The phylogenetic relationships of neosuchian crocodiles and their implications for the convergent evolution of the longirostrine condition

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Since their origin in the Late Triassic, crocodylomorphs have had a long history of evolutionary change. Numerous studies examined their phylogeny, but none have attempted to unify their morphological characters into a single, combined dataset. Following a comprehensive review of published character sets, we present a new dataset for the crocodylomorph clade Neosuchia consisting of 569 morphological characters for 112 taxa. For the first time in crocodylian phylogenetic studies, quantitative variation was treated as continuous data (82 characters). To provide the best estimate of neosuchian relationships, and to investigate the origins of longirostry, these data were analysed using a variety of approaches. Our results show that equally weighted parsimony and Bayesian methods cluster unrelated longirostrine forms together, producing a topology that conflicts strongly with their stratigraphic distributions. By contrast, applying extended implied weighting improves stratigraphic congruence and removes longirostrine clustering. The resulting topologies resolve the major neosuchian clades, confirming several recent hypotheses regarding the phylogenetic placements of particular species (e.g. *Baryphracta deponiae* as a member of Diplocyonodontinae) and groups (e.g. Tethysuchia as non-eusuchian neosuchians). The longirostrine condition arose at least three times independently by modification of the maxilla and premaxilla, accompanied by skull roof changes unique to each longirostrine clade.


INTRODUCTION

Crocodylomorpha is a paucispecific clade in modern faunas, which was thought to include only 23 extant species (Oaks, 2011), although recent genetic work has increased this number to at least 25 (Hekkala et al., 2011; Shirley et al., 2018). By contrast, the rich fossil record of Crocodylomorpha indicates that it was previously much more diverse and widespread, with over 600 named species (Alroy et al., 2018). This clade comprises a paraphyletic array of early diverging taxa (‘sphenosuchians’) and the monophyletic Crocodyliformes (Brochu et al., 2009), with the latter including the three extant crocodylian families.

Although extant 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 of Crocodylomorpha diverged during the first 100 million years of its evolutionary history and exhibited numerous unique modifications to their ancestral bauplan. Species range from fully terrestrial (Tennent et al., 2016) through amphibious to fully marine (De Andrade & Sayão, 2014) and, although extant forms are exclusively carnivorous (including the piscivorous Gavialidae), some extinct species are suggested to have been herbivorous or omnivorous (Ösi et al., 2007; Sereno & Larsson, 2009; Melstrom & Irmis, 2019). Several species possessed...
unusual snout shapes (Gasparini et al., 2006) from ‘pug-nosed’ forms such as Simosuchus (Buckley et al., 2000) to extremely long- and thin-snouted taxa such as Dyrosaurus and the extant Gavialis. Body sizes ranged from <1 m, as in the Atoposauridae (Schwarz-Wings et al., 2011), to giant forms such as Sarcosuchus imperator de Broin & Taquet, 1966 with body lengths >11 m (Sereno et al., 2001). This morphological and ecological diversity is paralleled by expansions and contractions in geographical ranges that occurred during the Mesozoic and Palaeogene, 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).

Crocodile species richness was coupled strongly with peaks in global thermal maxima (Brochu, 2013). Crocodylian species richness continued to increase through time (Mannion et al., 2015), with peaks in global thermal maxima (Brochu, 2013). Given the rich fossil record of crocodylomorphs, their morphological and ecological diversity, wide spatiotemporal range and apparent responsiveness to environmental perturbations, it is unsurprising that there has been considerable interest in crocodylomorph evolution, especially in recent years. While substantial progress has been made towards the goal of a robust, well-resolved phylogeny for the group, many problems remain (see below). Disagreements over phylogenetic relationships have impacted negatively upon our understanding of macroevolutionary patterns: for example, within Eusuchia, the geographical origins of both alligatoroids and crocodyloids continue to be widely debated (Brochu, 1999, 2003; Salisbury et al., 2006; Martin & Buffetaut, 2008; Oaks, 2011; Holliday & Gardner, 2012; Martin et al., 2014; Wang et al., 2016).

Neosuchia is a clade within a larger grouping, Mesoeucrocodylia (Fig. 1), which also includes Notosuchia, plus a number of smaller clades and several paraphyletic grades (De Andrade et al., 2011; Pol & Larsson, 2011). Neosuchia was first defined as ‘Atoposauridae, Goniopholidae [sic], Pholidosauridae, Dyrosauridae, Bernissartia, Shamosuchus, and eusuchians’ (Benton & Clark, 1988: 27). The most recent, widely accepted definition of Neosuchia (used throughout the text here) is ‘all crocodyliforms more closely related to Crocodylus niloticus than to Notosuchus terrestris’ (Sereno et al., 2001: 4). Although this definition results in the inclusion or exclusion of certain groups depending on the preferred phylogenetic topology (such as Thalattosuchia, Sebecia and Dyrosauridae: Martin et al., 2010), it currently contains approximately 480 species according to the Paleobiology Database (PBDB: Alroy et al., 2018). We limit this study to Neosuchia, because this clade represents the majority of the long, intricate evolutionary history of crocodylomorphs, contains the bulk of their species richness and encompasses a wide range of skull morphologies (Fig. 2).

The aims of this study are three-fold: (1) to provide a new, comprehensive character list with uniformly worded, clearly defined and illustrated character states for the analysis of neosuchian interrelationships, (2) to identify the analytical approaches that provide the best estimate of neosuchian relationships (e.g. the use of continuous data, extended implied weighting, the application of different tree-building methods, such as maximum parsimony and Bayesian inference) and (3) to investigate patterns of character state assembly and homoplasy during the multiple origins of longirostry in Neosuchia. We start by briefly summarizing current problems in our understanding of neosuchian phylogeny and the difficulties caused by longirostry, and then present our rationale for the assembly and analysis of a comprehensively revised character set. A suite of different analytical protocols are implemented, grounded in theoretical and methodological literature, and the relative accuracy of the resulting topologies is assessed by determining their fit to stratigraphy. Finally, we discuss the implications of our results for morphological phylogenetic analyses in general, neosuchian phylogeny and systematics, our understanding of the spatiotemporal distributions of major neosuchian clades and the evolution of the longirostrine condition.

**Previous studies of crocodylomorph relationships**

The first detailed cladistic analyses of Crocodylomorpha were undertaken during the 1980s (e.g. Clark & Matthew, 1986; Benton & Clark, 1988; Buscalioni & Sanz, 1988). These were followed by further studies that lead to analyses with marked increases in character and species numbers, and numerous new phylogenetic hypotheses were 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; Larsson & Gado, 2000; Ortega et al., 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 subsequent phylogenetic studies derived most of their morphological characters from these earlier works, often without critical re-examination of either the characters or the 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 & Gardner, 2012; Montefeltro et al., 2013; Turner & Pritchard, 2015; Wilberg, 2015a; Martin et al., 2016a; Wang et al., 2016; Wu et al., 2018). Table 1 presents an overview of selected crocodylomorph phylogenetic studies, illustrating the increase in taxon and character sampling over time.

Within Neosuchia, the affinities of various taxa remain unclear, despite the large number of studies available (Fig. 3). This includes the positions of early diverging non-eusuchians (such as Bernissartia and Mahajangasuchus: Lauprasert et al., 2009; De Andrade et al., 2011) and eusuchians (such as Hylaeochampsa and Alloposuchus: Buscalioni et al., 2011). The placements of Boverisuchus and Borealsuchus are also contested. Boverisuchus is often associated with either Crocodylia (Bronzati et al., 2012) or Planocephalidae (Brochu, 2013). The position of Borealsuchus is unclear in its relation to Gavialoidea, being resolved either as the sister-taxon of the latter (Buscalioni et al., 2011; Puértolas et al., 2011) or outside Crocodylia (Bronzati et al., 2012).

An attempt has been made to generate a consensus of these studies using a supertree meta-analysis (Bronzati et al., 2012). Although supertrees can be useful tools for integrating previous phylogenies, this approach has been criticized because robust methods to test these trees are lacking and their topologies might 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 Borealsuchus (as mentioned above), can be placed in ‘compromise’ positions in the supertree as a result of widely differing placements in the source trees.

The phylogenetic studies listed in Table 1 are also potentially problematic in terms of character sampling, construction and treatment. For example, all previous analyses have discretized quantitative characters rather than treating them as continuous data. Furthermore, many previous datasets contain multiple examples of suboptimally constructed characters, such as complex multistate composite characters (see

Composite characters should be atomized and converted into several binary characters, according to Wilkinson (1995), Sereno (2007) and Brazeau (2011), although care has to be exercised with assumptions of character independence (Wilkinson, 1995; Vogt, 2018) and an increase in inapplicable scores (analytically equivalent to increased missing data), resulting from reductive character construction (Maddison, 1993; Strong & Lipscomb, 1999; Seitz et al., 2000). Finally, many characters have been proposed without their individual states being clearly illustrated: given the potential subjectivity of scoring these characters, this lack of clarity is likely to have led to inconsistent scoring of the same character in different analyses. Therefore, a detailed examination and re-evaluation of the available characters for elucidating crocodylomorph phylogeny is long overdue.

### The ‘Longirostrine Problem’

One of the major problems in neosuchian phylogenetics is posed by the evolution of longirostrine taxa: several species, such as members of Tethysuchia, Gavialoidea and Tomistominae, possess markedly thin, elongated snouts, which are regarded as potential adaptations to piscivory (Iordansky, 1973). This superficial similarity between taxa can cause artificial clustering of longirostrine species into clades whose branching patterns are incongruent with their stratigraphic records (Clark, 1994; Jouve, 2009; Meunier & Larsson, 2016), although molecular evidence supports a sister-taxon relationship for the extant longirostrine species Gavialis and Tomistoma (Roos et al., 2007; Piras et al., 2010). Several methods have been suggested to deal with this problem, including the removal of some longirostrine groups to explore the position of other longirostrine clades (Martin et al., 2016b) and the a priori deletion of characters associated with the longirostrine condition, combined with the removal of several longirostrine taxa from the analysis to avoid artificial associations (Jouve, 2009). Despite the strong homoplastic signal in characters associated with the longirostrine condition, they still retain potential phylogenetic information and, ideally, should not be totally discarded. Although a priori deletion of taxa might remove some of the confounding homoplastic signal, it is also likely to simultaneously reduce the representation of genuinely informative character states.

One method to deal with problems of homoplasy is Implied Weighting (Goloboff, 1993), which is an addition to the maximum parsimony methods based on Farris (1969). It allows the retention of potentially homoplastic characters throughout an analysis, downweighting them to different extents, depending on a preset penalty factor (k) and the distribution of states across the trees being ‘considered’ during the analysis. An improved version of the algorithm, Extended Implied Weighting (‘EIW’), is able to cope better with missing data (Goloboff, 2014). However, O’Reilly et al. (2016, 2018b) and Puttick et al. (2017) stated that Implied Weighting performed worse than equal-weights parsimony and Bayesian models (see also: Congreve & Lamsdell, 2016). In contrast, Goloboff et al. (2017) argued that EIW outperforms all other

### Table 1. Selected previous studies of crocodylomorph phylogeny.

<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 et al. (2001)</td>
<td>Mesoeucrocodylia</td>
<td>20</td>
<td>72</td>
</tr>
<tr>
<td>Wu et al. (2001)</td>
<td>Crocodyliformes</td>
<td>32</td>
<td>131</td>
</tr>
<tr>
<td>Jouve et al. (2006)</td>
<td>Crocodylomorpha</td>
<td>47</td>
<td>234</td>
</tr>
<tr>
<td>Salisbury et al. (2006)</td>
<td>Crocodylia</td>
<td>46</td>
<td>176</td>
</tr>
<tr>
<td>Hill et al. (2008)</td>
<td>Dyrosauridae</td>
<td>14</td>
<td>39</td>
</tr>
<tr>
<td>Jouve (2009)</td>
<td>Crocodyliformes</td>
<td>75</td>
<td>143</td>
</tr>
<tr>
<td>Hastings et al. (2010)</td>
<td>Crocodyliformes</td>
<td>16</td>
<td>82</td>
</tr>
<tr>
<td>De Andrade et al. (2011)</td>
<td>Crocodylomorpha</td>
<td>104</td>
<td>486</td>
</tr>
<tr>
<td>Brochu et al. (2012)</td>
<td>Eusuchia</td>
<td>96</td>
<td>179</td>
</tr>
<tr>
<td>Bronzati et al. (2012)*</td>
<td>Crocodyliformes</td>
<td>184</td>
<td>-</td>
</tr>
<tr>
<td>Montefeltro et al. (2013)</td>
<td>Neosuchia</td>
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<td>484</td>
</tr>
<tr>
<td>Adams (2014)</td>
<td>Crocodyliformes</td>
<td>90</td>
<td>301</td>
</tr>
</tbody>
</table>

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methods, including Bayesian analyses, and parsimony has been found to yield more stratigraphically congruent results than Bayesian analyses (Sansom et al., 2018). Despite the recent debate over the effectiveness of weighted parsimony vs. Bayesian analyses and their usefulness in dealing with homoplasy, neither has been applied extensively to neosuchian phylogenetics. Here, we apply both methods in an attempt to tackle 'the longirostrine problem'.

**Phylogenetic abbreviations**

CI, Consistency Index; EIW, Extended Implied Weighting; GER, Gap Excess Ratio; MPT(s), Most Parsimonious Tree(s); MP, Maximum Parsimony; MSM*, Manhattan Stratigraphic Measure; NTS, New Technology Search; OTU, Operational Taxonomic Unit; RCI, Relative Completeness Index; RI, Retention Index; TL, Tree Length.

**Anatomical abbreviations**

An, angular; Ar, articular; At, atlas; Ax, axis; Bso, basioccipital; D, dentary; Ecp, ectopterygoid; Exo, exoccipital; F, frontal; Fe, femur; Hu, humerus; Il, ilium; J, jugal; L, lacrimal; Mc, metacarpal; Mx, maxilla; N, nasal; Na, neural arch; Ocn, occipital condyle; Pa, palatine; Par, parietal; Pf, prefrontal; Pi, pisiform; Pmx, premaxilla; Po, postorbital; Pt, pterygoid; Q, quadrate; Qi, quadratojugal; Ra, radius; Ral, radiale; Sa, surangular;
Sp, splenial; Spo, supraoccipital; Sq, squamosal; Ul, ulna; Ulr, ulnare; Vce, vertebral centrum.

Institutional abbreviations
AMNH, American Museum of Natural History, New York, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LDUCZ, Grant Museum of Zoology, University College London, UK; MNHN, Museum National d’Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; YPM, Peabody Museum of Natural History, Yale University, New Haven, USA.

MATERIAL AND METHODS
DATA COLLECTION
A total of 112 neosuchian taxa were included in this study. Morphological characters were scored first-hand from 152 specimens representing 108 taxa, with a further four taxa (Iharkutosuchus mahadii Ösi et al., 2007, Isisfordia duncani Salisbury et al., 2006, Koumpiodontosuchus aprosdokiti Sweetman et al., 2015 and Pietraroiasuchus ormezzanoi Buscalioni et al., 2011) scored from descriptions in the literature.

As outgroup choice has been shown to influence taxon placement in crocodylomorph analyses (Wilberg, 2015a), multiple species outside Neosuchia were selected (N = 8, counting Thalattosuchia), with Protosuchus richardsoni Brown, 1933 set as the outgroup to all other taxa (TNT only allows a single outgroup to be designated). A further four non-neosuchians were included (Araripesuchus gomesii Price, 1959, Comahuesuchus brachybbuccalis Bonaparte, 1991, Notosuchus terrestris Woodward, 1896 and Sebecus icaeorhinus Simpson, 1937), because they represent a range of clades that are currently thought to lie outside Neosuchia, but are more closely related to Neosuchia than Protosuchus (Bronzati et al., 2012). In addition, three thalattosuchian species (Gracilinectes leedsi Andrews, 1913, Pelagosaurus typus Bronn, 1841 and Steneosaurus bollensis Cuvier, 1824) have been included in the dataset, because Thalattosuchia has been resolved in various positions both in and outside Neosuchia (Benton & Clark, 1988; Wu et al., 2001; Pol & Gasparini, 2009; Young & De Andrade, 2009; Wilberg, 2015a). The analysis also included 19 extant taxa representing all three crocodylian families.

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

All measurements and scorings 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), Montefeltro et al. (2013) and references therein. These characters were traced back to their original descriptions and new characters were added based on personal observations and a survey of the more recent literature. Each character was evaluated to establish that it describes 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) to enhance clarity and repeatability.

After removing obvious duplicates, the original character list contained 1419 discrete characters. All of these characters were checked against specimens of extant crocodylians in the collections of LDUCZ and NHMUK and individually re-evaluated in terms of how accurately they could be replicated and operationalized. This led to the removal of numerous characters for one or more of three major reasons: (1) they represented autapomorphies for OTUs in the dataset and were thus uninformative for resolving neosuchian phylogeny, (2) they were hidden duplicates of other characters, describing the same morphologies but with different definitions or (3) they were describing ambiguous morphological variation that could not be applied consistently. A list of these discarded characters, with justifications for their exclusion, can be found in the Supporting Information (S2).

Twenty-three new characters were formulated, nine based on personal observation of specimens and 14 based on features identified in other systematic descriptions (Wu et al., 2001; Brochu, 2007, 2011; Jouve et al., 2008a; Martin et al., 2010, 2014; Buscalioni et al.,...
The original character list contained many complex multistate composite characters. An example of this is character 6 of 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 presence/absence of the premaxillary bar (see characters 95 and 96 in our character list, available in full as Supporting Information [S1]).

Further problems in character scoring and repeatability have been caused previously not only by unclear wording, but also by the use of character states that are difficult to operationalize; for example, those that employ undefined qualitative 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 continuum rather than via distinct stages (Wiens, 2001) it is more appropriate to convert discretized quantitative characters into continuous ones. Continuous data are less influenced by worker subjectivity (Parins-Fukuchi, 2017) and are a more accurate representation of evolutionary processes that usually occur along a sliding scale rather than in separate, distinct stages (Wiens, 2001). Moreover, continuous characters have been found to have a positive impact on obtaining phylogenies by reducing homoplasy (Jones & Butler, 2018). Such data 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)."
The height of mandibular symphysis to maximum length of mandibular symphysis [character 54a; after Jouvet et al. (2005, 2008a), character 17]. The original characters 53a and 54a were, therefore, excluded and are marked as such in the full character list.

The final morphological character list used as the basis for our subsequent analyses contains 569 characters (487 discrete and 82 continuous) and is available in the Supporting Information (S1). To facilitate the use of this character list, 163 characters have been illustrated in order to enhance clarity and repeatability of character-state scoring in future analyses. A second version of the full dataset was generated with all continuous characters discretized into separate states according to their original character descriptions, in order to evaluate the influence of the alternative treatments of quantitative characters (i.e. continuous data vs. discretized versions) on phylogenetic reconstruction. The full.tnt files of both datasets are available in the Supporting Information (S4).

**Data transformations and character settings**

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. This is because it is necessary to adjust the relative weights of quantitative characters when expressed as continuous data (e.g. ratios) (Goloboff et al., 2006). 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 multistate characters were treated as ordered because 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, 288, 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 the Supporting Information (S1).

**Phylogenetic analyses**

Maximum parsimony (MP) 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) (Goloboff, 2014) in TNT. We used New Technology Search (NTS) with sectorial searches, ratchet, drifting and tree-fusing algorithms enabled on their default settings. The consensus was required to stabilize 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 two different k-values, k = 3 and k = 12. k = 3 represents the standard setting for TNT, while k = 12 was recommended as a potentially better alternative by Goloboff et al. (2017), as it does not downweight putative homoplasic characters as strongly as lower k-values and produces more accurate trees in a modelled environment.

In addition to unconstrained analyses, we also performed a MP+EIW analysis of the complete dataset using a backbone topological constraint. This backbone (Fig. 4) reflects the currently accepted consensus on neosuchian phylogeny (based on morphology), as found in Brochu (2011) and Bronzati et al. (2012). The constrained analysis was carried out to compare our new phylogenetic trees with established hypotheses. Statistical comparison of the lengths of unconstrained and constrained MPTs was carried out using a Templeton test (Templeton, 1983) via the TempletonTest.run script by Alexander N. Schmidt-Lebuhn (phylo.wikidot.com/tntwiki).

In order to identify unstable taxa and the characters responsible for their instability, we applied the command perprune (Goloboff & Szumik, 2015), which is based on the iterperce script by Pol & Escapa (2009).

**Figure 4.** Backbone tree used in the constrained analysis of the complete dataset CW3.
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 Ramirez, 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. Character-state mapping was performed using MESQUITE v.3.2 (Maddison & Maddison, 2017).

We also performed Bayesian inference using MrBayes v. 3.2 (Ronquist & Huelsenbeck, 2003; Ronquist et al., 2012). Because MrBayes does not allow for the use of continuous variables, only the rediscretized version of the dataset was analysed via this method. The dataset was analysed using the following commands: 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. [2012]) and mcmc ngen = 1000000 samplefreq = 10000 printfreq = 10000 diagnfreq = 10000. After the initial number of 1 000 000 generations, the standard deviation (SD) still proved too high (above 0.01). The SD never dropped below 0.2 so the analyses were stopped after 10 000 000 generations, with a burn-in of 1 000 000.

**Stratigraphic congruence**

We used stratigraphic congruence as an independent measure to compare different tree topologies. In accordance with the findings of Pol et al. (2004), we did not employ statistical tests between the different support measures, and only compared tree topologies based on the same species sets. Stratigraphic congruence for each of the resulting trees was calculated using the package strap (Bell & Lloyd, 2014) in the R environment, applying the command StratPhyloCongruence with 1000 permutations each for resampled and randomly generated trees. Taxon ages were taken from the PBDB (Alroy et al., 2018) and adjusted to be congruent with the International Chronostratigraphic (ICS) chart (Cohen et al., 2013) and any updates based on the recent literature, and are listed in full in the Supporting Information (S4).

For those taxa with only one occurrence in the fossil record, uncertainties in dating were taken into account by using the midpoint ages of their inferred stratigraphic ranges. Several taxa, such as *Dyrosaurus phosphaticus* Thomas, 1893, displayed genuine stratigraphic ranges with multiple occurrences in the fossil record and were entered into the ages file as such.

Stratigraphic congruence was calculated using three metrics: Relative Completeness Index (RCI) (Benton & Storrs, 1994), Manhattan Stratigraphic Measure (MSM*) (Siddall, 1998; Pol & Norell, 2001) and Gap Excess Ratio (GER) (Wills, 1999). The 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 total branch length of the time-scaled tree can be explained by actual taxon 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 congruence of a given tree’s topology. The GER is similar to MSM* in that it operates with a hypothetical tree of best stratigraphic congruence and topology of a given tree. However, it also takes into account suboptimal trees and calculates stratigraphic congruence with optimal and suboptimal tree topologies compared to the target tree that is being tested for stratigraphic congruence.

**RESULTS**

For ease of reference and discussion throughout, our various phylogenetic analyses are here referred to via a simple system of abbreviations (see Table 2).

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Dataset</th>
<th>Method</th>
<th>EIW</th>
<th>k-value</th>
<th>No. of MPTs</th>
<th>TL</th>
<th>CI</th>
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<td>EIW</td>
<td>k-value</td>
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<td>CI</td>
<td>RI</td>
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<td>12</td>
<td>12</td>
<td>2363</td>
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</tbody>
</table>

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PHYLOGENETIC ANALYSES

The results of the tree searches (Table 2) generally fall into three different categories (Fig. 5): (1) topologies where the longirostrine groups are clustered together (analyses without EIW, and with EIW under \( k = 12 \)), (2) topologies where the longirostrine groups are resolved as distinct clades in different positions (analyses with EIW and \( k = 3 \)) and (3) topologies whose strict consensus trees are characterized by numerous polytomies (Bayesian analysis, rediscretized dataset without EIW).

Taxon pruning and the use of RogueNaRok (Aberer et al., 2013) yields limited and unclear results as tree resolution is not significantly improved following the removal of potential ‘rogue’ taxa. Only a handful of taxa are shown to affect consensus tree resolution when removed. These taxa are either members of Tethysuchia (Dyrosaurus, Rhabdognathus and Pholidosaurus) or Crocodyloidea (Crocodylus affinis, C. elliotti, C. cf. clavis and C. megarhinus), in which all taxa of the latter clade have similar scores. A full list of apomorphies for each node in the unconstrained tree topology of the complete dataset analysis can be found in the Appendix.

STRATIGRAPHIC CONGRUENCE

The trees resulting from analysis CW3 (complete dataset with EIW and \( k = 3 \)) yield the best results with respect to stratigraphic congruence (with RCI values above –300 for the unconstrained, and ranging from –296 to –312 for the constrained analysis MPTs), followed by RW3 (rediscretized dataset with EIW and \( k = 3 \)) (RCI > -400) (see Table 3). In both cases, changing the \( k \)-value from 3 to 12 results in worse stratigraphic congruence analyses for each parsimony and Bayesian analysis performed. EIW, Extended Implied Weighting; GER, Gap Excess Ratio; MSM, Manhattan Stratigraphic Measure; RCI, Relative Completeness Index. The p-values for all stratigraphic congruence values (not shown) were all \( P < 0.05 \)

<table>
<thead>
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<th>Abbreviation</th>
<th>Dataset</th>
<th>Method</th>
<th>EIW k-value</th>
<th>RCI</th>
<th>GER</th>
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</tbody>
</table>

Figure 5. Illustration of the two major tree topologies obtained. The analyses yielded the following topologies in their strict consensus trees: A, unweighted analyses B, analyses using extended implied weighting with \( k = 3 \). Outlines drawn by the lead author.
congruence (RCI ranging from −610 to −695). The trees obtained from analyses C (complete dataset with equal weights parsimony) and R (rediscretized dataset with equal weights parsimony) yield considerably worse stratigraphic congruence values, with RCI ranging from −540 to −730 and −768 to −1020, respectively (Table 3).

TOPOLOGICAL DETAILS
Analyses C, R and RB result in clustering of most longirostrine taxa. In contrast, analyses CW3 and RW3 result in all major longirostrine clades appearing in distinctly separate regions of the tree. However, individual lineages and subclades differ greatly in their positions or internal structure. The results of the Templeton test show that the trees resulting from the constrained version of analysis CW3 are not significantly worse explanations of the data than those generated by the unconstrained analysis of CW3.

Araripesuchus, Comahuesuchus and Notosuchus are consistently resolved as a monophyletic notosuchian outgroup, associated with Shamosaurus, Theriosuchus and Sebecus. Thalattosuchus and Tethysuchia are paraphyletic in the results of analyses CW3 and RW3, although the relationship between taxa varies between analyses. All thalattosuchian taxa are consistently resolved as outgroups to Neosuchia. Hyposaurus, Congosaurus, Dybosaurus and Rhabdognathus form an unresolved monophyletic group in analyses CW3 and RW3 (Fig. 6), and Elosuchus, Sarcosuchus and Pholidosaurus occur in various positions in the trees [see Supporting Information (S3)].

Susischus anatoceps Salisbury et al., 2003 is consistently placed as the closest sister-group to Goniopholididae in analyses CW3 and RW3 (Fig. 6). Sunosuchus and Vectisuchus are included in Goniopholididae in analysis RW3. They are placed as sister-taxon to Goniopholididae in the unconstrained version of CW3.

In all weighted analyses, Bernissartia fagesii Dollo, 1883 is consistently found as the sister-taxon to all Eusuchia (Fig. 6). However, the clade including Hylaeochampsa is resolved as the sister-group to Brevirostres (Crocodyloidea + Alligatoroidea), except for the constrained version of CW3 where the backbone tree forces it to be the sister-group to the remaining eusuchians.

Analyses CW3 and RW3 yield monophyletic Gavialoidea and Gavialinae with similar species compositions, although with slight differences in internal relationships. Marccosuchus zennarii Jonet & Wouters, 1977 is resolved in Gavialoidea in CW3 (Fig. 6), but as part of Tomistominae in RW3. Both place Tomistoma dowsoni Fourtou, 1918 in Gavialoidea.

In addition, Crocodyloidea and Alligatoroidea are monophyletic in analyses CW3 and RW3. However, the greatest difference lies in the position of Diplocynodontinae: CW3 resolves it as the sister-group to Crocodylia, whereas RW3 places it as the sister-group to Alligatoridae, as is also enforced in the constrained version of analysis CW3. In addition, the position of the two species of Planocrania varies markedly between CW3 and RW3: as sister-group to Diplocynodontinae (RW3) or sister-group to Crocodylidae (CW3) (Fig. 6). Similarly, Eoalligator chunyi Young, 1964 is resolved in different positions, as either the sister-group to the remaining Brevirostres (CW3) or more deeply nested within Alligatoridae (RW3). Leidyosuchus canadensis Lambe, 1907 and L. gilmorei Mook, 1842 are placed either as the sister-group to all remaining Alligatoridae (RW3) or Diplocynodontinae (CW3). Both CW3 and RW3 show a paraphyletic Alligatorinae (with slightly different internal relationships) and monophyletic Caimaininae.

Tomistominae is consistently placed within Crocodylidae, as the sister-group to Crocodylinae, although the internal relationships of Crocodylinae vary across different analyses, especially with respect to the positions of Crocodylus siamensis Schneider, 1801 and C. novaguineae Schmidt, 1928.

Support values
Support values for the trees stemming from analysis CW3 are low overall, with few groups receiving high support for any of the three measures used (bootstrap, jackknife and Bremer). The best-supported groups for CW3 include: Notosuchus and Comahuesuchus (bootstrap = 97, jackknife = 98), the two species of Eosuchus (bootstrap = 77, jackknife = 72) and the two species of Planocrania (bootstrap = 74, jackknife = 85). See Figure 6 for all support values.

DISCUSSION

METHODOLOGICAL IMPLICATIONS

Extended implied weighting
Extended implied weighting with $k = 3$ consistently yielded results with better stratigraphic congruence than the same dataset analysed without EIW or with $k = 12$, a pattern repeated across all datasets (Table 3). Higher stratigraphic fit does not always reliably indicate accurate phylogenetic position (Smith, 2000; Geiger et al., 2001). Therefore, it is used here as an auxiliary criterion, independent of phylogeny, thus providing some basis for selecting between alternative topologies (as seen in: Ausich et al., 2015; Randle & Sansom, 2017). The
Figure 6. Strict consensus tree obtained by the unconstrained extended implied weights analysis of the complete dataset CW3 with $k = 3$. Support values are in the following order: Bootstrap/Jackknife/Bremer value.
largescale differences in the stratigraphic congruence values seen in our results, in conjunction with the non-clustering of longirostrine taxa, clearly suggest that the CW3 and RW3 trees represent a substantial improvement when compared to the C, R, CW12, RW12 and RB phylogenies. All analyses using EIW with $k = 3$ (CW3 and RW3) resolved Thalattosuchia, Tethysuchia, Gavialoidea and Tomistominae as separate longirostrine clades. The same datasets analysed without EIW (C, R, RB) or EIW and $k = 12$ (CW12, RW12) often yielded a single clade clustering all long- and slender-snouted taxa [for the different topologies see Supporting Information (S3); Fig. 5]. This extreme clustering of longirostrine taxa could stem from the use of continuous data (see below), with the use of EIW negating their effect. However, the rediscretized dataset analysed without EIW (R) exhibits the same pattern of clustering [see Supporting Information (S3)]. It is apparent that the usage of EIW with a low $k$-value plays a key role in obtaining trees whose topologies are less determined by homoplasic 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), our results for those analyses conducted with lower $k$-values display higher stratigraphic congruence. Both the complete and rediscretized datasets analysed with $k = 3$ (RCI $-273.8$ to $-275.7$ and $-329.1$ to $-365.6$, respectively) yielded more stratigraphically congruent trees than those analysed with $k = 12$ (RCI $-610.8$ to $-611.8$ and $-670.9$ to $-694.4$, respectively) (Table 3). The latter trees once again clustered longirostrine species together. This result reflects a high degree of homoplasy, either caused by the addition of continuous characters to the new dataset, or in neosuchian evolution as a whole (introduced as strong secondary signal by snout shape), since lower $k$-values are known to downweigh homoplastic characters more strongly (Goloboff et al., 2017). Here, we suggest that the latter explanation (i.e. that EIW has successfully identified and mitigated a homoplasys-driven secondary signal) is better supported, especially given other recent evidence that the treatment of quantitative characters as continuous data tends to reduce homoplasy (Jones & Butler, 2018).

Parsimony is the most commonly used method in reconstructing phylogenies using morphological data, although it has been argued that this is due to force of habit rather than the selection of the best method available (Congreve & Lamsdell, 2016). Recent debate has questioned the usefulness of parsimony in phylogenetic reconstruction in comparison with Bayesian methods and whether one outperforms the other (see: Wright & Hillis, 2014; O’Reilly et al., 2016, 2018a, 2018b; Goloboff et al., 2017; Puttick et al., 2017, Sansom et al., 2018; Yang & Zhu, 2018; Smith, 2019). Our results add to this debate by supporting the utility of EIW when analysing morphological data, particularly in cases where strong homoplasy might overprint the true phylogeny. In contrast, Bayesian analyses of the same datasets produced large numbers of polytomies and trees where longirostrine clades cluster together (representing either hard polytomies and a close relationship between longirostrine taxa, or incorrect tree reconstruction).

**Treatment of quantitative characters**

The trees obtained by analysing CW3 (the complete dataset, including both continuous and discrete characters, with EIW) yielded consistently higher stratigraphic congruence values for all three measures than those resulting from the rediscretized dataset (Table 3). Without EIW, the stratigraphic congruence values fall within similar ranges for the continuous and rediscretized datasets, both of which show clustering of longirostrine taxa. The use of continuous characters causes general skull shape to play a strong role in tree reconstruction, potentially contributing to the extreme clustering of longirostrine taxa. However, as this clustering is also observed in the analyses without continuous characters (R, RW12 and RB), our results point to improved accuracy in tree reconstruction when using continuous characters in conjunction with EIW.

During the rediscretization of the continuous characters, it became apparent that most of these characters (as deployed in previous studies) had been constructed on the basis of arbitrarily defined boundaries between character states. These arbitrary limits usually did not reflect true differences or gaps in the continuous variation of measurement-based ratios. An example can be seen in Fig. 7, for character 3 (based on character 3 from Hastings et al. (2010): thickness of anterior margin of external nares in relation to external nares: less than half anteroposterior length (0); same or greater than half anteroposterior length (1). The boundary of 0.5 between the two states does not reflect a clear categorical variation in ratios obtained by measuring a variety of different species. The vast majority of continuous characters in our dataset show similar patterns of non-categorical variation [see continuous character scores in Supporting Information (S4)].

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

**Implications for Neosuchian Phylogeny and Systematics**

The most stratigraphically congruent tree found in our analyses (Fig. 6, based on CW3) resolved all of the major neosuchian clades proposed by previous
phylogenetic studies (for a list of studies see: Table 1). However, it differed from the majority of these in placing Diplocynodontinae as the sister-group to Brevirostres, rather than within Alligatoroidea, as well as resolving Tethysuchia and Thalattosuchia as paraphyletic. Most of the synapomorphies discussed below are skull and mandible characters, which is unsurprising as the character list is dominated by features in these anatomical regions (77.9% of all characters). Moreover, postcranial material is less frequently (or sometimes never) preserved for many of the species in the dataset.

**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. 8). Our analyses support the placement of Tethysuchia as an early diverging neosuchian clade rather than within Alligatoroidea, as well as resolving Tethysuchia and Thalattosuchia as paraphyletic.

Most of the synapomorphies discussed below are skull and mandible characters, which is unsurprising as the character list is dominated by features in these anatomical regions (77.9% of all characters). Moreover, postcranial material is less frequently (or sometimes never) preserved for many of the species in the dataset.

**Figure 7.** Scatterplot of all the character scores for character 3 in our character list [see Supporting Information (S1)]. Each point represents the obtained ratio for one of our measured specimens (distance between anterior margin of nares and anterior margin of rostrum in dorsal view to maximum anteroposterior length of external nares in dorsal view). Colours mark character scores in the rediscretised version, according to character 3 in Hastings et al. (2010): black, character state 0 (anterior margin of external nares less than half of anteroposterior length of external nares; ratio <0.5); grey, character state 1 (anterior margin of external nares greater than half of anteroposterior length of external nares; ratio > 0.5).

In contrast to the results presented by Young et al. (2016), both species of Elosuchus/Fortignathus are found in Pholidosauridae in our CW3 trees, instead of F. felixi as a dyrosaurid. Elosuchus is grouped with Sarcosuchus and Pholidosaurus on the basis of the ventral edge of the premaxilla being situated deeper than that of the maxilla in lateral view (character 112), a zigzag-shaped frontoparietal suture on the interfenestral bar (character 195) and a well-developed anterolateral process on the postorbital (character 200). In contrast to the tree of De Andrade et al. (2011), Elosuchus does not form a clade with Vectisuchus, so we find no support for 'Elosuchidae', despite most of our character scores being similar to those of Andrade et al. (2011). In the CW3 tree, Vectisuchus forms a clade with the two species of Sunosuchus (Fig. 6), outside both Tethysuchia and Goniopholididae [where it was placed by Tykoski et al. (2002) and our RW3 analysis].

In addition to supporting a monophyletic Pholidosauridae, our CW3 analysis also resolves
Dyrosauridae as monophyletic, supporting the conclusions of Hastings et al. (2010) and Martin et al. (2016b). However, within this grouping, Dyrosaurus, Congosaurus and Rhabdognathus form a polytomy.

Terminonaris robusta Wu et al., 2001, which is typically classified as a pholidosaurid (e.g. Puértolas et al., 2011; Martin et al., 2016b), groups instead with the thalattosuchian Steneosaurus bollensis Cuvier, 1824 (Fig. 8). This relationship might result from the amount of missing data for our examined specimen of Terminonaris, as, despite possessing relatively complete skulls, many features were unscorable.

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Unstable early diverging neosuchian taxa

In addition to incomplete taxon sampling (covering 105 of 480 neosuchian taxa), which can lead to issues associated with long-branch attraction (Bergsten, 2005), the most prevalent problem in this study, as with many other fossil datasets, is the high proportion of missing data. Our dataset contains 49.7% missing data, the most complete taxon being Crocodylus porosus (7.7% of entries marked with ‘?’, resulting from inapplicable characters) and the most incomplete being Congosaurus compressus (extremely fragmentary material with 94.3% missing data). It is possible that this factor has led to varying placements of multiple taxa such as Shamosuchus djadochaensis Mook, 1924 [an early diverging neosuchian according to Pol et al. (2009)], Crocodiliaeus robustus Jouard, 1857 [a pholidosaur according to Young et al. (2011)] and Theriosuchus pusillus Owen, 1878 [an early diverging neosuchian recently removed from Atoposauridae by Tennant et al. (2016)]. Shamosuchus and Theriosuchus are resolved as the sister-group of Notosuchus in our CW3 and RW3 analyses, whereas Crocodiliaeus is placed as the sister-group of Crocodylidae (CW3, see Fig. 6) and within Alligatoridae [RW3, see Supporting Information (S3)].

Hylaeochampsidae

Our CW3 and RW3 analyses resolve Hylaeochampsidae in a novel position as the sister-group of Brevirostres (Fig. 6), rather than in its more typical placement as the sister-group of Crocodylia (Buscalioni et al., 2011). In addition, the susisuchids Isisforida duncani and Koumpiodontosuchus aprosdokiti (Sweetman et al., 2015; Turner & Pritchard, 2015) are placed as sister-taxon of Hylaeochampsidae in both CW3 and RW3, separate from Bernissartia. This association is based on the following characters: concave rostrum contour (character 86); anterior process of frontal truncated (character 182); squamosals extending to orbit margin and overlapping postorbitals (character 227); posterior edge of quadrate gently concave in dorsal view (character 283); paroccipital process dorsolaterally directed at a 45° angle in occipital view (character 290); prezygapophyseal processes of the anterior to middle cervical vertebrae flat or slightly convex (character 487); and a concave surface of the anterior centrum of the first caudal vertebra (character 501).

Goniopholididae and Susisuchus

The phylogenetic relationships of Goniopholididae in the CW3 analysis places a clade consisting of Vectisuchus and the two species of Sunosuchus as the sister-group to Goniopholididae + the remaining neosuchians (Fig. 6). Previously, these two genera have been identified either as two of the most shallowly nested goniopholidids (De Andrade et al., 2011; also found in the constrained version of analysis CW3) or a more deeply nested goniopholidid in the case of Sunosuchus (Martin et al., 2016b; although its placement was not discussed in the latter paper).

One novel aspect of our results is the identification of Susisuchus anatoceps as the sister-taxon of Goniopholididae in both our CW3 and RW3 analyses. Susisuchus has previously been placed outside Neosuchia (Jouve, 2009) or as part of Susisuchidae at the base of Neosuchia (Fortier & Schultz, 2009; Turner & Pritchard, 2015). The two synapomorphies supporting the association of Susisuchus and Goniopholididae in our trees are: dorsal process of premaxillae extending beyond third maxillary alveolus (character 108) and caudal vertebrae with amphicoelous centra from second vertebra onward (character 503).

Borealosuchus and Planocaniidae

Our CW3 and RW3 analyses resolves Borealosuchus as the sister-taxon of Brevirostres, similar to the results presented in Brochu (2001) (Fig. 6). This is in contrast to Pol et al. (2009), where it is one of the earliest diverging eusuchian lineages (Holliday & Gardner, 2012) and formed a polytomy with Gavialoidea; and Puértolas et al. (2011), where it was placed as the sister-group to Gavialoidea. Its position as the sister-taxon to Brevirostres in our analyses is based on: alveolar walls raised relative to ventral surface of maxilla (character 131); a weak postorbital bar (its width less than half of the bar height) (character 213); anterior edge of choanae closer to posterior edge of pterygoid flanges than suborbital fenestrae (character 352); and third maxillary alveolus larger in diameter than second alveolus (character 391). Our character scores mostly agree with those in previous studies, but they are overwhelmed by the addition of other characters in our revised dataset.

Planocaniidae sensu Brochu (2013), who defined it as consisting of both species of Planocrania + Boverisuchus, is not identified in any of our analyses. This is despite the fact that our scores include the same apomorphies that grouped the three species together in Brochu (2013): labiolingually compressed teeth on both maxilla and dentary (characters 396 and 414). However, in our analysis, these two characters do not provide a strong enough signal to resolve Planocaniidae. Both CW3 and RW3 analyses place the two Planocrania species as the sister-group of Crocodylidae on the basis of the lateral carotid foramen opening dorsal to the basisphenoid lateral exposure (character 318) and parallel to subparallel lateral edges of the anterior half of the interfenestral bar between the suborbital fenestrae (character 366). Boverisuchus
is placed as the sister-taxon of Brevirostres, based on: a single projection of the postorbital bar (character 216); the posteriormost maxillary alveolus being closer to the anterior margin of the orbit than the posterior margin (character 394); and dentary teeth occluding lingually to maxillary teeth (character 425).

Gavialoidea
In line with the majority of recent morphological phylogenies (with the notable exception of Halliday et al., 2013), we find Gavialoidea and Tomistominae as separate lineages, with Gavialoidea as the sister-clade of Brevirostres and Tomistominae as the sister-clade of Crocodylinae, nested within Crocodyloidea (Fig. 6).

The overall branching pattern within Gavialoidea is similar in both the CW3 and RW3 analyses and resembles that found in Jouve et al. (2015), with the exception of Piscogavialis jugaliperforatus Kraus, 1998, which is resolved in an earlier diverging position and forming a clade with Rhampbosuchus. The separation of thoracosours from Gavialoidea proposed by Lee & Yates (2018) (based on incorporating stratigraphy directly into phylogenetic analysis) is not supported, possibly because our analysis did not incorporate stratigraphic data directly into tree reconstruction and/or because of differences in taxon sampling and character construction and scoring. Instead, our results provide a number of synapomorphies uniting thoracosours and gavialoids: large supratemporal fenestrae, covering more than 50% of the skull roof surface (character 224); no parietopostorbital suture on dorsal skull roof (character 244); and an anterior notch at the jugal-lacrimal contact, paralleling the jugal-lacrimal suture on dorsal skull roof (character 317); and anterior median palatine process (character 370). This latter clade is united by: foramen for the palatine ramus of CN-V large (at least 50% or more of adjacent alveolus length) (character 137); 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).

Two or three taxa are grouped within Gavialoidea in our CW3 analysis, despite their previous referrals to Tomistominae: Maroccosuchus zennaroi Jonet & Wouters, 1977 [an early diverging tomistomine according to Jouve et al. (2015) and our RW3 analysis] and two species of Gavialosuchus [both tomistomines according to Brochu & Storrs (2012)]. The examined Maroccosuchus specimen (IRSNB R408) had limited access and was more fragmentary than other specimens described in the literature. This resulted in several of the characters usually uniting it with Tomistominae (such as the extent of the pterygoid wings and the morphology of the choanae; see Jouve et al., 2015) being scored as unknown, changing the position of Maroccosuchus in our CW3 tree. Gavialosuchus eggenburgensis Toula & Kail, 1885 (in the unconstrained CW3 and RW3 analyses) and G. antiquus Leidy, 1852 are grouped with the Gavialidae + Thoracosaurus clade on the basis of: the frontoparietal suture being entirely on the skull table (character 193); barely visible posterior walls of supratemporal fenestrae in dorsal view (character 225); dorsal and ventral rims of groove for external ear valve musculature flaring anteriorly (character 230); parietopostorbital suture present on dorsal skull roof (character 244); no midline crest on basioccipital plate below occipital condyle (character 304); basisphenoid with large pendulous tubera (character 305); dentary symphysis extending beyond eighth dentary alveolus (character 400); lateral edges of dentary oriented longitudinally, with convex anterolateral corner and extensive transversely oriented anterior edge (character 401); and distal rami of mandible strongly curved medially at mid-length, giving the mandible a broad Y-shaped outline (character 468).

A third taxon, Tomistoma dowsoni, had not been included in any phylogenetic analyses until this study, although differences in skull morphology from other Tomistoma species had been noted (Jouve et al., 2015). Both CW3 and RW3 analyses resolve T. dowsoni as part of Gavialoidea, most closely related to Piscogavialis.

Crocodyloidea
In our CW3 and RW3 analyses, Crocodyloidea is composed of three clades: Tomistominae, Crocodylinae and an early diverging crocodyloid clade consisting of Brachyurancamps, Crocodylus affinis Marsh, 1871, C. elliotti Leidy, 1871, C. cf. clavis Cope, 1871 and Prodiplocynodon (Fig. 6). This latter clade is united by: foramen for the palatine ramus of CN-V large (at least 50% or more of adjacent alveolus length) (character 137); 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 we identify in Tomistominae are similar to those found by Brochu (1999), Jouve et al. (2008b) and Buscalioni et al. (2011). However, unlike the topologies generated by Brochu (2004) and Jouve et al. (2015), three of the four Tomistoma species scored in our dataset (all except T. dowsoni) were resolved as the most deeply nested tomistomines in both CW3 and RW3 (Fig. 6; Supporting Information (S3)). This includes T. petrolica Yeh, 1958, which had been placed in an earlier diverging position elsewhere (Brochu & Storrs, 2012; but not discussed). These tomistomines cluster together based on the following characters: a small pit posterior to the external nares (character 107); linear lateral margins of maxillae in dorsal view (character 127); a straight ventral edge of the maxillae in lateral view (character 128); anterior margin of the nasal located posterior relative to the level of the first maxillary tooth (character 152); absence of a parietopostorbital suture from the skull roof (character 244); and thin and long teeth, at least three times longer than wide (character 397).
The interrelationships of Crocodylinae are highly variable across our different analyses. The topologies we found with our CW3 analysis differ from those published by others, on the basis of both morphological (Brochu & Storrs, 2012) and molecular (Meredith et al., 2011; Oaks, 2011) (Fig. 9) datasets, and do not

Figure 9. Summary of the competing hypotheses of crocodyloid phylogenetic relationships 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.
cluster species geographically [e.g. into ‘Old World’ and ‘New World’ groups, as found by Meredith et al. (2011)]. These interrelationships are supported by few synapomorphies for the groups in Crocodyliae, but there are a high number of shifts within continuous characters. In this case, the reliance of continuous characters on overall skull shape appears to be a potential cause for the unique interrelationships found. In addition, most discrete characters that act as synapomorphies for the different clades of Crocodyliae are located in the posterior skull and/or mandible (e.g. features of the basioccipital and dentary). However, many of these clades are based on continuous characters and are thus variable between analyses.

In addition, several ‘traditional’ non-crocodylian taxa, such as C. depressifrons de Blainville, 1855, Asiatosuchus grangeri Mook, 1940 (both crocodilyids according to: Delfino & Smith, 2009; Brochu & Storrs, 2012; Wang et al., 2016) and Eoalligator huiningensis Young, 1982 (a crocodyloid according to: Wu et al., 2018), are resolved as part of a monophyletic group nested deeply within Crocodyliae in both the CW3 and RW3 analyses. However, this group is united only by a single character state: a ‘neck’ formed by the pterygoid surface being pushed inward, lateral and anterior to the internal choana (character 357).

**Alligatoroidea**

Two of the largest deviations from ‘traditional’ crocodylian phylogenies seen in our trees occur in Alligatoroidea. The CW3 analysis resolves Diplomynodontinae as the sister-group to all Brevirostre, instead of placing it in Alligatoroidea (as in: Delfino & Smith, 2012; Brochu, 2013; and our RW3 trees, as well as the constrained CW3 trees). Leidyosuchus gilmorei + Leidyosuchus canadensis is placed as the sister-group of Diplomynodontinae in the CW3 analysis. This association is supported by the following characters: frontal preventing contact between postorbital and parietal on skull table (character 193); spina quadratejugalis positioned high between posterior and superior angles of infratemporal fenestra (character 270); and dentary alveoli 3 and 4 confluent (character 420). This is in contrast to the relationship proposed by Delfino & Smith (2012) where Leidyosuchus is placed as the sister-taxon of Diplomynodontinae + Globidonta (but not discussed in their paper). However, our results agree with Delfino & Smith (2012) in finding that Baryphracta deponiae is nested deeply within Diplomynodon.

We agree with Wu et al. (2018) that Eoalligator and Asiatosuchus are not synonymous (contra Wang et al., 2016). Our findings corroborate the identification of Asiatosuchus as a crocodyloid (Delfino & Smith, 2009; Wang et al., 2016) and also suggest a possible crocodyloid position for Eoalligator huiningensis (see above). However, E. huiningensis is placed as the sister-taxon to Brevirostres in the CW3 analysis.

The largest differences between our results and those of previous analyses are found in the relationships within Globidonta. Although Caimaninae is resolved as monophyletic, Alligatorinae is paraphyletic in both the CW3 and RW3 analyses, in marked contrast to the analysis of Brochu (2013) and its derivatives (e.g. Skutschas et al., 2014; Wang et al., 2016) (Fig. 6). The overall relationships in Alligatorinae that are supported here resemble those in Wu et al. (1996), although that study did not include any caimanines. As with Crocodyliae, there are few discrete synapomorphies supporting the internal alligatorine groups in our trees: instead, there are a large number of shifts in continuous characters. Our results mainly reflect the patterns of overall skull shape within Alligatorinae (e.g. the shorter snouts of both A. sinensis Fauvel, 1879 and caimanis), potentially because of the influence of continuous data, although Alligatorinae remains paraphyletic in the phylogenies based on the discretized datasets (RW3 and RW12).

**Molecules vs. morphology**

Our reconstructed morphological phylogenies differ from recently proposed molecular trees for extant crocodilian taxa in a number of ways. As outlined above, relationships differ most notably within the Crocodyliae, the paraphyly of Alligatorinae, as well as in providing a different topology for the well-known Gavialis–Tomistoma problem (see below). The results of molecular analyses, based on both nuclear and mitochondrial data, have usually been consistent between different studies and corresponded to biogeographical patterns (Oaks 2011). One possible explanation for the differences between the molecular and morphological trees lies in the use of continuous characters, as we have discussed previously. The relationships within the Crocodyliae and Alligatorinae are usually determined by shifts between continuous character states, which follow changes in the general outlines of the skull for the most part. In addition, a simple parsimony analysis of our dataset without EIW, and with continuous characters removed, yielded a large unresolved tree (data not shown). A second analysis of our dataset without continuous characters but with the use of EIW (k = 3) resulted in a similar topology to the CW3 tree, with a paraphyletic Alligatorinae and unique relationships within Crocodyliae. This indicates that the use of continuous characters does not constitute
the sole reason for the differences between molecular trees and our morphological phylogenies. Additional reasons for these differences could include: (1) EIW potentially penalizes the characters that underpin the relationships in the affected subfamilies and/or (2) errors caused in molecular phylogenetic topologies because they exclude fossil species.

**Temporal implications**

The temporal ranges implied by our phylogenies (Fig. 10) are influenced strongly by the differing positions of Hylaeochampsidae and *Crocodilaemus robustus* within our trees. The node ages obtained here are usually older than those derived from molecular phylogenetic estimates (e.g. Roos et al., 2007; Oaks, 2011).

Our results indicate that the origin of Neosuchia occurred in the Early Jurassic, at least 180 million years ago (Mya), which is consistent with other estimates (Pol et al., 2009; Montefeltro et al., 2013). The origination time of Eusuchia is strongly influenced by the placement of *Crocodilaemus*: if the latter is the sister-taxon of Brevirostres, as in the tree based on the CW3 analysis, eusuchian origins are pushed back to the early Late Jurassic (around 160 Mya). However, if *Crocodilaemus* is removed, the CW3 tree places eusuchian origins in the early part of the Early Cretaceous, around 130 Mya (Fig. 10). The latter is similar to the timing implied by the constrained CW3 trees. This estimate is congruent with those from Pol et al. (2009) and Lee & Yates (2018). The placement of Hylaeochampsidae and *Crocodilaemus robustus* also adds long ghost ranges of ~70 Myr to Gavialoidea and the Borealosuchus clade in the unconstrained CW3 tree. In contrast, the differing placements of Diplocynodontinae do not affect the origination time of Crocodylia, which is estimated to have taken place ~90–100 Mya. This estimate agrees with the recent discovery of the earliest potential crocodylian, from the Cenomanian (Mateus et al., 2018).

In agreement with Brochu (2003), Martin & Delfino (2010) and Brochu et al. (2012), all of the major crocodylian lineages (crocodyloids, including tomostomines, alligatoroids and gavialoids) appeared before the K/Pg boundary. In addition to the three extant lineages, the fossil record shows that

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**Figure 10.** Summarized and timescaled strict consensus tree from the unconstrained CW3 analysis. Original image created with the R package *strap* (Bell & Lloyd, 2014). Image modifications and skull outline drawings by the lead author.
Tethysuchia and Sebecosuchia both survived the K/Pg boundary, as also noted by Pol & Larsson (2011) and reflected in our tree topologies. The origin of Tomistominae is extended much further back in time by our analyses. Instead of appearing after the K/Pg boundary (e.g. Brochu, 2003; Salisbury et al., 2006), our CW3 trees consistently place the split of this major group from the remaining Crocodylidae in the Late Cretaceous around 81 Mya or earlier (Fig. 10). This also adds a long (27 million years) ghost range to the base of the tomistomine lineage. The early split of tomistomines from the remaining crocodyliform lineage might be due to the placement of Hylaeochampsidae, which, in turn, pulls back the origination date for Brevirostres as a whole. In addition, many previous studies have based their origination estimates on the appearance dates of the first fossils in a group [such as Brochu (2003) and Salisbury et al. (2006)], rather than using statistical time-calibration methods, including ghost lineages, for calculating the timing of lineage splits.

**Convergent evolution of longirostrine and the assembly of the long and narrow snout**

The longirostrine problem, and the probably inaccurate taxon clustering it creates in crocodyliform phylogenies, has been recognized for several decades (Clark, 1994; Jouve, 2009; Meunier & Larsson, 2016). There have been previous studies of the functional morphology and convergence of longirostrine crocodyliform snouts (e.g. Salas-Gismondi et al., 2016; Ballell et al., 2019). Furthermore, insights into the longirostrine condition have come from recent work on the embryological development of extant crocodylian skulls by Morris et al. (2019). These authors found that heterochrony is responsible for the convergent trends in crocodylian snout evolution and that the longirostrine shape can be achieved by several different ontogenetic trajectories during development. However, to date, no previous analysis has examined in detail the character-state changes that occurred during the parallel assembly of elongate snouts in neosuchians.

Here, we find that the occurrence of rampant homoplasy in snout length is also supported by the stratigraphic distribution of longirostrine taxa. One of the most striking examples of the impact of longirostrine characters on phylogenetic topology is illustrated by the placement of Thalattosuchia. This group has been placed almost everywhere in the crocodyliform tree, from nesting within Neosuchia (often in association with other longirostrine clades, such as members of 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). We observed similar patterns in our unweighted and Bayesian analyses, with Thalattosuchia clustering with other longirostrine clades (Fig. 4). However, Thalattosuchia is found to lie outside Neosuchia in all of our weighted analyses.

Our results are consistent with Brochu’s (2001) proposal that long-snouted forms evolved on at least three occasions within Neosuchia: in Gavialoidea, Tomistominae and Tethysuchia. Additionally, longirostry evolved independently in at least three taxa within the otherwise short-snouted Crocodylinae: Euthedon arambourgi Ginsburg & Buffetaut, 1978, Mecistops cataphractus Cuvier, 1825 and Crocodylus johnstoni (the latter was not examined first-hand and is, therefore, missing from our 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 above). Molecular studies reduce the number of independent origins of the longirostrine condition by at least one, with Gavialoidea and Tomistominae usually forming a clade (Piras et al., 2010; see below).

Character-state mapping on the strict consensus tree of the unconstrained CW3 analysis (Fig. 6) revealed that at least 24 characters are associated with the evolution of longirostrine clades (Fig. 11; see Table 4 for detailed character descriptions). Twelve of these characters appear to be linked to the evolution of longirostry in all three clades, as well as the three other independently occurring longirostrine species listed above. These features include skull and mandibular characters approximately equally. Preorbital ridges are lost at the base of all longirostrine clades and several others, 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 a median projection of the premaxilla extending into the maxilla in the form of a sharp process (character 123). Furthermore, the maxillary teeth all remain the same size (character 386). 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 play large roles. The splenial is usually involved extensively in the symphysis (characters 400 and 428), together with a relatively straight and long dentary (characters 401 and 402), leading to the characteristic ‘Y’-shaped mandibular symphysis in all longirostrine taxa (character 468).
All of these changes occur independently at the base of each longirostrine clade. Although such ‘sudden’ and apparently coordinated state transformations might be an artefact generated by taxon sampling and specimen incompleteness, it is conceivable that these results point to a genuine, relatively rapid shift in snout morphology during a short time-interval, rather than a slower assembly of the longirostrine snout across several nodes.

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 long-snouted lineages (i.e. although some posterior skull character-states evolve at the base of longirostrine clades, they do not typically display the repeated coherent homoplasy seen in the more anterior portions of the snout and mandible). Tethysuchia, in particular, possesses several supratemporal region characters associated with its longirostrine condition (195 and 200) that are absent in other ‘long-snouted’ clades, indicating 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-shaped 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). A complex skull roof surface is also found outside Neosuchia in Thalattosuchia, which contains many marine species (Wilberg, 2015b). In addition to the other skull roof changes, the placement of the postorbital is more anterior when compared to other neosuchians (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 gavialoids and tethysuchians. These changes are accompanied by bilateral tubera of the basioccipital (character 305), as well as a deep fork in the axial hypapophysis (character 479) in both Tethysuchia and Gavialoidea. The only anterior skull character that is uniquely shared by Gavialoidea and several tethysuchian taxa is the height of the alveolar wall of the fourth dentary tooth, which is level with that of the adjacent dentary alveoli (character 419). In addition, several posterior skull characters are unique to Gavialinae, such as an abrupt expansion of the orbits (character 88), a prominent notch at the ventral margin of the orbit (character 256) and a strongly arched posteroventral margin of the angular (character 442). However, the ‘telescoping’ and wide separation of the orbits has previously been revealed to be a potentially homoplastic feature in Gavialoidea (Salas-Gismondi et al., 2016).

Figure 11. Characters associated with the evolution of the longirostrine condition mapped onto a simplified version of our neosuchian tree, based on analysis CW3. Note that character numbers do not denote synapomorphies for the clades; rather, these refer to characters that are shared by longirostrine clades. See Table 3 for detailed character state descriptions and positions. Outlines drawn by the lead author.
Table 4. Characters states revealed by character mapping to be common to one or more longirostrine clades with details of character state, character description and exact occurrence in the phylogenetic tree. Based on the strict consensus trees of the unconstrained CW3 analysis (Fig. 6)

<table>
<thead>
<tr>
<th>Character number</th>
<th>Character state</th>
<th>Character description</th>
<th>Details of position</th>
</tr>
</thead>
<tbody>
<tr>
<td>87</td>
<td>0</td>
<td>Preorbital ridges absent</td>
<td>Ancestral for all longirostrine clades, plus Alligatoroidea and Diplomynodontinae</td>
</tr>
<tr>
<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 <em>Euthedodon</em> and <em>Mecistops</em></td>
</tr>
<tr>
<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>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>131</td>
<td>1</td>
<td>Alveolar walls of maxillary level with ventral surface</td>
<td>In all Gavialoidea and Tomistominae, plus several Tethysuchia and goniopholidids</td>
</tr>
<tr>
<td>149</td>
<td>0</td>
<td>Nasal not in contact with external nares</td>
<td>In all longirostrine clades and Goniopholididae</td>
</tr>
<tr>
<td>386</td>
<td>0</td>
<td>All maxillary teeth of similar size</td>
<td>In all longirostrine clades and <em>Euthedodon</em></td>
</tr>
<tr>
<td>400</td>
<td>2</td>
<td>Extensions of symphysis beyond 8th alveolus</td>
<td>In all longirostrine clades</td>
</tr>
<tr>
<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>402</td>
<td>0</td>
<td>Dorsal edge of dentary straight or slightly concave</td>
<td>In all longirostrine clades</td>
</tr>
<tr>
<td>428</td>
<td>2</td>
<td>Splenial involved extensively in symphysis</td>
<td>In all longirostrine clades and Goniopholididae</td>
</tr>
<tr>
<td>468</td>
<td>1</td>
<td>Mandible broadly ‘Y’-shaped</td>
<td>In all longirostrine clades and Goniopholididae</td>
</tr>
<tr>
<td>118</td>
<td>0</td>
<td>No ventral opening on ventral edge of premaxillo-maxillary contact</td>
<td>In all Tethysuchia and Alligatorida</td>
</tr>
<tr>
<td>195</td>
<td>1</td>
<td>Frontoparietal suture on interfenestral bar zigzag in shape</td>
<td>In all Tethysuchia and <em>Tomistoma</em></td>
</tr>
<tr>
<td>200</td>
<td>1</td>
<td>Well-developed anterolateral process on postorbital</td>
<td>In all Tethysuchia</td>
</tr>
<tr>
<td>208</td>
<td>0</td>
<td>‘Complex’ supratemporal roof dorsal surface</td>
<td>In all Tethysuchia + Thalattosuchia</td>
</tr>
<tr>
<td>254</td>
<td>0</td>
<td>Postorbital bar placed anteriorly on jugal</td>
<td>In all Tethysuchia</td>
</tr>
<tr>
<td>89</td>
<td>0</td>
<td>Skull table surface slopes ventrally at maturity</td>
<td>In derived Gavialoidea and <em>Pholidosaurus</em> and <em>Dyrosaurus</em></td>
</tr>
<tr>
<td>224</td>
<td>0</td>
<td>Supratemporal fenestrae large, covering more than 50% of skull roof</td>
<td>In all Tethysuchia and several gavialoids</td>
</tr>
<tr>
<td>305</td>
<td>1</td>
<td>Basioccipital with large bilateral pendulous tubera</td>
<td>In all Tethysuchia and Gavialoidea</td>
</tr>
<tr>
<td>419</td>
<td>0</td>
<td>4\textsuperscript{th} dentary alveolus wall on level with adjacent dentary alveoli</td>
<td>In all Gavialoidea and <em>Sarcosuchus</em> and <em>Rhabdognathus</em></td>
</tr>
<tr>
<td>479</td>
<td>1</td>
<td>Hypapophysis of axis with deep fork</td>
<td>In all scored Tethysuchia and Gavialoidea</td>
</tr>
<tr>
<td>230</td>
<td>1</td>
<td>Groove of external ear valve musculature flaring anteriorly</td>
<td>In all Gavialoidea and Tomistominae</td>
</tr>
<tr>
<td>371</td>
<td>1</td>
<td>Anterior median process of palatines into maxilla in form of thin wedge</td>
<td>In all Gavialoidea and Tomistominae</td>
</tr>
<tr>
<td>384</td>
<td>1</td>
<td>Flat depressions the size of small alveoli between maxillary and premaxillary alveoli</td>
<td>Only in <em>Gavialis</em>, Mecistops, <em>Rhabdognathus</em> and <em>Tomistoma</em>, Ancestral state retained outside Eusuchia and in <em>Gavialis</em>, <em>Eogavialis</em> and <em>Tomistoma</em></td>
</tr>
<tr>
<td>397</td>
<td>1</td>
<td>Thin and long teeth which are at least three times longer than wide</td>
<td>Ancestral state retained outside Eusuchia and in <em>Gavialis</em>, <em>Eogavialis</em> and <em>Tomistoma</em></td>
</tr>
</tbody>
</table>

Gavialoids and tomistomines share two posterior skull characters that are potentially related to the formation of a long snout. The groove for the external ear valve musculature is flared anteriorly in both clades (character 230). Furthermore, the anterior process of the palatines into the maxilla takes the form of a thin wedge (character 371). There are two characters, 384 and 397, with shared character-states between Gavialis and Tomistoma, but that are absent in their direct ancestors (Table 4). This provides some evidence for their long-snoutedness as a homoplastic condition, in direct contrast to hypotheses derived from molecular evidence alone (Piras et al., 2010).

Molecular studies have consistently grouped Gavialis and Tomistoma as sister-taxa, postulating a single origin of longirostrity at least for extant forms (Roos et al., 2007; Piras et al., 2010; Oaks 2011). Recently, new fossil taxa have been described that exhibit both gavialine and tomistomine features, providing support for the molecular hypotheses (Iijima & Kobayashi, 2019). However, studies using these evolutionary hypotheses potentially for two reasons: (1) morphological data, in general, is potentially biased towards phylogenetic signals that override the characters connecting Gavialis and Tomistoma (Iijima & Kobayashi, 2019) and/or (2) the topology favoured by molecular or total evidence analyses is incorrect, because it fails to sufficiently sample fossil taxa near the bases of the tomistomine and gavial lineages that reinforce separate origins (see below).

The most important aspect of the longirostrine problem in both molecular and morphological analyses is taxon sampling: most analyses combining molecular and morphological evidence (e.g. Gold et al., 2014; Iijima & Kobayashi, 2019) only investigated Crocodylia. However, if Gavialis and Tomistoma are constrained to be sister-taxa in accordance with molecular phylogenies, total evidence analyses including longirostrine groups outside Crocodylia (such as Tethysuchia) cluster all longirostrine taxa together (Groh et al., unpublished material), regardless of their stratigraphic position. Future investigations of the ‘Tomistoma–Gavialis problem’ should take these factors into account.

Overall, based on the results in this study, the evolution of the longirostrine condition seems to have been remarkably constrained, at least with regards to the anterior portion of the skull, and occurred in a broadly similar fashion in each of the different clades. Modifications to the premaxilla, maxilla, dentary and splenial were of primary importance in the convergent construction of the long-snouted condition. In contrast, the median parts of the skull and mandible between the anterior and posterior parts remained mostly unmodified, although changes involving the orbits can be related to different feeding mechanisms (e.g. in some gavialoid species: Salas-Gismondi et al., 2016). 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. Furthermore, Tethysuchia and Gavialoidea exhibit more similarities in their snout assembly than Gavialoidea and Tomistominae (Table 4). Once again, this emphasizes the dissimilarities between the latter two groups. These results partially corroborate the findings of Morris et al. (2019), who observed that Gavialis and Tomistoma are the only exceptions to a pattern of otherwise conserved regions of morphospace during early and median skeletal development stages of extant crocodylian species. In addition, these authors found that a number of different developmental pathways could lead to similar snout morphologies, emphasizing the depth of convergence in crocodylian skull evolution, which is consistent with our conclusions here.

In order to test our results further, the genetic patterns underpinning longirostrine snout development should be investigated in both Gavialis and Tomistoma, which would provide new data that could potentially resolve the ongoing Gavialis–Tomistoma debate (Gatesy et al., 2003; Piras et al., 2010; Gold et al., 2014).

CONCLUSIONS

In this case study we demonstrate that the combined application of continuous data and EIW can result in improved stratigraphic fit of phylogenetic trees, in spite of the presence of a strong homoplastic signal (at least compared to other vertebrate groups). Even though several studies confirm their utility (e.g. Parins-Fukuchi, 2017; Jones & Butler, 2018), the influence of continuous characters on large-scale phylogenetic studies is still largely unexplored, and future work should concentrate on determining the effects of continuous characters and EIW on 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 test them rigorously before including them in phylogenetic analyses.

Our new neosuchian phylogeny is generally consistent with those derived from previous analyses, confirming the placement of Tethysuchia at the base of Neosuchia. However, it deviates from established phylogenetic hypotheses in the identification of alligatorine paraphyly, the lack of resolution within
Croodylinae, and in the uncertain positions of Diplocynodontinae and Hylaeochampsiidae. In addition, the origin of Tomistominae is estimated to have occurred earlier than in most previous studies. Future datasets should aim to include additional members of clades that were either unrepresented or represented by only a single taxon in this phylogeny, such as Atoposauridae.

Character mapping reveals that the longirostrine condition was assembled in similar ways across the neosuchian tree by transformation of the anterior portions of the snout and mandible. However, posterior skull transformations are often unique to individual longirostrine clades and might represent adaptations to their different habitats and lifestyles. Future work should be aimed at investigating the genetic mechanisms that underlie long snout evolution and the particular ways in which evolution of longirostry might have occurred in different environments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site.

Document S1. Full osteological character list with illustrations.

Document S2. List of rejected osteological characters from previous publications and the reasons for rejection.

Document S3. Strict consensus trees presented for all analyses.

Document S4. All .tnt files used for analysis and the tree file with the corresponding ages of the examined species used in strap.

Appendix

List of Synapomorphies

Synapomorphies are given for discrete characters and were obtained by using the ‘List Synapomorphies’ function in TNT v.1.5. Character numbers refer to the original character list of 569 characters [see Supporting Information (S1)]. Synapomorphies are listed for the tree in Figure 5, using the unconstrained analysis of CW3. For clade labels and phylogenetic definitions, see Figure 5. Character consistency indices (obtained with CharStats.run) are given after each character.

Notosuchia: Premaxillae loosely sutured anterior to nares (C92.1, CI = 1.00); anterior rostral contour concealed relative to external nares (C96.0, CI = 0.3);
perinarial fossa on premaxillae present (C102.1, CI = 1.0); no constriction of snout at maxilla-premaxilla contact (C113.0, CI = 0.1); two parallel ridges creating recess on lateral wall of premaxillary notch (C116.1, CI = 0.5); large and aligned neurovascular foramina on lateral surface of maxillae (C13.1, CI = 0.5); antorbital fenestra (C159.1, CI = 0.5); descending ornamented process at posterolateral edge of squamosal (C235.1, CI = 1.0); lateral surface of jugal exposed lateral to maxilla in ventral view (C258.0, CI = 0.3); major axis of quadrate ventrally directed (C273.1, CI = 1.0); subquadrangular morphology of distal end of quadrate in cross section (C280.1, 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 = 0.1); paroccipital process curves downwards strongly in occipital view (C290.3, CI = 0.2); unsculpted region below dentary tooththrow (C403.1, CI = 0.5); supraacetabular crest on ilium (C526.0, CI = 0.3); no antorlarial process on dorsal parasagittal osteoderms (C551.0, CI = 0.2); centro of vertebrae cylindrical in shape (C567.0, CI = 0.5).

_Dyrosauridae:_ Maxillae project posterior to the level of postorbital bar (C141.1, CI = 0.3); postorbital bar slightly anterodorsally inclined (20° or less) (C211.1, CI = 0.3).

_Polidosauridae:_ Ventral edge of premaxilla is deeper than ventral edge of maxilla in lateral view (C112.1, CI = 0.3); zigzag shaped frontoparietal suture on interfenestral bar (C195.1, CI = 0.2); well-developed anterolateral process of the postorbital (C200.1, CI = 0.5).

_Goniopholididae excl. Sussisuchus:_ Depression on posteroventral surface of maxilla (C134.1, CI = 0.5).

‘Deeply nested’ _Goniopholididae_ (Goniopholis, Amphicotylus, Anteophthalmosuchus): Crest dorsal to orbit on prefrontal-lacrimal (C168.1, CI = 0.1); quadratejugal forms posterior angle of infratemporal fenestra (C265.0, CI = 1.0); thin and long teeth, which are at least three times longer than wide (C397.1, CI = 0.2).

_Hylaeochampsidae:_ Posterior process on dorsal surface of maxilla (C144.1, CI = 0.07); no contact between lacrimal and nasal at medial edge (C160.0, CI = 0.1); lateral extension of lacrimal almost reaching the medial border of the orbit edge (C163.1, CI = 0.1); jugal does not exceed the anterior margin of orbit (C253.0, CI = 0.1); prominent and dorsally directed boss on the posterior surface of paroccipital process (C298.0, CI = 0.5); paroccipital process lateral to cranioquadrate opening barely extended posteriorly in dorsal view (C299.0, CI = 0.5).

_Borelosuchus:_ Anterior median palatine process into maxilla in form of thin wedge (C371.1, CI = 0.1); dientary alveoli 3 and 4 confluent (C420.0, CI = 0.3); splenial reaches fifth dientary tooth (C427.0, CI = 0.1); lingual foramen on surangular-articular suture (C443.1, CI = 0.1).

_Crocdyliia incl. Hylaeochampsidae:_ Frontoparietal suture on skull table entirely (C193.2, CI = 0.1); parietopostorbital suture present within supratemporal fossa (C245.1, CI = 1.0); otic aperture closed posteriorly and of triangular shape, with dorsally directed apex (C323.1, CI = 0.5); palatines do not participate in anterior margin of choanae (C355.0, CI = 0.2); angular extends beyond posterior margin of orbits in lateral view (C438.1, CI = 0.2); hypapophyseal keel present until eleventh cervical vertebra behind atlas (C483.1, CI = 0.3); all cervical vertebrae procoelous (C490.2, CI = 0.7); all thoracic vertebrae procoelous (C492.1, CI = 1.0); postacetabular process on ilium directed posteriorly (C530.1, CI = 1.0); osteoderm edges sutured to one another (C544.1, CI = 0.5).

_Gavialoidea incl. Maroccosuchus:_ Frontoparietal suture entirely on skull table (C193.2, CI = 0.1); posterior walls of supratemporal fenestrae barely visible in dorsal view (C225.0, CI = 0.6); doral and ventral rims of groove for external ear valve musculature flaring anteriorly (C230.1, CI = 0.5); parietopostorbital suture present on doral skull roof (C244.1, CI = 0.09); no midline crest on basioccipital plate below occipital condyle (C304.0, CI = 0.07); basioccipital with large pendulous tubera (C305.1, CI = 0.1); dentary symphysis extends beyond eighth dentary alveolus (C400.2, CI = 0.1); lateral edges of dentary oriented longitudinally, with convex anterolateral corner and extensive transversely oriented anterior edge (C401.2, CI = 0.3); distal rami of mandible strongly curved medially at mid-length, giving the mandible a broad Y-shape (C468.1, CI = 0.3).

_Gavialinae:_ Ventral opening on ventral edge of premaxillo-maxillary contact (C118.1, CI = 0.06); transversely flattened postorbital bar (C210.0, CI = 0.06); prominent notch in ventral margin of orbits (C256.1, CI = 1.0); thin and long teeth, which are at least three times longer than wide (C397.1, CI = 0.2).

_Brevirostres + Diplocynodontinae:_ Humeral shaft sigmoidal, with a pronounced posterior curvature of shaft on proximal area of humerus (C515.1, CI = 0.5).

_Brevirostres (Crocdyloidea + Alligatoroidea):_ Dentary symphysis extends to sixth through eighth alveolus (C400.1, CI = 0.1); dorsal midline osteoderms rectangular (C548.1, CI = 0.7); more than one keel on presacral dorsal osteoderms (C556.1, CI = 1.0).

_Crocdyloidea:_ Squamosal and quadrate extend dorsally along posterior margin of external auditory
meatus (C338.0, CI = 0.2); sulcus on anterior braincase wall lateral to basisphenoid rostrum (C315.1, CI = 0.5); interalveolar space between second and third dentary alveoli greater than that between first and second dentary alveoli (C417.1, CI = 0.1); anterior perforation on mandibular ramus of cranial nerve V on splenial absent (C431.1, CI = 0.1); one side of dorsal anterior forked process of surangular into dentary shorter than the other (C445.0, CI = 0.3); anterior margins of turbeculum 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 = 0.3); follicle gland pores on ventral osteoderms absent (C560.1, CI = 1.0).

Crocodyliidae: No posterior wall on median Eustachian foramen on basisphenoid (C318.1, CI = 0.3); lateral edges of palatines in anterior half of interfenestral bar parallel to subparallel (C366.0, CI = 0.07).

Tomistominae: Premaxillary ventral projections with sharp tips (C123.1, CI = 0.2); dorsal and ventral rims of groove for external ear valve musculature flaring anteriorly (C230.1, CI = 0.5); anterior suborbital fenestra extension posterior to anterior two-thirds of alveoli (C372.0, CI = 0.08); all dentary alveoli immediately posterior to fourth of similar size (C424.3, CI = 0.2); extensive involvement of splenial in mandibular symphysis (C428.2, CI = 0.2).

Crocodylinae: No extension of quadratojugal to superior angle of infratemporal fenestra (C267.0, CI = 0.2); otoccipitals participate in basioccipital tubera (C301.1, CI = 0.08).

Diplacynodontinae incl. Leidyosuchus: Frontal prevents contact between postorbital and parietal on skull table (C193.0, CI = 0.1); spina quadratojugalis positioned high between posterior and superior angles of infratemporal fenestra (C270.1, CI = 0.3); dentary alveoli 3 and 4 confluent (C420.0, CI = 0.3).

Diplacynodontinae excl. Leidyosuchus: Preorbital ridges reduced (C87.1, CI = 0.1); parietal and squamosal approach each other on posterior wall of supratemporal fenestra without making contact (C218.1, CI = 0.3); temporal canal hidden in dorsal view and overlapped by rim of supratemporal fossa (C226.1, CI = 0.08); lingual foramen for articular artery and alveolar nerve on surangular–articular suture (C443.1, CI = 0.2); posterior tip of iliac blade deep, less than twice as long as it is high (C523.1, CI = 1.0).

Alligatoridae: Premaxillae form less than ventral half of internarial bar (C101.1, CI = 0.2); no constriction of snout at premaxillo–maxillary contact (C113.0, CI = 0.1); no opening on ventral edge of premaxillo–maxillary contact (C118.0, CI = 0.06); maxillary alveoli heterodont (C390.1, CI = 0.1).

Caimaninae: Dorsal contour of rostrum concave in lateral view (C86.2, CI = 0.1); external nares confluent (C97.1, CI = 0.2); contact of lacrimals with nasal at medial edge (C160.1, CI = 0.1); no transverse ridge of frontals (C191.0, CI = 0.2); rim of supertemporal fenestrae overhangs fenestrae (C222.1, CI = 0.3); quadratojugal does not extend to superior angle of infratemporal fenestra (C267.0, CI = 0.2); dorsal exposure of supraoccipital (C286.1, CI = 0.07); dorsal margin of supraoccipital same height as dorsal margin of squamosal (C288.1, CI = 0.1); occipitals participate in basioccipital tubera (C301.1, CI = 0.08); ectopterygoid–pterygoid flexure remains throughout ontogeny (C332.1, CI = 1.0); last premaxillary tooth anterior to first maxillary tooth (C382.0, CI = 0.1); no anterior perforation on splenial for cranial nerve V (C431.1, CI = 0.1); 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 = 0.1); 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 = 0.1); 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 = 0.3); four contiguous dorsal osteoderms per row at maturity (C549.0, CI = 0.5); paired ossifications suturing osteoderms of ventral armour together (C562.1, CI = 0.3).

LIST OF EXAMINED SPECIMENS

*: extinct species

Alligator meffordi*: 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 092673
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

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Amphicotylus lucasii: AMNH FR 5782 (as Goniopholis lucasii)
Anteophthalmosuchus hooleyi: NHMUK PV R3876
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 OR37712
Borealosuchus formidabilis: YPM VP 016512 (as Leidyosuchus formidabilis)
Borealosuchus wilsoni: AMNH FR 7637 (as Leidyosuchus wilsoni), USNM 12990
Boverisuchus vorax: AMNH FR 29993 (as Pristichampsa vorax), USNM 12957 (as Pristichampsus rollinatii)
Brachychampsa montana: AMNH FR 5032, USNM 7068
Brachyuranochampsa zangerli: AMNH FR 6048, AMNH FR 16609, YPM VP 00246
Brochuchus pigotti: NHMUK PV R7729
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 R14104 (cast)
Congosaurus compressus: MNHN TGE 4034, MNHN TGE 4036, MNHN TGE 4198
Crocodilaemus robustus: USNM 15828, USNM 537820
Crocodylus acutus: NHMUK 1975.997
Crocodylus affinis: USNM 18390, YPM VP 001345
Crocodylus clavis: AMNH FR 1212, USNM 12719
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 R3327
Crocodylus moreletii: NHMUK 1861.4.1.4
Crocodylus niloticus: NHMUK 1861.4.1.5
Crocodylus porosus: NHMUK 1921.4.1.17, NHMUK 1921.4.1.168, NHMUK 1920.1.1626
Crocodylus siamensis: NHMUK 1921.4.1.17, NHMUK 1921.4.1.168, NHMUK 1920.1.1626
Crocodylus silvalensis: AMNH FR 1915, NHMUK PV OR39705
Diplocynodon hantoniensis: AMNH FR 27632 (cast), NHMUK PV OR30393
Diplocynodon remensis: IRSNB R289, MNHN F BR 4020, MNHN MB 051, MNHN BR 2622, MNHN BR 10085, MNHN BR 13976, 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)
Dollosuchoides densmorei: IRSNB 1748
Dyrosaurus phosphaticus: NHMUK 1901–11, MNHN APH 27, MNHN APH 25, MNHN APH 23, MNHN unnumbered skull
Eosuchus cherifiensis: MNHN MRS 340, MNHN SAM 129
Eosuchus felixi: MNHN INA 21 (may be Fortignathus), MNHN INA 25, MNHN INA 3
Eoalligator chunyi: IVPP V2716
Eoalligator hysudricus: IVPP V4058
Eocaiman cavernensis: AMNH FR 3158
Eogavialis africanaum: 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
Euthecodon arambourgi: MNHN ZEL 001
Eutretauranosuchus delfsi: AMNH FR 570
Gavialis gangeticus: NHMUK 1935.6.4.1, NHMUK 2005.1601
Gavialis hysudricus: NHMUK PV OR39808, NHMUK PV OR39805
Gavialis lewisi: YPM VP 003226
Gavialis silvalensis: NHMUK PV OR39805
Gavialis silvalensis: NHMUK PV OR39805
Gavialosuchus eggenburgensis: NHMUK PV R797 (cast)
Goniopholis felix: YPM VP 000517
Goniopholis simus: NHMUK PV OR41098
Gracilinesastes leedsi: NHMUK PV R2042, NHMUK PV R3014, NHMUK PV R3015, NHMUK PV R4762 (as Metriorhynchus laeve)
Hylaeochampsa vectiana: NHMUK PV R177
Hyposaurus natator oweni: YPM VP 000985
Kentisuchus spenceri: NHMUK PV OR37717
Leidyosuchus canadiensis: NHMUK PV OR39705
Leidyosuchus gilmorei: AMNH FR 5352
Listrognathosuchus multidentatis*: AMNH FR 5179
(as Leidyosuchus multidentatis)
Maroccosuchus zennaroi*: IRSNB R408
Mecistops cataphrac tus: 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 OR48301, NHMUK PV OR48217
Navajosuchus novomexicanus*: AMNH FR 5186
Notosuchus terrestris*: NHMUK PV R14105
Osteolaemus tetraspis: LDUCZ X122, NHMUK 1862.6.30.5, NHMUK 1983.1130, NHMUK 1862.6.30.6
Paleosuchus trigonatus: NHMUK 1868.10.8.1
Pelagosaurus typus*: NHMUK PV R14437, NHMUK PV R19375, NHMUK PV R32598, NHMUK PV R32599, NHMUK PV R32600, NHMUK PV R32601, NHMUK PV R36841
Pholidosaurus purbeckensis*: NHMUK PV R3414, NHMUK PV OR28432
Piscogavialis jugaliperforatus*: SMNK 1282 PAL
Planocrania datangensis*: IVPP V 5016
Planocrania hengdongensis*: IVPP V 6074
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 OR5265, NHMUK PV OR39802
Sarcosuchus imperator*: MNHN unnumbered complete skeleton in main exhibition
Sebecus icæorhinus*: AMNH FR 3159, AMNH FR 3160, AMNH FR 3162
Shamosuchus djadochtaensis*: AMNH FR 6412
Steneosaurus bollensis*: SMNS complete unnumbered skeleton, SMNS 15391
Sunosuchus junggarensis*: IVPP V10606
Sunosuchus miaoi*: IVPP V500
Susisuchus anatoceps*: SMNK 3804 PAL
Terminonaris browni*: AMNH FR 5851 (as Teleorhinus browni)
Thecachamps a americana*: AMNH FR 5662, AMNH FR 5663 (as Gavialosuchus americanus), USNM 24939 (as Tomistoma americana)
Thecachamps a antiqua*: USNM 24938 (as Gavialosuchus americanus)
Theriosuchus pusillus*: NHMUK PV OR48330
Thoracosaurus macrorhynchus*: MNHN 1902–22, NHMUK PV R2798, NHMUK PV OR28296a, NHMUK PV OR28296b
Thoracosaurus neocesariensis*: NHMUK PV OR 41842 (cast)
Tomistoma cai rense*: SMNS 10575, SMNS 50742, SMNS 50739, SMNS 50379a, SMNS 50734
Tomistoma dowsoni*: NHMUK PV R4769
Tomistoma petrolica*: IVPP V2303, IVPP V5015, IVPP unnumbered full skull
Tomistoma schlegeli: LDUCZ X1227, NHMUK 1848.10.31.19, NHMUK 1860.11.6.8, NHMUK no number, in wooden box
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 R2026

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