizontally oriented (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 452)

C535. Tibia, morphology in anterior or posterior view: straight (0); markedly bowed laterally (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 451)

C536. Fibula, morphology of proximal-most portion of fibular head: straightsided to weakly developed posteriorly (0); very sharply projecting posteriorly, forming distinct extension (1) (Turner 2006; in Montefeltro et al. 2013, character 450)
C537. Astragalus, morphology of the fibular facet: subrectangular with subequal anterior and posterior margins (0); trapezoidal with the proximodistal height of its anterior margin lower than the posterior margin (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 457)

C538. Astragalus, morphology of anterior margin of the tibial facet: well developed ridge reaching medially to the ball-shaped region for the articulation of metatarsal I-II: present (0), absent (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 453)

C539. Astragalus, morphology of anterior margin of the tibial facet: closing the proximomedial corner of the anterior hollow of the astragalus: present (0), absent (1) (after Pol et al. 2012; in Montefeltro et al. 2013, character 453)

C540. Astragalus, astragalar-tarsal ligament pit (sensu Sertich & Groenke, 2010) at the distal end of the anterior hollow: not differentiated from the rest of the anterior hollow of the astragalus (0); distinct depression separated from the anterior hollow by an obliquely oriented ridge running along the proximolateral margin of the astragalar-tarsal ligament pit (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 455)

C541. Calcaneum, morphology of posterior astragalar facet: subtriangular with proximal and lateral margins forming a right-angle and an oblique medioplantar edge (0); proximal and plantar edges subparallel to each other connected through a broad and rounded medial margin (1) (Pol et al. 2012; in Montefeltro et al. 2013, character 458)
Osteoderms

C542. Osteoderms, longitudinal keels on dorsal surfaces: present (0); absent (1)  
(after Clark 1994, character 101)

C543. Osteoderms, extent of longitudinal keels on dorsal surfaces: extending to  
anterior half (0); restricted to posterior edge of osteoderm (1) (Pol et al. 2009;  
in Montefeltro et al. 2013, character 463)

C544. Osteoderms, edges: some or all imbricated (0); sutured to one another (1)  
(Clark 1994, character 98)

C545. Osteoderms, size of lingual osmoregulatory pores: small (0); large, at least  
twice the size of small ones (1) (Brochu 1999, character 158)

Figure 162: single  
disarticulated  
osteoderm in ventral  
view from Alligator sp.  
(character 545, state 0)

C546. Nuchal shield, morphology: grades continuously into dorsal shield (0);  
differentiated from dorsal shield (1) (after Brochu 1999, character 38)

C547. Nuchal osteoderms, number: four (0), six (1), eight (2) (after Brochu 1999,  
character 38) [ORDERED]

C548. Dorsal midline osteoderms, morphology: rounded (0); rectangular (1) (adapted  
from Norell and Clark, 1990, character 16 and Clark, 1994, character 95; in  
Brochu 1999, character 36)
C549. Dorsal osteoderms, number of contiguous osteoderms per row at maturity:
   four (0), six (1), eight (2); ten (3) (adapted from Norell and Clark 1990,
   character 12 and Clark 1994, character 97; in Brochu 1999, character 37)

[ORDERED]

   absent (0); present (1) (Turner & Sertich 2010; in Montefeltro et al. 2013,
   character 469)

C551. Dorsal parasagittal osteoderms, morphology: without articular anterior
   process (0), with a discrete convexity on anterior margin (1); with a well-
   developed process located anterolaterally (2) (modified from Clark 1994; in
   Pol & Norell 2004, character 96) [ORDERED]

C552. Dorsal osteoderms, number of rows: two parallel rows (0), more than two (1),
   more than four with accessory ranges of osteoderms (2) (modified from Clark
   1994; in Pol & Norell 2004, character 97) [ORDERED]

C553. Dorsal osteoderms, continuity of armour: dorsal armour continues uniformly
   from neck to tail (0); dorsal armour shows a narrowing or gap at the cervico-
   thoracic junction (1) (Jouve et al. 2006, character 233)

C554. Dorsal medial osteoderms, morphology of lateral margins: linear (0); serrated
   and curved, sutured with the lateral osteoderm (sends an acute process
   laterally) (1) (Jouve et al. 2008, character 37)

C555. Osteoderms, morphology of lateral margins: horizontal (0); thick and vertical
   (1) (Jouve et al. 2006, character 232)
C556. Presacral dorsal osteoderms, number of keels on transverse bands: one (0), more than one (1) (modified from Ortega et al. 2000, character 115; in Jouve et al. 2006, character 234)

C557. Median pelvic keel osteoderms, order: form two parallel rows along most of tail length (0); form single row along tail (1); merge with lateral keel scales to form Y-shaped keel (2) (Poe 1997; in Brochu 1999, character 157)

[UNORDERED]

C558. Ventral collar osteoderms, size relative to other ventral scales: enlarged, ratio of ventral collar to other ventral scale diameters larger than 1:1 (0); not enlarged, diameter ratio 1:1 (1) (after Poe, 1997; in Brochu 1999, character 156)

C559. Ventral collar osteoderms, number of rows: one (0), two (1) (after Poe, 1997; in Brochu 1999, character 156)

C560. Ventral osteoderms, follicle gland pores: present (0); absent (1) (after Brochu 1999, character 155)

C561. Ventral armor: absent (0); present (1) (modified from Buscalioni et al. 1992, character 21; in Brochu 1999, character 39)

C562. Ventral armor, state of osteoderms: osteoderms single (1); osteoderms consist of paired ossifications that suture together (2) (modified from Buscalioni et al. 1992, character 21; in Brochu 1999, character 39)

[UNORDERED]

C563. Ventral trunk osteoderms: absent (0); present (1) (Clark 1994, character 100)
C564. Tail osteoderms: dorsal only (0); tail completely surrounded by osteoderms (1)  
(Clark 1994, character 99)

C565. Appendicular osteoderms: absent (0); present (1) (Pol & Norell 2004; in Jouve 2009, character 306)

**General Postcranial**

C566. Tongue, keratinized surface: present (0); absent (1) (after Brochu 1999, character 159)

C567. Vertebra, morphology of centra: cylindrical, dorsal and ventral edges parallel in lateral view (0); spool-shaped, dorsal and ventral edges indented in lateral view (1) (Buscalioni & Sanz 1988; in Clark 1994, character 113)

*Figure 163*: Cervical vertebrae in right lateral view from *Croocyclus cf. clavis.*  
(character 567, state 1)

C568. Posterior cervical vertebrae, height of peduncle of neural arch compared to pedicel height of each of the thoracic, sacral and anteriormost caudal vertebrae: equal, ratio 1:1 (0); taller, ratio larger than 1:1 (1) (Salisbury et al. 2006, character 169)

C569. M. caudofemoralis, with single head (0); with double head (longus and brevis) (1) (Brochu 1999, character 160)
### Appendix B

### Character scores

**Alligator mcgrewi:**  
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**Alligator mefferdi:**  
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**Alligator mississippiensis**: 0.277-0.318 0.737-0.796 0.500-0.559 1.196-1.353
0.170-0.333 1.269-1.556 1.000 0.229-0.254 0.381-0.447 2.075-2.143 0.032-0.034 14.000-16.000 4.000 0.190-0.234 0.660 0.000 0.616-0.633 14.000-16.000 0.328-0.467 0.526-0.729 0.706-1.200 0.465-0.559 0.569-0.667 0.250 0.254-0.275 0.593-0.737 0.183-0.190 0.921-0.980 0.389-0.451 0.761-0.880 0.543-0.681 0.559-0.667 0.333-0.474 0.030-0.042 0.020-0.103 0.460-0.488 0.367-0.430 24.536-54.668 0.647-0.723 0.637-0.667 0.224-0.257 1.000-1.077 0.627-0.663 0.466-0.521 0.667-1.000 0.082-0.115 0.804-1.000 0.358-0.671 0.214-0.714 0.171-0.284 0.559-0.591 0.912-1.029 0.800-21.000 20.000-22.000 0.386-0.408 0.378-0.579 0.647-0.723 0.637-0.667 0.224-0.257 1.000-1.077 0.627-0.663 0.466-0.521 0.667-1.000 0.082-0.115 0.804-1.000 0.358-0.671 0.214-0.714 0.171-0.284 0.559-0.591 0.912-1.029 0.800-21.000 20.000-22.000 0.386-0.408 0.378-0.579

**Alligator prenasalis**: 0.299 0.603 0.200 1.360 0.210 1.340 1.016 0.387 0.532
2.229 0.053 14.000 4.000 0.293 0.000 0.540 0.237 0.904 14.000 0.692 ? ?
Alligator sinensis: 0.295 0.836 0.524 1.381 1.167 1.271 1.000 0.295 0.443
2.316 0.050 13.000 4.000 0.220 0.000 0.604 0.000 0.631 12.000 0.308 0.490
1.292 0.452 0.519 0.230 0.197 0.735 0.237 0.941 0.429 1.167 0.591 0.739
0.429 0.024 0.000 0.551 0.557 0.615 0.761 0.241 0.859 0.683 0.522 1.231
0.096 0.473 0.555 0.306 0.316 0.657 0.870 0.762 40.000 0.442 0.522 0.000

Allognathosuchus heterodon: 0.245 0.735 0.365 0.882 0.182 1.172 1.000
? 0.618 1.905 ? ? 4.000 0.197 0.000 0.511 ? ? ? ? ? 0.810
0.500 0.293 0.714 0.201 ? ? ? ? ? 0.500 ? ? 0.640 0.441 ? ? 0.672
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**Allognathosuchus mooki**: 0.275 0.400 0.144 1.281 0.232 1.034 1.000 0.350

**Allognathosuchus wartheni**: 0.256 0.594 0.354 1.385 0.190 1.032 1.000
**Amphicotylus felix:** 0.167 0.750 0.356 1.250 0.638 1.419 1.065 0.000 0.644 0.173 0.647 0.379 0.485 0.939 1.000 0.330 0.853 0.129 0.000 0.552 0.679 0.941 43.907 0.698 0.713 0.149 0.330 1.044 43.907 0.698 0.713 0.149 0.330 1.044

**Amphicotylus lucasii:** 0.215 0.640 0.424 1.030 0.141 0.781 1.534 0.466 0.776 1.538 0.031 18.000 5.000 0.267 0.000 0.625 17.000 1.000 1.000 0.448 0.939 1.000 0.053 0.330 0.534 48.642 0.464 0.692 0.198 0.397 1.014 0.627 0.706 0.625 0.053 0.433 0.534 48.642 0.464 0.692 0.198 0.397 1.014 0.627 0.706 0.625 0.053 0.433 0.534
Anteophthalmosuchus hooleyi: 0.360 1.600 1.000 0.272 0.500 0.067 11.000 4.000 0.000 0.472 0.000 0.647 11.000 0.924 0.141 3.226 0.500 0.463 0.231 0.190 1.000 0.247 0.600 0.729 0.591 0.000 0.629 0.300 52.516 0.452 0.769 0.233 0.821 0.722 0.672 0.857 0.121 0.615 0.652 0.957 0.728 0.588 0.231 0.190 1.000 0.247 0.600 0.729 0.591 0.000 0.629 0.300 52.516 0.452 0.769 0.233 0.821 0.722 0.672 0.857 0.121 0.615 0.652 0.957 0.728 0.588

Arambourgia gaudryi: 0.360 1.600 1.000 0.272 0.500 0.067 11.000 4.000 0.000 0.472 0.000 0.647 11.000 0.924 0.141 3.226 0.500 0.463 0.231 0.190 1.000 0.247 0.600 0.729 0.591 0.000 0.629 0.300 52.516 0.452 0.769 0.233 0.821 0.722 0.672 0.857 0.121 0.615 0.652 0.957 0.728 0.588

Araripesuchus gomesii: 0.360 1.600 1.000 0.272 0.500 0.067 11.000 4.000 0.000 0.472 0.000 0.647 11.000 0.924 0.141 3.226 0.500 0.463 0.231 0.190 1.000 0.247 0.600 0.729 0.591 0.000 0.629 0.300 52.516 0.452 0.769 0.233 0.821 0.722 0.672 0.857 0.121 0.615 0.652 0.957 0.728 0.588
Asiatosuchus grangeri:

Asiatosuchus nanlingensis:

### Baryphracta deponiae:

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### Bernissartia fagesii:

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344
| Borealsuchus wilsoni: | 0.160-0.189 0.931 0.800 1.333 0.222-0.339 ? 1.261-1.451 0.239-0.529 0.804 1.545-2.097 0.035-0.045 17.000-20.000 4.000 0.187-0.203 0.000 0.564-0.687 ? ? 15.000 ? ? ? ? 1.537 0.957-1.235 0.336-0.391 0.721-0.922 0.110-0.138 ? 0.255-0.370 0.352-0.467 0.420 0.542 0.020-0.674 ? 0.059 0.441-0.526 0.630 37.019-58.112 0.429-0.576 0.578-0.679 0.183-0.202 0.317-0.351 1.025-1.120 0.629-0.686 ? ? 0.333-0.667 ? ? 0.553-0.612 1.079 0.800 23.000 0.171 0.262 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1?0?0011001?21100??0??000?1010100??10?1??12011000000???00?000? 1??0?0?0110??0?010?000?0????0000?0000?0111000000??1?0001 1??1010020010000?0110?0000000??0200?0000?0?1?01001??1011?1?0 001011000001001120??0011?011110?0000?0?????0??00?110?000? 00?0?0?1?1?01????0010010?1?00200??????1100?10??01000?10?0010?1?1? ??01?00100010100100110000220010????????001001?001?00100001100 000?00?0??????????????0110100201001000?00100??00000101?00??00 1?1??1??0????????????????10?11??0????????0???11? 

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Brachyuranochampsa zangerli:  
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352
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**354**
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0.035 14.000 5.000 0.248-0.282 0.000 0.588-0.701 0.833-0.972 1.102-1.131
11.000-13.000 0.493-0.692 0.641-0.922 1.439-1.593 0.536-0.713 1.196-1.438
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0.582 0.528-0.596 0.120-0.889 0.513-0.688 0.021-0.047 0.000 0.438-0.502 0.295
0.378 49.072-54.238 0.694-0.769 0.764-0.818 0.209-0.273 0.681-0.986 0.563
0.693 0.433-0.507 0.471-0.947 0.060-0.130 0.446-0.656 0.324-0.464 0.623
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12.000-13.000 0.512-0.732 0.483-0.660 1.290-2.517 0.522-0.684 1.455-1.656
0.585-0.716 0.366-0.431 0.633-0.717 0.141-0.149 0.651-0.706 0.404-0.429 0.526-0.541 0.579-0.610 0.735-1.083 0.525-0.550 0.022-0.031 0.000 0.438-0.463 0.305-0.392 35.728-46.059 0.644-0.750 0.618-0.738 0.205-0.215 0.602-0.664 0.732-0.753 0.540-0.550 0.625-0.826 0.097-0.121 0.453-0.709 0.238-0.443 0.353-0.492 0.122-0.387 0.542-0.557 0.722-0.814 0.571-0.605 27.000-31.000 0.413-0.518 0.543-0.727

Crocodylus sivalensis: 0.290-0.309 0.873-0.991 0.623-0.755 1.020-1.396
0.206-0.214 0.824 1.073-1.125 0.445-0.448 0.438 2.603-3.065 0.036-0.050 14.000
5.000 0.190-0.240 0.000 0.622-0.644 14.000 0.190-0.240 0.000 0.622-0.644 14.000
0.204 0.381-0.448 0.344-0.384 0.672-0.806 0.164-0.175 0.560-0.667 0.440 0.610 0.514-0.585 0.716 0.366-0.431 0.633-0.717 0.141-0.149 0.651-0.706 0.404-0.429 0.526-0.541 0.579-0.610 0.735-1.083 0.525-0.550 0.022-0.031 0.000 0.438-0.463 0.305-0.392 35.728-46.059 0.644-0.750 0.618-0.738 0.205-0.215 0.602-0.664 0.732-0.753 0.540-0.550 0.625-0.826 0.097-0.121 0.453-0.709 0.238-0.443 0.353-0.492 0.122-0.387 0.542-0.557 0.722-0.814 0.571-0.605 27.000-31.000 0.413-0.518 0.543-0.727

1
Diplocynodon darwinii: 0.230 0.545 0.333 0.944 0.256 0.917 1.035 0.341

0.576 2.500 0.035 17.000 5.000 0.281 0.000 0.628 ？？？？？？？？？？？？？？？？？？？？？？？？？？

0.259 0.176 0.684 0.149 0.800 0.372 0.471 0.473 0.473 0.649 ？？？？？？？？？？？？？？？？？？？？？？？？？？？

64.138 0.452 0.792 0.152 0.680 0.786 0.556 ？？？？？？？？？？？？？？？？？？？？？？？？？？？

Diplocynodon hantoniensis: 0.278 0.615 0.371 1.238 0.155 1.472 1.472

0.340 ？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？？

358
Diplocynodon remensis: 0.724 0.481 0.852 1.055 1.184 0.306 1.760

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**Eogavialis gavialoides**: 0.078-0.099 0.806-0.868 0.778-0.806 1.056-1.167 0.057 0.298-0.374 1.388-1.636 0.409-0.571 0.273-0.612 1.000-2.500 0.008-
Eosuchus lerichei: 0.099 0.651 0.556 0.815 0.179 0.305 1.483 0.483 0.862
1.357 0.019 ? 4.000 0.316 0.000 0.721 0.718 1.327 12.000 0.346 0.682 1.433
0.230 0.920 0.793 0.215 0.795 0.102 0.731 0.402 0.537 0.523 0.532 0.932
0.023 0.036 0.397 0.793 56.390 0.745 0.738 0.165 0.271 0.799 0.594 0.609
0.128 0.740 0.000 ? 0.360 0.416 0.810 0.947 ? ? ? ? ? ? ? ? ? ? ?

363
Eosuchus minor: 0.098 0.872 0.893 1.036 0.239 0.362 1.205 0.590 0.718
1.739 0.020 18.000 4.000 0.293 0.000 0.688 1.115 1.117 16.000 0.526 0.407
1.409 0.888 0.821 0.590 0.181 0.722 0.112 0.621 0.451 0.659 0.443 ? 0.833
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Euthecodon arambourgi: 0.085 0.887 0.893 0.929 0.938 0.291 1.606 0.788
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366
Gavialosuchus antiquus: 1.589 0.527 1.364 0.593 0.222 0.947 0.222 0.593 0.527 0.222 0.947 0.593 0.222

Gavialosuchus eggenburgensis: 0.194 0.282 1.364 0.782 0.203 0.955 0.512 0.603 0.820 0.203 0.955 0.512 0.603 0.820

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Leidyosuchus multidentatus:
**Maroccosuchus zennaroi:**

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Navajosuchus novomexicanus: 0.209 0.640 0.276 1.095 1.042 1.000
0.260 0.600 1.500 4.000 0.231 0.548 0.867 0.520
0.656 0.440 0.260 0.600 1.500 4.000 0.231 0.548

Notosuchus terrestris: 0.264 0.615 0.000 1.828 1.773 1.000 0.641 0.718
2.517 0.192 0.350 0.378 0.723 1.348 0.588 0.343 0.893 0.641
0.342 0.825 0.270 0.538 1.538 0.481 0.306 0.900 0.000 0.966 0.410
0.658 0.795 0.310 0.534 0.500 0.871 0.212 0.789 16.000 0.211

Osteolaemus tetraspis: 0.245-0.248 0.564-0.608 0.247-0.313 1.250-1.588
0.245-0.248 0.564-0.608 0.247-0.313 1.250-1.588

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Pholidosaurus purbeckensis:

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Planocrania datangensis: 0.164 0.737 0.339 0.913 ? 0.633 1.086 0.400
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? 0.220 0.920 0.657 0.307 0.721 0.185 ? ? ? 0.603 0.833 0.628 ? ? ?
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Planocrania hengdongensis: 0.172 ? ? 1.000 ? ? 1.316 0.321 ? ?
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Prodiplocynodon langi: 0.205 0.623 0.321 0.906 0.253 ? 1.205 0.364 ?
1.809 0.041 15.000 5.000 0.267 0.000 0.612 ? ? ? ? ? ? 0.432 0.247
Protosuchus richardsoni: 0.109 0.288
Rhabdognathus keiniensis: 0.230
Rhabdognathus sp: 0.957 0.905

Rhamphosuchus crassidens:

Sarcosuchus imperator: 0.258 0.859 0.449 1.861 0.877 0.348 0.011 0.786 1.070 0.090 0.457
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379
Steneosaurus bollensis: 0.061-0.089 0.406-0.486 0.000 1.000-1.400 ? 0.508-
0.673 1.429-1.455 ? 0.633-0.909 ? ? ? ? 0.000 0.717-0.733 ? ? ? ? ?
? ? 1.950-2.065 1.306-1.773 0.254-0.283 0.710-0.727 0.079-0.083 ? ? ? ? ?
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### Sunosuchus miaoii

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Theriosuchus pusillus: 0.247 0.526 0.283 1.151
Thoracosaurus macrorhynchus: 0.090 0.952 0.344 0.781

Theriosuchus pusillus: 0.247 0.526 0.283 1.151
Thoracosaurus macrorhynchus: 0.090 0.952 0.344 0.781
Thoracosaurus neocesariensis: 0.000 0.258 1.446 0.336 0.833 0.420 0.430 0.146

Tomistoma cairense: 0.000 0.577 1.111 0.613 0.000 1.583 0.202 0.667 0.441 0.377 0.584 0.560 0.640 0.578 0.000 0.000 50.364 0.750 0.670 0.206 0.887 0.495 1.105 0.100 0.563 0.000 0.000 50.364 0.750 0.670 0.206
Tomistoma dowsoni: 0.106 0.891 0.813 0.750 ? 0.390 1.667 0.818 0.970
1.579 0.009 16.000 ? 0.303 0.000 0.708 0.676 1.203 15.000 0.321 ? ? 0.909
1.313 1.273 0.341 0.872 0.090 0.842 ? ? ? 0.894 ? ? ? 1.030 57.251
0.683 0.870 0.131 0.268 0.842 ? ? ? 0.486 0.542 ? ? ? ? ? ? ? ?

Tomistoma petrolica: 0.118 0.500 0.211 0.800 0.375 0.429 1.556 0.667
0.815 2.156 0.015 16.000 ? 0.265 0.000 0.706 ? ? ? ? ? ? 0.818
0.667 0.182 0.837 0.120 0.517 0.329 0.506 0.518 0.556 0.721 ? 0.000 0.339
0.741 ? 0.481 0.646 0.156 0.273 1.456 0.717 ? ? ? ? ? 0.387 ? ?

Tomistoma schlegelii: 0.077-0.098 0.737-1.068 0.806-1.000 0.704-0.806
0.158-0.184 0.223-0.270 1.333-1.500 0.789-0.842 0.579-0.727 1.479-1.857 0.010-
Vectisuchus leptognathus: 0.325

Voay robustus: 0.339 0.586 0.432 0.946 0.178 1.261 1.144 0.375-0.392
Appendix C

Supplementary information

C.1 List of Synapomorphies

Synapomorphies given for discrete characters, obtained by using the 'List synapomorphies' function in TNT v 1.5. Character numbers refer to the original character list of 569 characters. Synapomorphies are listed for the tree in Fig. 2.3, using analysis IV. For clade labels and phylogenetic definitions, see Fig. 2.3. Character consistency indices are given after each character. For a full list of synapomorphies for each node, see the online-only supplementary material.

Notosuchia: premaxillae loosely sutured anterior to nares (C92.1, CI=1.0); perinarial fossa on premaxillae present (C102.1, CI=1.0); posterolateral process of squamosal depressed from skull table (C234.1, CI=0.0033); descending ornamented process at posterolateral edge of squamosal (C235.1, CI=1.0); posterior posterolateral process of squamosal tapered (C236.0, CI=0.0014); major axis of quadrate ventrally directed (C273.1, CI=1.0); ventral orientation of quadrate body distal to otoccipital-quadrate contact (C.277.0, CI=1.0); quadrate with two distinct faces in posterior view (C281.1, CI=1.0); dorsal margin of paroccipital process anterior to quadrate condyle (C289.1, CI=0.13); three sacral vertebrae (C498.1, CI=1.0); no articular anterior process on dorsal parasagittal osteoderms (C551.0, CI=0.22).
**Tethysuchia excl.** *Terminonaris*: medial tubercles on posterior margin of external nares (C99.1, CI=0.14); zigzag-shaped frontoparietal suture on interfenestral bar (C195.1, CI=0.33); long and acute anterolateral process on postorbitals (C200.1, CI=1.0).

**Dyrosauridae excl.** *Elosuchus*: inner antero-posterior margins of maxillae linear over the anterior 2/3 (C125.2, CI=0.14); complex dorsal supratemporal roof surface (C208.0, CI=0.17); elongated posteriorly directed process at posterior edge of squamosal (C237.1, CI=1.0); quadratojugal forms lateral extension to quadrate condyles and participates in mandibular joint (C272.1, CI=0.25); no dorsal exposure of supraoccipital (C286.0, CI=0.1); paroccipital process curves downwards strongly (C290.3, CI=0.21); large bilateral posterior prominences on exoccipital and supraoccipital (C296.1, CI=0.5); paired grooves along ventral surface of basioccipital (C307.1, CI=1.0); seventh alveolus on dentary smaller than other alveoli (C422.1, CI=0.5).

**Pholidosauridae incl.** *Elosuchus*: medial tubercles on posterior margin of anterior nares in ventral position (C100.2, CI=0.33); upper toothrow of mandible nearly straight (C413.1, CI=0.11).

**Pholidosauridae**: orbits positioned laterally (C180.1, CI=0.14); quadratojugal-jugal suture situated at posterior angle of infratemporal fenestra (C265.1, CI=0.11); pterygoids do not participate in anterior margin of choanae (C356.0, CI=0.25).

**Goniopholididae excl.** *Susisuchus*: depression on posterolateral surface of maxilla (C134.1, CI=0.33); lateral margins of osteoderms thick and vertical (C555.1, CI=0.33).

**Most derived Goniopholididae** (*Goniopholis, Amphicotylus, Anteophthalmosuchus*): lateral fossa excavating the alveolus of the last premaxillary tooth (C114.1, CI=0.33); crest dorsal to orbit on prefrontal-lacrimal (C168.1, CI=0.14); lateral margins of upper temporal bard strongly sinuisoidal (C207.1, CI=0.17); quadratojugal forms posterior angle of infratemporal fenestra (C265.0, CI=0.11).
**Borealosuchus**: anterior median palatine process into maxilla in form of thin wedge (C371.1, CI=0.11); dentary alveoli 3 and 4 confluent (C420.0, CI=0.33); surangular extends to posterior end of retroarticular process (C450.0, CI=0.14); peduncle of neural arch on posterior cervical vertebrae larger than all other vertebral pedicels (C568.1, CI=0.33).

**Planocrainiidae**: anterior opening of temporal canal exposed in dorsal view (C226.0, CI=0.09); strongly compressed dentary teeth (C414.1, CI=0.5); dentary teeth occlude lingually to maxillary teeth (C425.0, CI=0.2).

**Gavialoidea + Crocodyloidea + Alligatoroidea**: dorsal longitudinal ridge on frontals restricted to central portion (C190.1, CI=0.2); frontoparietal suture on skull table entirely (C193.2, CI=0.14); frontoparietal suture concavoconvex (C194.0, CI=0.08); parieto-postorbital suture present on skull roof (C244.1, CI=0.13); lateral edges of anterior half of interfenestral bar between suborbital fenestrae flared anteriorly (C366.1, CI=0.08); crest present on dorsal surface of axis neural spine (C480.0, CI=0.33).

**Gavialoidea incl. Maroccosuchus**: ventral opening on ventral edge of premaxillo-maxillary contact (C118.1, CI=0.08); dorsal and ventral rims of groove for external ear valve musculature flaring anteriorly (C230.1., CI=0.5); spina quadratojugalis reduced or absent in maturity (C269.1, CI=0.11); basioccipital with large pendulous tubera (C305.1., CI=0.17); interalveolar space between third and fourth dentary alveoli roughly equal to space between second and third (C418.0, CI=0.08).

**Gavialidae (excl. Gryposuchinae)**: ventral opening on ventral edge of premaxillo-maxillary contact (C118.1, CI=0.08); prominent notch in ventral margin of orbits (C256.1, CI=1.0).

**Crocodyloidea + Alligatoroidea**: premaxillary ventral projections rounded (C123.0, CI=0.25); prefrontal pillar expanded anteroposteriorly (C175.1, CI=1.0); posterior margin of otic aperture invaginate (C324.1., CI=0.5); sulcus between articular and surangular absent (C454.1, CI=0.33); dorsal edges of coronoid
oriented almost horizontal (C463.1, CI=0.33); prominent hypapophysis on first postaxial vertebra (C484.0, CI=1.0); proximal edge of deltopectoral crest on humerus is concave and emerges abruptly from proximal end of humerus (C509.1, CI=0.33); nuchal shield differentiated from dorsal shield (C546.1, CI=1.0); six contiguous dorsal osteoderms per row at maturity (C549.1, CI=0.5); more than four rows of dorsal osteoderms with accessory ranges of osteoderms (C552.2, CI=1.0); dorsal armour with narrowing or gap at cervico-thoracic junction (C553.1, CI=1.0); peduncle of neural arch on posterior cervical vertebrae larger than all other vertebral pedicels (C568.1, CI=0.33).

**Crocodyloidea**: sulcus on anterior braincase wall lateral to basisphenoid rostrum (C315.1, CI=0.33); anterior perforation on mandibular ramus of cranial nerve V on splenial absent (C431.1, CI=0.13); surangular extends to posterior end of retroarticular process (C450.0, CI=0.14); tall dorsal keel on proatlas absent (C470.1, CI=0.2); anterior margins of tuberculum and capitulum of sacral vertebrae nearly in same plane (C499.1, CI=1.0); dorsal margin of iliac blade rounded with modest dorsal indentation (C522.1, CI=0.29); follicle gland pores on ventral osteoderms absent (C560.1, CI=1.0).

**Crocodylidae**: rostrum contour concave in lateral view (C86.2, CI=0.11); medial process of prefrontal pillar constricted at base (C176.1, CI=1.0); paroccipital process with horizontal medial edge and sharply inclined terminal third at 45° angle (C290.1, CI=0.21); no posterior wall on median Eustachian foramen on basisphenoid (C318.1, CI=0.25); posterior pterygoid processes small (C346.0, CI=0.33); lingual foramen on surangular-articular suture (C443.1, CI=0.18); interclavicle with moderate dorsoventral flexure (C508.1, CI=0.33).

**Tomistominae**: premaxillary ventral projections with sharp tips (C123.1, CI=0.25); dorsal and ventral rims of groove for external ear valve musculature flaring anteriorly (C230.1, CI=0.5); squamosal prongs long, covering large part of paroccipital process (C233.1, CI=0.08).

**Crocodylinae**: quadratojugal-jugal suture lies at posterior angle of infratem-
poral fenestra (C265.1, CI=0.11); posterior notch on suborbital fenestrae (C373.1, CI=0.14); anterior process dorsal to lingual foramen on articular-surangular suture (C453.1, CI=0.5).

**Alligatoroidea:** two or more projections of premaxillae at premaxilo-maxillary contact (C122.2, CI=0.13); inner antero-posterior margins of maxillae linear for anterior 2/3 or less (C125.1, CI=0.14); foramen aerum on dorsal surface of quadrate (C275.1, CI=0.14); ectopterygoid stops abruptly ventral to postorbital bar (C329.1, CI=0.25); dentary teeth occlude lingually to maxillary teeth (C425.0, CI=0.2); both sides of forked process of surangular onto dentary equal (C445.1, CI=0.5); posterior end of postacetabular process of ilium subrectangular (C531.1, CI=0.33); six nuchal osteoderms (C547.1, CI=0.33); single osteoderms on ventral armour (C562.0, CI=0.33).

**Diplocynodontinae incl. Leidyosuchus:** frontal prevents contact between postorbital and parietal on skull table (C193.0, CI=0.14); parieto-postorbital suture absent from skull roof (C244.0, CI=0.13); dentary alveoli 3 and 4 confluent (C420.0, CI=0.33).

**Diplocynodontinae excl. Leidyosuchus:** preorbital ridges reduced (C87.1, CI=0.11); no contact of external nares with nasal (C149.0, CI=0.1); linear frontoparietal suture (C194.1, CI=0.08); parietal and squamosal approach each other on posterior wall of supratemporal fenestra without making contact (C218.1, CI=0.33); lingual foramen for articular artery and alveolar nerve on surangular-articular suture (C443.1, CI=0.18); distal region of articular surface for ulnare on radiale triangularly shaped (C521.1, CI=1.0).

**Alligatoridae:** premaxillae form less than ventral half of internarial bar (C101.1, CI=0.17); no constriction of snout at premaxillo-maxillary contact (C113.0, CI=0.17); no opening on ventral edge of premaxillo-maxillary contact (C118.0, CI=0.08); no contact of nasal with lacrimals at medial edge (C160.0, CI=0.13); parietal and squamosal meet along posterior wall of supratemporal fenestra (C218.2, CI=0.33); jugal edge producing anterior notch at contact with lacrimal (C250.1,
CI=0.1); prootic largely obscured by quadrate and laterosphenoid externally (C322.1, CI=0.33); maxilla broadly separates ectopterygoid from maxillary toothrow (C327.1, CI=1.0); palatine-pterygoid suture close to posterior angle of suborbital fenestra (C376.0, CI=0.5); last premaxillary tooth anteromedial to first maxillary tooth (C382.1, CI=0.11); maxillary alveoli heterodont (C390.1, CI=0.14); intercentrum of atlas plate-shaped (C472.1, CI=1.0).

**Caimaninae:** dorsal contour of rostrum concave in lateral view (C86.2, CI=0.11); external nares confluent (C97.1, CI=0.17); internarial bar not bisecting nares (C151.0, CI=0.2); contact of lacrimals with nasal at medial edge (C160.1, CI=0.13); no transverse ridge of frontals (C191.0, CI=0.2); rim of suprtemporal fenestrae overhangs fenestrae (C222.1, CI=0.33); quadratojugal does not extend to superior angle of infratemporal fenestra (C267.0, CI=0.14); dorsal exposure of supraoccipital (C286.1, CI=0.1); dorsal margin of supraoccipital same height as dorsal margin of squamosal (C288.1, CI=0.11); occipitals participate in basioccipital tubera (C301.1, CI=0.09); ectopterygoid-pterygoid flexure remains throughout ontogeny (C332.1, CI=1.0); last premaxillary tooth anterior to first maxillary tooth (C382.0, CI=0.11); no anterior perforation on splenial for cranial nerve V (C431.1, CI=0.13); angular does not extend beyond anterior end of foramen intermandibularis caudalis (C435.1, CI=1.0); angular-surangular suture passes broadly along ventral margin of external mandibular fenestra (C441.1, CI=0.2); contact of surangular-angular suture with articular dorsal to ventral tip (C448.1, CI=1.0); surangular extends to posterior end of retroarticular process (C450.0, CI=0.14); ventral process of coronoid remains largely on medial surface of mandible (C464.1, CI=1.0); thin medial laminae at anterior end of atlantal ribs (C474.1, CI=1.0); six nuchal osteoderms (C547.1, CI=0.33); four contiguous dorsal osteoderms per row at maturity (C549.0, CI=0.5); paired ossifications suturing osteoderms of ventral armour together (C562.1, CI=0.33).
C.2 List of examined specimens

†: extinct species

*Alligator mcgrewii*†: AMNH FR 8700, AMNH FR 7905

*Alligator mefferdi*†: AMNH FR 7016

*Alligator mississippiensis*: NHMUK X.184, NHMUK 1868.2.12.6, NHMUK 1873.2.21.2

*Alligator prenasalis*†: YPM VP 014063, YPM VP 026273

*Alligator sinensis*: IVPP V1335

*Allognathosuchus heterodon*†: AMNH FR 5157, FR 2088, FR 1257, USNM 16832, USNM 2508, USNM 13680, USNM 16835

*Allognathosuchus mooki*†: AMNH FR 6780

*Allognathosuchus wartheni*†: YPM VP 016989

*Amphicotylus lucasii*†: AMNH FR 5782 (as *Goniopholis lucasii*)

*Anteophthalmosuchus hooleyi*†: NHMUK R 3876

*Arambourgia gaudryi*†: MNHN QU17155

*Araripesuchus gomesii*†: AMNH FR 24450

*Asiatosuchus grangeri*†: AMNH FR 6606, AMNH FR 6607, AMNH FR 6608

*Asiatosuchus nanlingensis*†: IVPP V.2772, IVPP V.2773

*Bernissartia fagesii*†: IRSNB 1538, NHMUK PV OR 37712

*Borealosuchus formidabilis*†: YPM VP 016512 (as *Leidyosuchus formidabilis*)
Borealosuchus wilsoni†: AMNH FR 7637 (as Leidyosuchus wilsoni), USNM 12990

Boverisuchus vorax†: AMNH FR 29993 (as Pristichampsia vorax)) USNM 12957 (as Pristichampsus rollinatii)

Brachychampsia montana†: AMNH FR 5032, USNM 7068

Brachyuranochampsia zangerli†: AMNH FR 6048, AMNH FR 16609, YPM VP 000246

Brochuchus pigotti†: NHMUK PV R 7729

Caiman crocodilus: NHMUK 1946.4.463, NHMUK 1898.9.26.1, NHMUK 1846.4.21.10

Caiman latirostris: NHMUK 2009.1, NHMUK 1886.10.4.2, NHMUK 2008.270

Comahuesuchus brachybuccalis†: NHMUK PV R 14104 (cast)

Congosaurus compressus†: MNHN TGE 4034, MNHN TGE 4036, MNHN TGE 4198

Crocodilaemus robustus†: USNM 15828, USNM 537820

Crocodylus cf. clavis†: AMNH FR 1212, USNM 12719

Crocodylus acutus: NHMUK 1975.997

Crocodylus affinis†: USNM 18390, YPM VP 001345

Crocodylus depressifrons†: MNHN G 160

Crocodylus elliotti†: USNM 141, USNM 923, YPM VP 010075

Crocodylus intermedius: NHMUK 1851.8.25.29, NHMUK 1862.10.19.1

Crocodylus megarhinus†: AMNH FR 5061, AMNH FR 5095, YPM VP 058532, NHMUK PV R 3327

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Crocodylus moreletii: NHMUK 1861.4.1.4

Crocodylus niloticus: NHMUK 1967.1076, NHMUK 1934.6.3.1, NHMUK 1897.6.24.1

Crocodylus novaeguineae: NHMUK 1886.5.20.1, NHMUK 1886.5.20.2

Crocodylus palustris: NHMUK 1897.12.31.1 (as Crocodylus palustris kim-bula), NHMUK 1848.2.5.9, NHMUK 1861.4.1.5

Crocodylus porosus: NHMUK 1847.3.5.33, NHMUK 1969.1590, NHMUK 1857.4.2.187

Crocodylus rhombifer: AMNH FR 16623, AMNH FR 16638, AMNH FR 6178, AMNH FR 6179

Crocodylus siamensis: NHMUK 1921.4.1.17, NHMUK 1921.4.1.168, NHMUK 1920.1.1626

Crocodylus silvalensis†: AMNH FR 1915

Crocodylus sivalensis†: NHMUK PV R 39705

Diplocynodon hantoniensis†: AMNH FR 27632 (cast), NHMUK PV OR 30393

Diplocynodon remensis†: IRSNB R289, MNHN F BR 4020, MNHN MB 051, MNHN BR 2622, MNHN BR 10085, MNHN BR 15976, MNHN BR 15200, MNHN BR 1645, MNHN BR 13106, MNHN BR 2617, MNHN BR 4021, MNHN BR 3171, MNHN BR 15197, MNHN BR 15227, MNHN BR 3649, MNHN BR 3636, MNHN BR 4244, MNHN BR 13695, MNHN BR 3663, MNHN BR 3634, MNHN BR 13418, MNHN BR 3639, MNHN BR 3631

Diplocynodon ungeri†: SMNK (unnumbered skull) (as Diplocynodon steineri)
*Dollosuchoides densmorei*†: IRSNB 1748

*Dyrosaurus phosphaticus*†: MNHN 1901-11, MNHN APH 27, MNHN APH 25, MNHN APH 23, MNHN (unnumbered skull)

*Elosuchus cherifiensis*†: MNHN MRS 340, MNHN SAM 129

*Elosuchus felixi*†: MNHN INA 21, MNHN INA 25, MNHN INA 3

*Eoalligator chunyi*†: IVPP V.2716

*Eoalligator huiningensis*†: IVPP V.4058

*Eocaiman cavernensis*†: AMNH FR 3158

*Eogavialis africanum*†: SMNS 11785

*Eogavialis gavialoides*†: AMNH FR 5066, AMNH FR 5067, AMNH FR 5069 (as *Gavialis gavialoides*), YPM VP 006263 (as *Tomistoma gavialoides*)

*Eosuchus lerichei*†: IRSNB 1740, IRSNB R 49

*Eosuchus minor*†: USNM 321933, USNM 181577, USNM 299730, USNM 418486

*Euthecodon arambourgi*†: MNHN ZEL 001

*Eutretauranosuchus delfsi*†: AMNH FR 570

*Gavialis gangeticus*: LDUCZ X1206, NHMUK 1935.6.4.1, NHMUK 2005.1601

*Gavialis hysudricus*†: NHMUK PV OR 39805, NHMUK PV OR 39808

*Gavialis lewisi*†: YPM VP 003226

*Gavialosuchus eggenburgensis*†: NHMUK PV R 797 (cast)

*Goniopholis felix*†: YPM VP 000517

*Goniopholis simus*†: NHMUK PV OR 41098
Hylaeochamps vectiana†: NHMUK PV R 177

Hyposaurus natator†: YPM VP 000985

Kentisuchus spenceri†: NHMUK PV OR 37717

Leidyosuchus canadensis†: YPM VP 000284, NHMUK PV R 10904 (cast)

Leidyosuchus gilmorei†: AMNH FR 5352

Listrognathosuchus multidentatis†: AMNH FR 5179 (as Leidyosuchus multidentatis)

Maroccosuchus zennarioi: IRSNB R408

Mecistops cataphractus: NHMUK 1900.2.27.1, NHMUK 1904.9.9.2, NHMUK 1900.2.27.1, NHMUK 1862.6.30.8

Melanosuchus niger: NHMUK 1872.6.4.1, NHMUK (unnumbered specimen), NHMUK 45.8.25.125

Nannosuchus gracilidens†: NHMUK PV OR 48301, NHMUK PV OR 48217

Navajosuchus novomexicanus†: AMNH FR 5186

Notosuchus terrestris†: NHMUKPV R 14105

Osteolaemus tetraspis: LDUCZ X122, NHMUK 1862.6.30.5, NHMUK 1983.1130, NHMUK 1862.6.30.6

Paleosuchus trigonatus: NHMUK 1868.10.8.1

Pholidosaurus purbeckensis†: NHMUK PV R 3414, PV OR 28432

Piscogavialis jugaliperforatus†: SMNK 1282 PAL

Planocrania datangensis†: IVPP V.5016

Planocrania hengdongensis†: IVPP V.6074

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Prodiplocynodon langi†: AMNH FR 108

Protosuchus richardsoni †: AMNH FR 3024, AMNH FR 3025, AMNH FR 3026, AMNH FR 3027, AMNH FR 3028

Rhabdognathus keiniensis†: MNHN TGE 4031, MNHN TGE 3917, MNHN TGE 4360, MNHN TGE 4366

Rhabdognathus sp.†: MNHN TGE 4033

Rhamphosuchus crassidens†: NHMUK PV OR 5265, NHMUK PV OR 39802

Sarcosuchus imperator†: MNHN (unnumbered complete skeleton in main exhibition)

Sebecus icaeorhinus†: AMNH FR 3159, AMNH FR 3160, AMNH FR 3162

Shamosuchus djadochaensis†: AMNH FR 6412

Steneosaurus bollensis†: SMNS (complete unnumbered skeleton), SMNS 15391

Sunosuchus junggarensis†: IVPP V.10606

Sunosuchus miao†: IVPP V.500

Susisuchus anatoceps†: SMNK 3804 PAL

Terminonaris browni†: AMNH FR 5851 (as Teleorhinus browni)

Thecachampsia americana†: AMNH FR 5662, AMNH FR 5663 (as Gavialosuchus americanus), USNM 24939 (as Tomistoma americana)

Thecachampsia antiqua†: USNM 24938 (as Gavialosuchus americanus)

Theriosuchus pusillus†: NHMUK PV OR 48330

Thoracosaurus macrorhynchus†: MNHN 1902-22, NHMUK PV R 2798, PV OR 28296a, PV OR 28296b
Thoracosaurus neocesariensis†: NHMUK PV OR 41842 (cast)

Tomistoma cairensed: SMNS 10575, SMNS 50742, SMNS 50739, SMNS 50379a, SMNS 50734

Tomistoma dowsoni†: NHMUK PV R 4769

Tomistoma petrolica†: IVPP V.2303, IVPP V.5015, IVPP (unnumbered full skull)

Tomistoma schlegelii: LDUCZ X1227, NHMUK 1848.10.31.19, NHMUK 1860.11.6.8, NHMUK (unnumbered)

Vectisuchus leptognathus†: SMNS 50984

Voay robustus†: AMNH FR 3100, AMNH FR 3101, AMNH FR 3102, AMNH FR 3103, AMNH FR 3104, AMNH FR 3105, NHMUK PV R 2026

C.3 Rejected osteological characters

Montefeltro et al. 2013

Montefeltro et al. (2013), character 1: from Clark (1994)
Montefeltro et al. (2013), character 2: from Clark (1994)
Montefeltro et al. (2013), character 3: similar to ch. 1 in this list
Montefeltro et al. (2013), character 4: all character scores 0 in this dataset
Montefeltro et al. (2013), character 5: from in Clark (1994)
Montefeltro et al. (2013), character 6: similar to ch. 127 in this list
Montefeltro et al. (2013), character 7: from Wu et al. (2001)
Montefeltro et al. (2013), character 8: too subjective, reflected in several of this continuous characters
Montefeltro et al. (2013), character 9: from Clark (1994)
Montefeltro et al. (2013), character 10: from Clark (1994)
Montefeltro et al. (2013), character 12: from Clark (1994)
Montefeltro et al. (2013), character 13: from Clark (1994)
Montefeltro et al. (2013), character 14: all character scores the same in this dataset
Montefeltro et al. (2013), character 15: all character scores the same in this dataset
Montefeltro et al. (2013), character 17: from Clark (1994)
Montefeltro et al. (2013), character 18: odd gap in character state description; all character scores 1 in this dataset
Montefeltro et al. (2013), character 19: from Ortega et al. (2000)
Montefeltro et al. (2013), character 21: from Clark (1994)
Montefeltro et al. (2013), character 23: from Clark (1994)
Montefeltro et al. (2013), character 24: from Clark (1994)
Montefeltro et al. (2013), character 27: similar to Brochu (1999), ch. 88
Montefeltro et al. (2013), character 28: all character scores the same in this dataset
Montefeltro et al. (2013), character 29: from Clark (1994)
Montefeltro et al. (2013), character 31: subjective; similar to several other characters in character list
Montefeltro et al. (2013), character 32: from Clark (1994)
Montefeltro et al. (2013), character 33: from Clark (1994)
Montefeltro et al. (2013), character 34: from Brochu (1999)
Montefeltro et al. (2013), character 35: from Jouve (2009)
Montefeltro et al. (2013), character 37: from Clark (1994)
Montefeltro et al. (2013), character 38: too subjective; reflected in continuous characters
Montefeltro et al. (2013), character 40: from Clark (1994)
Montefeltro et al. (2013), character 41: all character scores the same in this dataset
Montefeltro et al. (2013), character 44: from Clark (1994)
Montefeltro et al. (2013), character 45: from Clark (1994)
Montefeltro et al. (2013), character 46: from Clark (1994)
Montefeltro et al. (2013), character 47: all character scores the same in this dataset
Montefeltro et al. (2013), character 48: from Clark (1994)
Montefeltro et al. (2013), character 49: from Wu et al. (2001)
Montefeltro et al. (2013), character 50: too subjective, similar to ch. 147 in this list
Montefeltro et al. (2013), character 52: all character scores the same in this dataset
Montefeltro et al. (2013), character 57: all characters scores the same in this dataset
Montefeltro et al. (2013), character 58: all character scores the same in this dataset
Montefeltro et al. (2013), character 59: from Clark (1994)
Montefeltro et al. (2013), character 60: from Clark (1994)
Montefeltro et al. (2013), character 62: all character scores the same in this dataset
Montefeltro et al. (2013), character 63: from Brochu (1999)
Montefeltro et al. (2013), character 64: too subjective; reflected in continuous characters
Montefeltro et al. (2013), character 67: subjective; reflected by several other discrete characters
Montefeltro et al. (2013), character 68: all character scores the same in this dataset
Montefeltro et al. (2013), character 69: all character scores the same in this dataset
Montefeltro et al. (2013), character 71: similar to Brochu (1999) ch. 103
Montefeltro et al. (2013), character 72: all character scores the same in this dataset
Montefeltro et al. (2013), character 73: all character scores the same in this dataset
Montefeltro et al. (2013), character 74: from Clark (1994)
Montefeltro et al. (2013), character 75: from Clark (1994)
Montefeltro et al. (2013), character 77: from Clark (1994)
Montefeltro et al. (2013), character 82: from Clark (1994)
Montefeltro et al. (2013), character 83: similar to ch. 174 in this dataset
Montefeltro et al. (2013), character 84: similar to ch. 176 in this dataset
Montefeltro et al. (2013), character 85: from Sereno et al. (2001)
Montefeltro et al. (2013), character 86: from Brochu (1999)
Montefeltro et al. (2013), character 88: from Clark (1994)
Montefeltro et al. (2013), character 89: from Clark (1994)
Montefeltro et al. (2013), character 90: from Clark (1994)
Montefeltro et al. (2013), character 92: from Clark (1994)
Montefeltro et al. (2013), character 93: from Clark (1994)
Montefeltro et al. (2013), character 94: from Norell (1988), in dataset
Montefeltro et al. (2013), character 95: from Norell (1988), in dataset
Montefeltro et al. (2013), character 97: from Clark (1994)
Montefeltro et al. (2013), character 99: from Brochu (1999)
Montefeltro et al. (2013), character 100: similar to ch. 246 in this dataset
Montefeltro et al. (2013), character 101: from Wu et al. (2001)
Montefeltro et al. (2013), character 103: character not consistent in its coding
Montefeltro et al. (2013), character 104: from Clark (1994)
Montefeltro et al. (2013), character 105: from Clark (1994)
Montefeltro et al. (2013), character 106: from Clark (1994)
Montefeltro et al. (2013), character 108: all character scores the same in this dataset
Montefeltro et al. (2013), character 111: all character scores the same in this dataset
Montefeltro et al. (2013), character 112: all character scores the same in this dataset
Montefeltro et al. (2013), character 114: from Clark (1994)
Montefeltro et al. (2013), character 115: very similar to ch. 234 in this list
Montefeltro et al. (2013), character 116: reflected by several other character in this list
Montefeltro et al. (2013), character 118: all character scores the same in this dataset
Montefeltro et al. (2013), character 120: similar to ch. 286 in this list
Montefeltro et al. (2013), character 122: from Clark (1994)
Montefeltro et al. (2013), character 123: similar to several characters in this list
Montefeltro et al. (2013), character 124: all character scores the same in this dataset
Montefeltro et al. (2013), character 125: from Ortega et al. (2000)
Montefeltro et al. (2013), character 126: in ch. 98 of this character list
Montefeltro et al. (2013), character 134: all character scores the same in this dataset
Montefeltro et al. (2013), character 135: all character scores the same in this dataset
Montefeltro et al. (2013), character 136: all character scores the same in this dataset
Montefeltro et al. (2013), character 137: similar to ch. 131 in this list

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Montefeltro et al. (2013), character 138: all character scores the same in this dataset
Montefeltro et al. (2013), character 139: already in list as ch. 132
Montefeltro et al. (2013), character 140: from Pol (1999)
Montefeltro et al. (2013), character 141: all character scores the same in this dataset
Montefeltro et al. (2013), character 144: from Pol (1999)
Montefeltro et al. (2013), character 146: all character scores the same in this dataset
Montefeltro et al. (2013), character 147: not applicable to the taxa in this dataset, see ch. 146
Montefeltro et al. (2013), character 148: from Pol (1999), in continuous characters
Montefeltro et al. (2013), character 149: from Clark (1994)
Montefeltro et al. (2013), character 151: similar to several continuous characters
Montefeltro et al. (2013), character 152: all character scores the same in this dataset
Montefeltro et al. (2013), character 153: not applicable to the taxa in this dataset, see ch. 152
Montefeltro et al. (2013), character 154: all character scores the same in this dataset
Montefeltro et al. (2013), character 155: all character scores the same in this dataset
Montefeltro et al. (2013), character 156: similar to ch. 211 in this list
Montefeltro et al. (2013), character 157: reflected in continuous ch. 32 in this list
Montefeltro et al. (2013), character 158: all character scores the same in this dataset
Montefeltro et al. (2013), character 159: all character scores the same in this dataset
Montefeltro et al. (2013), character 160: from Clark (1994)
Montefeltro et al. (2013), character 161: from Clark (1994)
Montefeltro et al. (2013), character 163: all character scores the same in this dataset
Montefeltro et al. (2013), character 165: all character scores the same in this dataset
Montefeltro et al. (2013), character 169: from Clark (1994)
Montefeltro et al. (2013), character 170: from Clark (1994)
Montefeltro et al. (2013), character 171: from Clark (1994)
Montefeltro et al. (2013), character 172: from Clark (1994)
Montefeltro et al. (2013), character 174: all character scores the same in this dataset
Montefeltro et al. (2013), character 177: all character scores the same in this dataset
Montefeltro et al. (2013), character 179: from Clark (1994)
Montefeltro et al. (2013), character 181: from Ortega et al. (2000)
Montefeltro et al. (2013), character 182: from Ortega et al. (2000)
Montefeltro et al. (2013), character 184: similar to ch. 227 in this character list
Montefeltro et al. (2013), character 185: similar to ch. 273 in this character list
Montefeltro et al. (2013), character 186: from Clark (1994)
Montefeltro et al. (2013), character 187: all character scores the same in this dataset
Montefeltro et al. (2013), character 189: from Clark (1994)
Montefeltro et al. (2013), character 190: all character scores the same in this dataset
Montefeltro et al. (2013), character 191: from Clark (1994)
Montefeltro et al. (2013), character 192: from Clark (1994)
Montefeltro et al. (2013), character 193: reflected in ch. 323 in this character list
Montefeltro et al. (2013), character 194: from Brochu (1999)
Montefeltro et al. (2013), character 195: all character scores the same in this dataset
Montefeltro et al. (2013), character 196: from Pol (1999)
Montefeltro et al. (2013), character 197: all character scores the same in this dataset
Montefeltro et al. (2013), character 198: from Clark (1994)
Montefeltro et al. (2013), character 199: from Brochu (1999)
Montefeltro et al. (2013), character 200: from Sereno et al. (2001)
Montefeltro et al. (2013), character 201: from Clark (1994)
Montefeltro et al. (2013), character 202: from Sereno et al. (2001)
Montefeltro et al. (2013), character 203: all character scores the same in this dataset
Montefeltro et al. (2013), character 204: unclear character, replaced by new characters 122 and 123
Montefeltro et al. (2013), character 206: all character scores the same in this dataset
Montefeltro et al. (2013), character 207: all character scores the same in this dataset
Montefeltro et al. (2013), character 208: all character scores the same in this dataset
Montefeltro et al. (2013), character 209: all character scores the same in this dataset
Montefeltro et al. (2013), character 210: all character scores the same in this dataset
Montefeltro et al. (2013), character 212: all character scores the same in this dataset
Montefeltro et al. (2013), character 213: same as Brochu (1999)
Montefeltro et al. (2013), character 214: similar to ch. 267 in this dataset
Montefeltro et al. (2013), character 215: from Clark (1994)
Montefeltro et al. (2013), character 216: from Clark (1994)
Montefeltro et al. (2013), character 217: from Brochu (1999)
Montefeltro et al. (2013), character 219: all character scores the same in this dataset
Montefeltro et al. (2013), character 220: similar to ch. 370 in this dataset
Montefeltro et al. (2013), character 221: from Wu et al. (1997)
Montefeltro et al. (2013), character 222: all character scores the same in this dataset
Montefeltro et al. (2013), character 227: similar to several characters in this dataset
Montefeltro et al. (2013), character 230: all character scores the same in this dataset
Montefeltro et al. (2013), character 231: from Clark (1994)
Montefeltro et al. (2013), character 232: from Wu et al. (1997)
Montefeltro et al. (2013), character 233: from Clark (1994)
Montefeltro et al. (2013), character 234: all character scores the same in this dataset
Montefeltro et al. (2013), character 235: all character scores the same in this dataset
Montefeltro et al. (2013), character 236: not applicable to the taxa in this dataset
Montefeltro et al. (2013), character 237: similar to ch. 326 in this dataset
Montefeltro et al. (2013), character 238: from Clark (1994)
Montefeltro et al. (2013), character 240: not applicable to the taxa in this dataset
Montefeltro et al. (2013), character 241: from Pol (1999)
Montefeltro et al. (2013), character 242: from Wu et al. (1997)
Montefeltro et al. (2013), character 243: from Clark (1994)
Montefeltro et al. (2013), character 244: all character scores the same in this dataset
Montefeltro et al. (2013), character 245: not applicable to the taxa in this dataset
Montefeltro et al. (2013), character 246: from Wu et al. (1997)
Montefeltro et al. (2013), character 247: from Ösi et al. (2007)
Montefeltro et al. (2013), character 248: similar to ch. 346 in this dataset
Montefeltro et al. (2013), character 249: all character scores the same in this dataset
Montefeltro et al. (2013), character 250: all character scores the same in this dataset
Montefeltro et al. (2013), character 251: all character scores the same in this dataset
Montefeltro et al. (2013), character 252: similar to ch. 329 in this dataset
Montefeltro et al. (2013), character 253: all character scores the same in this dataset
Montefeltro et al. (2013), character 256: all character scores the same in this dataset
Montefeltro et al. (2013), character 257: from Pol (1999)
Montefeltro et al. (2013), character 258: all character scores the same in this dataset
Montefeltro et al. (2013), character 259: from Pol (1999)
Montefeltro et al. (2013), character 260: similar to ch. 326 in this dataset
Montefeltro et al. (2013), character 262: from Clark (1994)
Montefeltro et al. (2013), character 263: from Clark (1994)
Montefeltro et al. (2013), character 264: from Pol (1999)

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Montefeltro et al. (2013), character 265: all character scores the same in this dataset
Montefeltro et al. (2013), character 266: from Clark (1994)
Montefeltro et al. (2013), character 268: from Wu et al. (1997)
Montefeltro et al. (2013), character 269: from Clark (1994)
Montefeltro et al. (2013), character 270: from Clark (1994)
Montefeltro et al. (2013), character 272: from Clark (1994)
Montefeltro et al. (2013), character 273: from Pol (1999)
Montefeltro et al. (2013), character 274: all character scores the same in this dataset
Montefeltro et al. (2013), character 276: all character scores the same in this dataset
Montefeltro et al. (2013), character 277: unable to properly score the character
Montefeltro et al. (2013), character 278: from Ösi et al. (2007)
Montefeltro et al. (2013), character 281: all character scores the same in this dataset
Montefeltro et al. (2013), character 282: from Brochu (1999)
Montefeltro et al. (2013), character 283: from Brochu (1999)
Montefeltro et al. (2013), character 284: all character scores the same in this dataset
Montefeltro et al. (2013), character 285: from Clark (1994)
Montefeltro et al. (2013), character 286: from Clark (1994)
Montefeltro et al. (2013), character 287: similar to ch. 49 in this dataset
Montefeltro et al. (2013), character 289: from Clark (1994)
Montefeltro et al. (2013), character 291: from Clark (1994)
Montefeltro et al. (2013), character 292: from Clark (1994)
Montefeltro et al. (2013), character 293: from Clark (1994)
Montefeltro et al. (2013), character 294: from Wu et al. (1997)
Montefeltro et al. (2013), character 295: from Clark (1994)
Montefeltro et al. (2013), character 296: from Clark (1994)
Montefeltro et al. (2013), character 297: from Clark (1994)
Montefeltro et al. (2013), character 299: similar to ch. 48 in this dataset
Montefeltro et al. (2013), character 300: all character scores the same in this dataset
Montefeltro et al. (2013), character 303: from Clark (1994)
Montefeltro et al. (2013), character 304: from Clark (1994)
Montefeltro et al. (2013), character 308: from Wu et al. 1997
Montefeltro et al. (2013), character 309: similar to ch. 285 in this dataset
Montefeltro et al. (2013), character 310: all character scores the same in this dataset
Montefeltro et al. (2013), character 311: all character scores the same in this dataset
Montefeltro et al. (2013), character 312: similar to ch. 407 in this dataset
Montefeltro et al. (2013), character 314: from Clark (1994)
Montefeltro et al. (2013), character 316: from Pol (1999)
Montefeltro et al. (2013), character 318: from Brochu (1999)
Montefeltro et al. (2013), character 319: from Brochu (1999)
Montefeltro et al. (2013), character 320: all character scores the same in this dataset
Montefeltro et al. (2013), character 321: all character scores the same in this dataset
Montefeltro et al. (2013), character 323: all character scores the same in this dataset
Montefeltro et al. (2013), character 324: not applicable to the taxa in this dataset
Montefeltro et al. (2013), character 325: similar to ch. 53 and 54 in this character list
Montefeltro et al. (2013), character 326: from Clark (1994)
Montefeltro et al. (2013), character 327: all character scores the same in this dataset
Montefeltro et al. (2013), character 330: complex character, reflected in several of this characters
Montefeltro et al. (2013), character 331: all character scores the same in this dataset
Montefeltro et al. (2013), character 332: from Pol (1999)
Montefeltro et al. (2013), character 333: all character scores the same in this dataset
Montefeltro et al. (2013), character 335: all character scores the same in this dataset
Montefeltro et al. (2013), character 336: all character scores the same in this dataset
Montefeltro et al. (2013), character 338: from Clark (1994)
Montefeltro et al. (2013), character 340: all character scores the same in this dataset
Montefeltro et al. (2013), character 341: all character scores the same in this dataset
Montefeltro et al. (2013), character 342: from Clark (1994)
Montefeltro et al. (2013), character 345: from Wu et al. (1997)
Montefeltro et al. (2013), character 348: from Clark (1994)
Montefeltro et al. (2013), character 351: from Clark (1994)
Montefeltro et al. (2013), character 352: from Clark (1994)

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Montefeltro et al. (2013), character 353: similar to ch. 458 in this dataset
Montefeltro et al. (2013), character 354: all character scores the same in this dataset
Montefeltro et al. (2013), character 355: similar to several characters in this dataset
Montefeltro et al. (2013), character 357: all character scores the same in this dataset
Montefeltro et al. (2013), character 358: all character scores the same in this dataset
Montefeltro et al. (2013), character 359: not applicable to the taxa in this dataset
Montefeltro et al. (2013), character 360: all character scores the same in this dataset
Montefeltro et al. (2013), character 361: all character scores the same in this dataset
Montefeltro et al. (2013), character 362: all character scores the same in this dataset
Montefeltro et al. (2013), character 364: similar to ch. 380 in this dataset
Montefeltro et al. (2013), character 365: all character scores the same in this dataset
Montefeltro et al. (2013), character 366: unclear character states; reflected in several of the characters here
Montefeltro et al. (2013), character 367: all character scores the same in this dataset
Montefeltro et al. (2013), character 368: similar to ch. 380 in this dataset
Montefeltro et al. (2013), character 369: from Clark (1994)
Montefeltro et al. (2013), character 370: after Sereno et al. (2001)
Montefeltro et al. (2013), character 371: from Clark (1994)
Montefeltro et al. (2013), character 372: all character scores the same in this dataset
Montefeltro et al. (2013), character 374: subjective description, all character scores the same in this dataset
Montefeltro et al. (2013), character 376: all character scores the same in this dataset
Montefeltro et al. (2013), character 377: same as ch. 399 in this dataset
Montefeltro et al. (2013), character 378: all character scores the same in this dataset
Montefeltro et al. (2013), character 379: similar to ch. 399 in this dataset
Montefeltro et al. (2013), character 380: similar to ch. 391 and 392 in this dataset
Montefeltro et al. (2013), character 381: from Clark (1994)
Montefeltro et al. (2013), character 383: from Clark (1994)
Montefeltro et al. (2013), character 385: from Pol (1999)
Montefeltro et al. (2013), character 386: from Brochu (1999)
Montefeltro et al. (2013), character 387: from Pol (1999)
Montefeltro et al. (2013), character 388: from Pol (1999)
Montefeltro et al. (2013), character 389: from Brochu (1999)
Montefeltro et al. (2013), character 390: from Clark (1994)
Montefeltro et al. (2013), character 391: from Clark (1994)
Montefeltro et al. (2013), character 393: all character scores the same in this dataset
Montefeltro et al. (2013), character 396: same as Montefeltro et al. (2013), ch. 392
Montefeltro et al. (2013), character 398: all character scores the same in this dataset
Montefeltro et al. (2013), character 399: all character scores the same in this dataset
Montefeltro et al. (2013), character 400: from Clark (1994)
Montefeltro et al. (2013), character 401: similar to ch. 497 in this dataset
Montefeltro et al. (2013), character 410: from Clark (1994)
Montefeltro et al. (2013), character 413: from Clark (1994)
Montefeltro et al. (2013), character 414: all character scores the same in this dataset
Montefeltro et al. (2013), character 415: from Brochu (1999)
Montefeltro et al. (2013), character 416: all character scores the same in this dataset
Montefeltro et al. (2013), character 417: all character scores the same in this dataset
Montefeltro et al. (2013), character 418: from Clark (1994)
Montefeltro et al. (2013), character 419: all character scores the same in this dataset
Montefeltro et al. (2013), character 420: all character scores the same in this dataset
Montefeltro et al. (2013), character 427: from Brochu (1999)
Montefeltro et al. (2013), character 428: all character scores the same in this dataset
Montefeltro et al. (2013), character 431: very subjective character, turned into continuous ch. 72
Montefeltro et al. (2013), character 433: similar to ch. 521 in this dataset
Montefeltro et al. (2013), character 435: all character scores the same in this dataset
Montefeltro et al. (2013), character 437: from Clark (1994)
Montefeltro et al. (2013), character 441: all character scores the same in this dataset
Montefeltro et al. (2013), character 444: from Clark (1994)
Montefeltro et al. (2013), character 445: from Clark (1994)
Montefeltro et al. (2013), character 446: from Clark (1994)
Montefeltro et al. (2013), character 447: all character scores the same in this dataset
Montefeltro et al. (2013), character 448: all character scores the same in this dataset
Montefeltro et al. (2013), character 454: all character scores the same in this dataset
Montefeltro et al. (2013), character 456: all character scores the same in this dataset
Montefeltro et al. (2013), character 459: from Clark (1994)
Montefeltro et al. (2013), character 460: from Clark (1994)
Montefeltro et al. (2013), character 461: from Clark (1994)
Montefeltro et al. (2013), character 462: from Clark (1994)
Montefeltro et al. (2013), character 464: from Clark (1994)
Montefeltro et al. (2013), character 465: similar to ch. 553 in this dataset
Montefeltro et al. (2013), character 466: all character scores the same in this dataset
Montefeltro et al. (2013), character 467: from Clark (1994)
Montefeltro et al. (2013), character 468: from Clark (1994)
Montefeltro et al. (2013), character 470: from Clark (1994)
Montefeltro et al. (2013), character 471: from Clark (1994)
Montefeltro et al. (2013), character 473: all character scores the same in this dataset
Montefeltro et al. (2013), character 474: all character scores the same in this dataset
Montefeltro et al. (2013), character 475: all character scores the same in this dataset
Montefeltro et al. (2013), character 476: all character scores the same in this dataset
Montefeltro et al. (2013), character 477: similar to ch. 184 in this dataset
Montefeltro et al. (2013), character 482: all character scores the same in this dataset

**Jouve 2009 (only the new characters at the end)**

Jouve (2009), character 302: subjective character, difficult to score or turn into continuous character
Jouve (2009), character 304: all character scores the same in this dataset
Jouve (2009), character 308: all character scores the same in this dataset
Jouve (2009), character 309: similar to ch. 4 in this dataset
Jouve (2009), character 310: similar to ch. 27 in this dataset
Jouve (2009), character 312: all character scores the same in this dataset
Jouve (2009), character 313: all character scores the same in this dataset
Jouve (2009), character 316: all character scores the same in this dataset
Jouve (2009), character 317: all character scores the same in this dataset
Jouve (2009), character 318: all character scores the same in this dataset
Jouve (2009), character 322: similar to ch. 299 in this dataset
Jouve (2009), character 327: similar to ch. 418 in this dataset
Jouve (2009), character 329: subjective and unclear wording of character
Jouve (2009), character 332: all character scores the same in this dataset
Jouve (2009), character 333: similar to ch. 333 in this dataset
Jouve (2009), character 334: all character scores the same in this dataset
Jouve (2009), character 335: all character scores the same in this dataset
Jouve (2009), character 337: similar to ch. 83 in this dataset
Jouve (2009), character 338: similar to ch. 189 in this dataset
Jouve (2009), character 339: all character scores the same in this dataset
Jouve (2009), character 343: all character scores the same in this dataset

**Hastings et al. 2010**

Hastings *et al.* (2010), character 1: reflected in continuous character 16 in this dataset
Hastings *et al.* (2010), character 7: from Clark (1994)
Hastings *et al.* (2010), character 9: distinctions between codings not clear upon examination of real specimens
Hastings *et al.* (2010), character 14: describes same morphological variation as ch. 113 in this dataset
Hastings *et al.* (2010), character 27: all character scores the same in this dataset
Hastings *et al.* (2010), character 28: all character scores the same in this dataset
Hastings *et al.* (2010), character 31: similar to ch. 386 in this dataset
Hastings *et al.* (2010), character 32: all character scores the same in this dataset
Hastings *et al.* (2010), character 41: distinctions between codings not clear upon examination of real specimens
Hastings et al. (2010), character 42: all character scores the same in this dataset
Hastings et al. (2010), character 43: all character scores the same in this dataset
Hastings et al. (2010), character 44: all character scores the same in this dataset
Hastings et al. (2010), character 47: from Clark (1994)
Hastings et al. (2010), character 49: from Jouve et al. (2006)
Hastings et al. (2010), character 51: all character scores the same in this dataset
Hastings et al. (2010), character 52: from Jouve et al. (2006)
Hastings et al. (2010), character 53: similar to ch. 296 in this dataset
Hastings et al. (2010), character 54: all character scores the same in this dataset
Hastings et al. (2010), character 55: all character scores the same in this dataset
Hastings et al. (2010), character 56: distinctions between codings not clear upon examination of real specimens
Hastings et al. (2010), character 58: from Jouve et al. (2006)
Hastings et al. (2010), character 60: similar to ch. 271 in this dataset
Hastings et al. (2010), character 61: all character scores the same in this dataset
Hastings et al. (2010), character 67: similar to ch. 421 in this dataset
Hastings et al. (2010), character 69: all character scores the same in this dataset
Hastings et al. (2010), character 71: similar to ch. 400 in this dataset
Hastings et al. (2010), character 73: from Jouve et al. (2006)
Hastings et al. (2010), character 74: reflected in continuous characters 53 and 54
Hastings et al. (2010), character 75: similar to ch. 442 and 458 in this dataset
Hastings et al. (2010), character 76: all character scores the same in this dataset
Hastings et al. (2010), character 77: similar to ch. 462 in this dataset
Hastings et al. (2010), character 78: similar to ch. 409 in this dataset
Hastings et al. (2010), character 79: all character scores the same in this dataset
Hastings et al. (2010), character 80: same as ch. 397 in this dataset
Hastings et al. (2010), character 81: all character scores the same in this dataset
Hastings et al. (2010), character 82: same as ch. 554 in this dataset

**Jouve et al. 2006**

Jouve et al. (2006), character 1: from Wu et al. (2001)
Jouve et al. (2006), character 2: from Wu et al. (2001)
Jouve et al. (2006), character 3: same as ch. 94 in this dataset
Jouve et al. (2006), character 5: from Wu et al. (2001)
Jouve et al. (2006), character 7: similar to ch. 16 in this dataset
Jouve et al. (2006), character 8: from Wu et al. (2001)
Jouve et al. (2006), character 9: same as ch. 96 in this dataset
Jouve et al. (2006), character 10: from Wu et al. (2001)
Jouve et al. (2006), character 11: from Wu et al. (2001)
Jouve et al. (2006), character 12: from Wu et al. (2001)
Jouve et al. (2006), character 13: from Wu et al. (2001)
Jouve et al. (2006), character 14: from Wu et al. (2001)
Jouve et al. (2006), character 15: reflected in ch 33 of continuous characters in this dataset
Jouve et al. (2006), character 16: same as ch. 264 in this dataset

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Jouve et al. (2006), character 17: from Wu et al. (2001)
Jouve et al. (2006), character 20: from Wu et al. (2001)
Jouve et al. (2006), character 21: all character scores the same in this dataset
Jouve et al. (2006), character 22: from Wu et al. (2001)
Jouve et al. (2006), character 23: similar to ch. 352 in this dataset
Jouve et al. (2006), character 25: from Wu et al. (2001)
Jouve et al. (2006), character 26: from Wu et al. (2001)
Jouve et al. (2006), character 28: from Wu et al. (2001)
Jouve et al. (2006), character 29: from Wu et al. (2001)
Jouve et al. (2006), character 30: from Wu et al. (2001)
Jouve et al. (2006), character 31: from Wu et al. (2001)
Jouve et al. (2006), character 33: all character scores the same in this dataset
Jouve et al. (2006), character 34: distinctions between codings not clear upon examination of real specimens; replaced by characters 122 and 123
Jouve et al. (2006), character 35: same as ch. 122 in this dataset
Jouve et al. (2006), character 36: from Wu et al. (2001)
Jouve et al. (2006), character 37: all character scores the same in this dataset
Jouve et al. (2006), character 38: from Wu et al. (2001)
Jouve et al. (2006), character 39: all character scores the same in this dataset
Jouve et al. (2006), character 40: from Wu et al. (2001)
Jouve et al. (2006), character 41: similar to ch. 132 in this dataset
Jouve et al. (2006), character 42: same as ch. 128 in this dataset
Jouve et al. (2006), character 43: same as ch. 389 in this dataset
Jouve et al. (2006), character 44: all character scores the same in this dataset
Jouve et al. (2006), character 45: from Wu et al. (2001)
Jouve et al. (2006), character 46: from Wu et al. (2001)
Jouve et al. (2006), character 47: from Wu et al. (2001)
Jouve et al. (2006), character 48: same as ch. 154 in this dataset
Jouve et al. (2006), character 49: same as ch. 157 in this dataset
Jouve et al. (2006), character 51: same as ch. 162 in this dataset
Jouve et al. (2006), character 53: from Wu et al. (2001)
Jouve et al. (2006), character 54: similar to ch. 174 in this dataset
Jouve et al. (2006), character 55: all character scores similar in this dataset
Jouve et al. (2006), character 56: same as ch. 204 in this dataset
Jouve et al. (2006), character 57: from Wu et al. (2001)
Jouve et al. (2006), character 58: from Wu et al. (2001)
Jouve et al. (2006), character 59: from Wu et al. (2001)
Jouve et al. (2006), character 61: from Wu et al. (2001)
Jouve et al. (2006), character 62: from Wu et al. (2001)
Jouve et al. (2006), character 63: all character scores the same in this dataset
Jouve et al. (2006), character 64: reflected in ch. 40 in this dataset
Jouve et al. (2006), character 65: same as ch. 253 in this dataset
Jouve et al. (2006), character 66: from Wu et al. (2001)
Jouve et al. (2006), character 67: same as ch. 252 in this dataset
Jouve et al. (2006), character 68: from Wu et al. (2001)
Jouve et al. (2006), character 70: from Wu et al. (2001)
Jouve et al. (2006), character 71: same as ch. 260 in this dataset
Jouve et al. (2006), character 73: same as ch. 255 in this dataset
Jouve et al. (2006), character 74: all character scores the same in this dataset
Jouve et al. (2006), character 76: from Wu et al. (2001)
Jouve et al. (2006), character 77: all character scores the same in this dataset
Jouve et al. (2006), character 78: similar to ch. 265 in this dataset
Jouve et al. (2006), character 80: similar to ch. 266 in this dataset
Jouve et al. (2006), character 81: same as ch. 269 in this dataset
Jouve et al. (2006), character 82: similar to ch. 272 in this dataset
Jouve et al. (2006), character 84: from Wu et al. (2001)
Jouve et al. (2006), character 86: from Wu et al. (2001)
Jouve et al. (2006), character 87: from Wu et al. (2001)
Jouve et al. (2006), character 88: from Wu et al. (2001)
Jouve et al. (2006), character 89: similar to ch. 286 in this dataset
Jouve et al. (2006), character 90: from Wu et al. (2001)
Jouve et al. (2006), character 91: similar to ch. 244 in this dataset
Jouve et al. (2006), character 92: from Wu et al. (2001)
Jouve et al. (2006), character 93: from Wu et al. (2001)
Jouve et al. (2006), character 94: same as ch. 226 in this dataset
Jouve et al. (2006), character 95: from Wu et al. (2001)
Jouve et al. (2006), character 96: from Wu et al. (2001)
Jouve et al. (2006), character 97: from Wu et al. (2001)
Jouve et al. (2006), character 98: similar to ch. 232 and 233 in this dataset
Jouve et al. (2006), character 99: same as ch. 289 in this dataset
Jouve et al. (2006), character 100: from Wu et al. (2001)
Jouve et al. (2006), character 101: from Wu et al. (2001)
Jouve et al. (2006), character 102: from Wu et al. (2001)
Jouve et al. (2006), character 103: from Wu et al. (2001)
Jouve et al. (2006), character 104: reflected in continuous ch. 49 in this dataset
Jouve et al. (2006), character 105: from Wu et al. (2001)
Jouve et al. (2006), character 106: from Wu et al. (2001)
Jouve et al. (2006), character 107: from Wu et al. (2001)
Jouve et al. (2006), character 108: from Wu et al. (2001)
Jouve et al. (2006), character 109: from Wu et al. (2001)
Jouve et al. (2006), character 111: from Wu et al. (2001)
Jouve et al. (2006), character 112: all character scores the same in this dataset
Jouve et al. (2006), character 113: similar to ch. 370 in this dataset
Jouve et al. (2006), character 114: from Wu et al. (2001)
Jouve et al. (2006), character 115: reflected in continuous ch. 38 in this dataset
Jouve et al. (2006), character 116: from Wu et al. (2001)
Jouve et al. (2006), character 117: from Wu et al. (2001)
Jouve et al. (2006), character 118: from Wu et al. (2001)
Jouve et al. (2006), character 119: from Wu et al. (2001)
Jouve et al. (2006), character 120: from Wu et al. (2001)
Jouve et al. (2006), character 121: from Wu et al. (2001)
Jouve et al. (2006), character 122: all character scores the same in this dataset
Jouve et al. (2006), character 123: similar to ch. 339 in this dataset
Jouve et al. (2006), character 124: from Wu et al. (2001)
Jouve et al. (2006), character 125: same as ch. 337 in this dataset
Jouve et al. (2006), character 127: same as ch. 345 in this dataset
Jouve et al. (2006), character 128: same as ch. 326 in this dataset
Jouve et al. (2006), character 129: from Wu et al. (2001)
Jouve et al. (2006), character 130: from Wu et al. (2001)
Jouve et al. (2006), character 132: from Wu et al. (2001)
Jouve et al. (2006), character 133: from Wu et al. (2001)
Jouve et al. (2006), character 134: all character scores the same in this dataset
Jouve et al. (2006), character 135: from Wu et al. (2001)
Jouve et al. (2006), character 136: from Wu et al. (2001)
Jouve et al. (2006), character 137: from Wu et al. (2001)
Jouve et al. (2006), character 138: from Wu et al. (2001)
Jouve et al. (2006), character 139: from Wu et al. (2001)
Jouve et al. (2006), character 140: from Wu et al. (2001)
Jouve et al. (2006), character 141: similar to ch. 279 in this dataset
Jouve et al. (2006), character 142: same as ch. 282 in this dataset
Jouve et al. (2006), character 143: all character scores the same in this dataset
Jouve et al. (2006), character 144: from Wu et al. (2001)
Jouve et al. (2006), character 145: similar to ch. 311 in this dataset
Jouve et al. (2006), character 146: from Wu et al. (2001)
Jouve et al. (2006), character 148: from Wu et al. (2001)
Jouve et al. (2006), character 149: same as ch. 316 in this dataset
Jouve et al. (2006), character 150: from Wu et al. (2001)
Jouve et al. (2006), character 151: similar to ch. 305 in this dataset
Jouve et al. (2006), character 152: same as ch. 306 in this dataset
Jouve et al. (2006), character 153: same as ch. 300 in this dataset
Jouve et al. (2006), character 154: from Wu et al. (2001)
Jouve et al. (2006), character 155: similar to ch. 350 in this dataset
Jouve et al. (2006), character 156: from Wu et al. (2001)
Jouve et al. (2006), character 157: from Wu et al. (2001)
Jouve et al. (2006), character 158: similar to ch. 409 in this dataset and continuous characters
Jouve et al. (2006), character 159: from Wu et al. (2001)
Jouve et al. (2006), character 160: states hard to tell apart in examined specimens
Jouve et al. (2006), character 161: reflected in several continuous and discrete characters
Jouve et al. (2006), character 162: from Wu et al. (2001)
Jouve et al. (2006), character 164: same as ch. 422 in this dataset
Jouve et al. (2006), character 165: from Wu et al. (2001)
Jouve et al. (2006), character 166: from Wu et al. (2001)
Jouve et al. (2006), character 167: similar to ch. 461 in this dataset
Jouve et al. (2006), character 168: from Wu et al. (2001)
Jouve et al. (2006), character 169: same as ch. 444 in this dataset
Jouve et al. (2006), character 170: from Wu et al. (2001)
Jouve et al. (2006), character 171: same as ch. 458 in this dataset
Jouve et al. (2006), character 172: from Wu et al. (2001)
Jouve et al. (2006), character 173: from Wu et al. (2001)
Jouve et al. (2006), character 175: from Wu et al. (2001)
Jouve et al. (2006), character 176: all character scores the same in this dataset
Jouve et al. (2006), character 177: all character scores the same in this dataset
Jouve et al. (2006), character 180: similar to ch. 57 in this dataset
Jouve et al. (2006), character 182: same as ch. 377 in this dataset
Jouve et al. (2006), character 183: reflected in continuous ch. 12 in this dataset
Jouve et al. (2006), character 185: same as ch. 385 in this dataset
Jouve et al. (2006), character 187: similar to ch. 391 and 392 in this dataset
Jouve et al. (2006), character 188: all character scores the same in this dataset
Jouve et al. (2006), character 189: same as ch. 390 in this dataset
Jouve et al. (2006), character 190: same as ch. 396 in this dataset
Jouve et al. (2006), character 191: from Sereno et al. (2001)
Jouve et al. (2006), character 193: from Sereno et al. (2001)
Jouve et al. (2006), character 194: from Sereno et al. (2001)
Jouve et al. (2006), character 195: all character scores the same in this dataset
Jouve et al. (2006), character 196: not applicable to the taxa in this dataset (see ch. 195)
Jouve et al. (2006), character 197: not applicable to the taxa in this dataset (see ch. 195)
Jouve et al. (2006), character 198: from Wu et al. (2001)
Jouve et al. (2006), character 199: from Wu et al. (2001)
Jouve et al. (2006), character 201: from Wu et al. (2001)
Jouve et al. (2006), character 203: from Wu et al. (2001)
Jouve et al. (2006), character 204: from Wu et al. (2001)
Jouve et al. (2006), character 205: from Wu et al. (2001)
Jouve et al. (2006), character 206: from Wu et al. (2001)
Jouve et al. (2006), character 208: from Wu et al. (2001)
Jouve et al. (2006), character 210: from Wu et al. (2001)
Jouve et al. (2006), character 211: from Wu et al. (2001)
Jouve et al. (2006), character 212: reflected in continuous ch. 71 in this dataset
Jouve et al. (2006), character 213: from Wu et al. (2001)
Jouve et al. (2006), character 214: reflected in continuous ch. 72 in this dataset
Jouve et al. (2006), character 215: reflected in continuous ch. 79 in this dataset
Jouve et al. (2006), character 216: same as ch. 515 in this dataset
Jouve et al. (2006), character 217: from Wu et al. (2001)
Jouve et al. (2006), character 218: from Wu et al. (2001)
Jouve et al. (2006), character 219: from Wu et al. (2001)
Jouve et al. (2006), character 220: from Wu et al. (2001)
Jouve et al. (2006), character 221: from Wu et al. (2001)
Jouve et al. (2006), character 222: from Wu et al. (2001)
Jouve et al. (2006), character 224: from Wu et al. (2001)
Jouve et al. (2006), character 225: all character scores the same in this dataset
Jouve et al. (2006), character 226: from Wu et al. (2001)
Jouve et al. (2006), character 227: from Wu et al. (2001)
Jouve et al. (2006), character 228: from Wu et al. (2001)
Jouve et al. (2006), character 229: from Wu et al. (2001)
Jouve et al. (2006), character 230: from Wu et al. (2001)
Jouve et al. (2006), character 231: from Wu et al. (2001)

Brochu 1999 + si et al. 2007 + Salisbury et al. 2006

(the latter two use characters 1-164 directly from Brochu (1999))
Brochu (1999), character 15: all character scores the same in this dataset
Brochu (1999), character 18: from Clark (1994)
Brochu (1999), character 24: character dependant on ontogeny; only mature individuals examined
Brochu (1999), character 35: similar to ch. 542 in this dataset
Brochu (1999), character 40: from Clark (1994)
Brochu (1999), character 43: from Clark (1994)
Brochu (1999), character 46: all character scores the same in this dataset
Brochu (1999), character 53: all character scores the same in this dataset
Brochu (1999), character 57: Hyoid not present in examined individuals
Brochu (1999), character 58: Hyoid not present in examined individuals
Brochu (1999), character 61: all character scores the same in this dataset
Brochu (1999), character 70: similar to ch. 213 in this dataset
Brochu (1999), character 71: from Clark (1994)
Brochu (1999), character 72: all character scores the same in this dataset
Brochu (1999), character 77: character dependant on ontogeny; only mature individuals examined
Brochu (1999), character 79: similar to ch. 95 in this dataset
Brochu (1999), character 82: similar to ch. 286 and 287 in this dataset
Brochu (1999), character 90: similar to ch. 367 in this dataset
Brochu (1999), character 91: same as ch. 327 in this dataset
Brochu (1999), character 92: all character scores the same in this dataset
Brochu (1999), character 96: from Clark (1994)
Brochu (1999), character 97: character dependant on ontogeny; only mature individuals examined
Brochu (1999), character 100: all character scores the same in this dataset
Brochu (1999), character 104: same as ch. 223 in this dataset
Brochu (1999), character 105: all character scores the same in this dataset
Brochu (1999), character 109: all character scores the same in this dataset
Brochu (1999), character 113: reflected in continuous ch. 51 of this dataset
Brochu (1999), character 128: similar to ch. 318 in this dataset
Brochu (1999), character 129: similar to ch. 317 in this dataset
Brochu (1999), character 146: from Clark (1994)
Brochu (1999), character 148: all character scores the same in this dataset
Brochu (1999), character 153: all character scores the same in this dataset

427
Brochu (1999), character 154: hard to score in examined specimens from outside
Brochu (1999), character 163: states hard to tell apart in examined specimens
Ösi et al. (2007), character 165: all character scores the same in this dataset
Ösi et al. (2007), character 167: all character scores the same in this dataset
Ösi et al. (2007), character 168: similar to ch. 174 and 176 in this dataset
Ösi et al. (2007), character 169: all character scores the same in this dataset
Salisbury et al. (2006), character 165: similar to ch. 385 in this dataset
Salisbury et al. (2006), character 168: similar to ch. 174 and 175 in this dataset
Salisbury et al. (2006), character 172: from Clark (1994)
Salisbury et al. (2006), character 175: similar to ch. 217 in this dataset
Salisbury et al. (2006), character 176: same as ch. 159 in this dataset

Clark 1994 (1-101) in Pol & Norell 2004

Clark (1994), character 3: very subjective; reflected by several continuous characters
Clark (1994), character 7: all character scores the same in this dataset
Clark (1994), character 8: all character scores the same in this dataset
Clark (1994), character 10: all character scores the same in this dataset
Clark (1994), character 12: all character scores the same in this dataset
Clark (1994), character 16: all character scores the same in this dataset
Clark (1994), character 17: reflected by continuous ch. 29 in this dataset
Clark (1994), character 32: all character scores the same in this dataset
Clark (1994), character 33: all character scores the same in this dataset
Clark (1994), character 34: all character scores the same in this dataset
Clark (1994), character 35: all character scores the same in this dataset
Clark (1994), character 37: all character scores the same in this dataset
Clark (1994), character 38: all character scores the same in this dataset
Clark (1994), character 43: all character scores the same in this dataset
Clark (1994), character 47: hard to examine in most of the skulls examined here
Clark (1994), character 48: very subjective, hard to tell states apart in most of the skulls examined here
Clark (1994), character 51: all character scores the same in this dataset
Clark (1994), character 52: all character scores the same in this dataset
Clark (1994), character 53: all character scores the same in this dataset
Clark (1994), character 54: all character scores the same in this dataset
Clark (1994), character 55: all character scores the same in this dataset
Clark (1994), character 56: similar to ch. 314 in this dataset
Clark (1994), character 58: all character scores the same in this dataset
Clark (1994), character 61: all character scores the same in this dataset
Clark (1994), character 62: all character scores the same in this dataset
Clark (1994), character 63: hard to examine from outside of skull in the specimens here
Clark (1994), character 69: all character scores the same in this dataset (no choanal groove, inside of choanae covered by ch. 353 in this dataset already)
Clark (1994), character 78: all character scores the same in this dataset
Clark (1994), character 79: similar to ch. 386 in this dataset
Clark (1994), character 80: all character scores the same in this dataset
Clark (1994), character 81: all character scores the same in this dataset
Clark (1994), character 82: all character scores the same in this dataset
Clark (1994), character 86: all character scores the same in this dataset
Clark (1994), character 87: all character scores the same in this dataset
Clark (1994), character 88: all character scores the same in this dataset
Clark (1994), character 92: similar to ch. 490 in this dataset
Clark (1994), character 94: similar to ch. 504 in this dataset
Pol & Norell (2004), character 102: similar to ch. 252 in this dataset
Pol & Norell (2004), character 107: same as ch. 12 in this dataset
Pol & Norell (2004), character 108: all character scores the same in this dataset
Pol & Norell (2004), character 109: reflected by several continuous characters
Pol & Norell (2004), character 115: same as ch. 498 in this dataset
Pol & Norell (2004), character 116: same as ch. 526 in this dataset
Pol & Norell (2004), character 117: same as ch. 519 in this dataset
Pol & Norell (2004), character 118: all character scores the same in this dataset
Pol & Norell (2004), character 119: all character scores the same in this dataset
Pol & Norell (2004), character 120: all character scores the same in this dataset
Pol & Norell (2004), character 121: all character scores the same in this dataset
Pol & Norell (2004), character 122: same as ch. 253 in this dataset
Pol & Norell (2004), character 123: same as ch. 98 in this dataset
Pol & Norell (2004), character 125: all character scores the same in this dataset
Pol & Norell (2004), character 128: same as ch. 155 in this dataset
Pol & Norell (2004), character 129: similar to ch. 370 in this dataset
Pol & Norell (2004), character 130: same as ch. 29 in this dataset
Pol & Norell (2004), character 131: all character scores the same in this dataset
Pol & Norell (2004), character 132: similar to ch. 311 in this dataset
Pol & Norell (2004), character 133: all character scores the same in this dataset
Pol & Norell (2004), character 134: same as ch. 334 in this dataset
Pol & Norell (2004), character 136: same as ch. 260 in this dataset
Pol & Norell (2004), character 138: same as ch. 133 in this dataset
Pol & Norell (2004), character 140: similar to ch. 396 in this dataset
Pol & Norell (2004), character 141: same as ch. 271 in this dataset
Pol & Norell (2004), character 142: same as ch. 255 in this dataset
Pol & Norell (2004), character 143: reflected in continuous ch. 32 in this dataset
Pol & Norell (2004), character 145: same as ch. 266 in this dataset
Pol & Norell (2004), character 146: all character scores the same in this dataset
Pol & Norell (2004), character 147: same as ch. 317 in this dataset
Pol & Norell (2004), character 149: same as ch. 349 in this dataset
Pol & Norell (2004), character 151: same as ch. 281 in this dataset

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Pol & Norell (2004), character 152: same as ch. 481 in this dataset
Pol & Norell (2004), character 153: same as ch. 63 in this dataset
Pol & Norell (2004), character 154: same as ch. 482 in this dataset
Pol & Norell (2004), character 156: same as ch. 403 in this dataset
Pol & Norell (2004), character 158: similar to ch. 228 in this dataset
Pol & Norell (2004), character 159: same as ch. 33 in this dataset
Pol & Norell (2004), character 160: all character scores the same in this dataset
Pol & Norell (2004), character 161: all character scores the same in this dataset
Pol & Norell (2004), character 162: all character scores the same in this dataset
Pol & Norell (2004), character 165: all character scores the same in this dataset
Pol & Norell (2004), character 166: from Wu et al. (2001)
Pol & Norell (2004), character 167: from Wu et al. (2001)
Pol & Norell (2004), character 168: from Wu et al. (2001)
Pol & Norell (2004), character 169: from Wu et al. (2001)
Pol & Norell (2004), character 170: from Wu et al. (2001)
Pol & Norell (2004), character 171: from Wu et al. (2001)
Pol & Norell (2004), character 172: from Wu et al. (2001)
Pol & Norell (2004), character 174: from Wu et al. (2001)
Pol & Norell (2004), character 175: from Wu et al. (2001)
Pol & Norell (2004), character 176: from Wu et al. (2001)
Pol & Norell (2004), character 177: from Wu et al. (2001)
Pol & Norell (2004), character 178: from Wu et al. (2001)
Pol & Norell (2004), character 179: all character scores the same in this dataset
Pol & Norell (2004), character 180: all character scores the same in this dataset
Pol & Norell (2004), character 182: all character scores the same in this dataset

Sereno et al. 2001

Sereno et al. (2001), character 16: similar to ch. 29 in this dataset
Sereno et al. (2001), character 27: similar to ch. 181 in this dataset

431
Sereno et al. (2001), character 48: similar to ch. 458 in out dataset

Hill et al. 2008 (new characters, 31-19)

Hill et al. (2008), character 31: similar to ch. 400 in this character list
Hill et al. (2008), character 33: similar to ch. 16 in this character list
Hill et al. (2008), character 34: all character scores the same in this dataset
Hill et al. (2008), character 36: subjective, difficult to score properly
Hill et al. (2008), character 37: similar to ch. 83 in this dataset
Hill et al. (2008), character 38: all character scores the same in this dataset

C.4 All phylogenetic trees
Strict consensus tree from analysis I, full dataset, equal weights
Strict consensus tree from analysis II, full dataset, EIW
Strict consensus tree from analysis III, full dataset with longirostrine characters removed, equal weights
Strict consensus tree from analysis IV, full dataset with longirostrine characters removed, EIW
Strict consensus tree from analysis IV, full dataset with longirostrine characters removed, EIW, k=6
Strict consensus tree from analysis IV, full dataset with longirostrine characters removed, EIW, k=12
Strict consensus tree from analysis V, continuous characters only, equal weights

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Strict consensus tree from analysis VI, continuous characters only, EIW
Strict consensus tree from analysis VII, discrete characters only, equal weights
Strict consensus tree from analysis VIII, discrete characters only, EIW
Strict consensus tree from analysis IX, rediscretised full dataset, equal weights
Strict consensus tree from analysis X, rediscretised full dataset, EIW
Strict consensus tree from analysis XI, rediscretised dataset, equal weights
445
Strict consensus tree from analysis XII, rediscretised dataset without longirostrine characters, EIW
50% majority rule consensus tree from Bayesian Analysis I, discrete characters only
50% majority rule consensus tree from Bayesian Analysis II,rediscretised dataset
50% majority rule consensus tree from Bayesian Analysis III, rediscretised dataset without longirostrine characters
C.5 Timelist of Neosuchia for divergence dating

Interval times:

\[
\text{start_time} \quad \text{end_time}
\]

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<tr>
<th>Interval</th>
<th>Start Time</th>
<th>End Time</th>
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<td>197</td>
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<tr>
<td>MJ2</td>
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<td>195</td>
</tr>
<tr>
<td>MJ3</td>
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<tr>
<td>MJ4</td>
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<tr>
<td>MJ5</td>
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<td>185</td>
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<tr>
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<td>Toa3</td>
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<td>Aal2</td>
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Val2 137 135
Val3 135 132.9
Hauterivian 132.9 129.4
Bar1 129.4 127
Bar2 127 125
Ap1 125 122
Ap2 122 119
Ap3 119 116
Ap4 116 113
ErAl1 113 111
ErAl2 111 109
LaAl1 109 106.5
LaAl2 106.5 103.5
LaAl3 103.5 100.5
Cen1 100.5 98
Cen2 98 96
Cen3 96 93.9
Tur1 93.9 91.5
Tur2 91.5 89.5
Coniacian 89.5 85.8
Santonian 85.8 83.6
Cam1 83.6 81
Cam2 81 78
Cam3 78 75
Cam4 75 72.1
Maa1 72.1 69
Maa2 69 66
Early_Danian 66 63.3
Late_Danian 63.3 61.6
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<td>Langhian</td>
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<td>Seravallian</td>
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**Taxon times**

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Alligator_mefferdi 73 73
Alligator_mississippiensis 75 79
Alligator_prenasalis 63 64
Alligator_sinensis 78 79
Allognathosuchus_heterodon 57 58
Allognathosuchus_mooki 53 53
Allognathosuchus_wartheni 57 58
Amphicotylus_felix 21 21
Amphicotylus_lucasii 21 21
Anteophthalmosuchus_hooleyi 29 30
Arambourgia_gaudryi 64 64
Araripesuchus_gomesii 35 36
Asiatosuchus_grangeri 62 62
Asiatosuchus_nanlingensis 55 55
Baryphracta_deponiae 60 61
Bernissartia_fagesii 23 30
Borealosuchus_formidabilis 47 56
Borealosuchus_wilsoni 57 59
Boverisuchus_vorax 57 62
Brachychampsa_montana 47 52
Brachyuranochampsa_zangerli 59 59
Brochuchus_pigotti 70 71
Caiman_crocodilus 79 79
Caiman_latirostris 74 79
Comahuesuchus_brachybuccalis 46 46
Congosaurus_compressus 53 59
Crocodilaemus_robustus 18 19
Crocodylus_acutus 79 79
Crocodylus_affinis 59 59
Crocodylus_cf_clavis 59 59
Crocodylus_depressifrons 56 61
Crocodylus_elliotti 78 78
Crocodylus_intermedius 79 79
Crocodylus_megarhinus 65 66
Crocodylus_moreletii 79 79
Crocodylus_niloticus 76 79
Crocodylus_novaguineae 79 79
Crocodylus_palustris 79 79
Crocodylus_porosus 77 79
Crocodylus_rhombifer 79 79
Crocodylus_siamensis 79 79
Crocodylus_sivalensis 76 78
Diplocynodon_darwinii 60 61
Diplocynodon_hantoniensis 57 66
Diplocynodon_remensis 56 56
Diplocynodon_ungeri 72 73
Dyrosaurus_phosphaticus 46 59
Elosuchus_cherifiensis 40 42
Elosuchus_felxi 41 41
Eoalligator_chunyi 55 55
Eoalligator_huiningensis 53 54
Eoaiman_cavernensis 60 62
Eogavialis_africanum 64 64
Eogavialis_gavialoides 66 66
Eosuchus_licerchei 56 64
Eosuchus_minor 56 58
Euthecodon_arambourgi 70 70
Eutretauranosuchus_delfsi 18 19
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C.6 Biogeography files for Neosuchia

BioGeoBEARS geography file

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465
BioGeoBEARS distance matrix

Time periods for distance-based analysis:
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Distance matrix:
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22.3 16.2 1.0 1.0 0.0 44.5 5.3
28.0 50.3 17.8 42.3 44.5 0.0 31.5
54.9 52.9 1.0 23.2 5.3 31.5 0.0

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10.4 0.0 51.8 29.0 16.7 39.1 55.8
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12.1 29.0 1.0 0.0 2.8 46.7 27.9
21.0 16.7 5.1 2.8 0.0 35.7 4.4
39.7 39.1 11.3 46.7 35.7 0.0 54.7
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END

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