

Origin, Diversity and Evolution of the Most Common Croodylians of Europe in the Paleogene Greenhouse Context

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ORIGIN, DIVERSITY AND EVOLUTION OF THE MOST COMMON CROCODYLIANS OF EUROPE IN THE PALEOGENE GREENHOUSE CONTEXT

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“the alligator-skin drums are resounding”

- From Shih-King, translated from the traditional Chinese by Fauvel, 1879

“I refer to the Diplocynodon species as the “rats” of the tertiary crocodile world.”

- Rauhe M., 1995

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EXTENDED ABSTRACT

Crocodylia is an iconic reptile vertebrate group whose extant representatives inhabit most of the continental land masses. Modern Europe is a notable exception, as no crocodyliform populations are found in this region of the world, which is greatly contrasting with the past biogeographical history of the group. The early Cenozoic, specifically, shows an exceptionally diverse crocodyliform fauna mainly dominated by alligatoroids. Morphological disparity, complex biogeography or even stratigraphically young age of the earliest-branching forms have been difficult to reconcile with consistently inferred phylogenetic relationships to alligatorids, an otherwise freshwater and small-bodied group in the Paleogene. The European putative alligatoroid genus *Diplocynodon* is recognised as the most common and best sampled crocodyliform in the Paleogene of Europe, as demonstrated by the extensive fossil record spread across multiple occurrences throughout the Cenozoic. This record hints at an exceptional survivorship of the genus from the late Paleocene to the middle Miocene, that perplexes the comprehensive investigation of the taxon systematics and taxonomy, indication of an overdue revision.

The thesis presents an expanded phylogeny with increased spatiotemporally coherence that reinterprets *Diplocynodon* spp. (recovered closely related to the North American *Borealosuchus*) as well as the North American *Deinosuchus* spp. and *Leidyosuchus canadensis* as stem-group crocodylians. The novel topology elucidates the evolution of osmoregulation in Crocodylia and its close relatives by inferring plesiomorphic saltwater tolerance for *Deinosuchus* and the crown-group, and secondary loss already in stem-group alligatorids. Divergence of Alligatoroidea coincided with extreme mid-Cretaceous sea level highs and the distribution of *Deinosuchus* across the American Western Interior Seaway can be best explained by marine dispersal. Phylogenetic body-length analysis using a head-width proxy reveals phyletic dwarfism early in alligatoroid evolution and a reasonable total length estimate for the most complete specimen of *Deinosuchus riograndensis*. Gigantism in crocodyliforms is suggested as being correlated with high-productive extensive aquatic ecosystems in the present and in the past.

The second and third chapters tackle the complex ingroup taxonomy of *Diplocynodon*. The diagnoses of currently accepted *Diplocynodon* species commonly include shared and/or irreproducible characters, hampering specific delimitations. Based on the review of all currently known species, the first taxonomic revision of the group since its inclusion in modern phylogenetic works is presented. An identification key to assist researchers with the identification of the valid species is additionally provided. Furthermore, the present work quantitatively reviews the state of the entire fossil record of *Diplocynodon* (based on two openly available databases) and discusses the waste-basket status of the taxon with respect to better taxonomical practices. Within *Diplocynodon*, the Eocene species *Diplocynodon darwini* Ludwig, 1877 has the largest sample in the Paleogene period, consisting of tens of complete well-preserved specimens, but yet critically lacks a detailed osteological description. The taxon is here redescribed for the first time based on type specimens collected 150 years ago and abundant excellently preserved material from the Messel and Geiseltal Konservat-Lagerstätten. Insights into the intraspecific variation in the taxon are provided in a detailed morphological description on the skeletal elements, including ontogenetic variation in temporally restricted populations. The complex ingroup taxonomy of *Diplocynodon* is furthermore explored and discussed through a review of previously published and newly retrieved phylogenies.

ERWEITERTE ZUSAMMENFASSUNG (DEUTSCH)

Kontinentaleuropa stellt heute eine Ausnahme dar, da es hier keine Krokodilpopulationen mehr gibt, was in starkem Kontrast zur biogeografischen Geschichte der Gruppe steht. Vor allem das frühe Känozoikum weist eine außergewöhnlich vielfältige Krokodilfauna auf, die hauptsächlich von Alligatoroiden dominiert wird. Morphologische Unterschiede, eine komplexe Biogeographie oder sogar ein stratigraphisch junges Alter der frühesten Formen lassen sich nur schwer mit den konsequent abgeleiteten phylogenetischen Verwandtschaftsverhältnissen der Alligatoroiden vereinbaren, die im Paläogen eine kleinwüchsige Süßwassergruppe waren. Die europäische mutmaßliche Alligatoroid Gattung *Diplocynodon* gilt als die häufigste und am besten untersuchte Gattung der Krokodyliforme im Paläogen Europas, welche durch umfangreiche Fossilienfunde an mehreren Fundorten im gesamten Känozoikum belegt ist. Diese Funde deuten auf ein außergewöhnlich langes Überleben der Gattung vom späten Paläozän bis zum mittleren Miozän hin, was die umfassende Untersuchung der Systematik und Taxonomie der Gattung vor ein Rätsel stellt, und ein deutlicher Hinweis auf eine längst überfällige Überarbeitung der Gattung ist.

Die Dissertation präsentiert eine erweiterte Phylogenie mit erhöhter räumlich-zeitlicher Kohärenz, die *Diplocynodon* spp. (eng verwandt mit der nordamerikanischen Gattung *Borealosuchus*) sowie die nordamerikanischen *Deinosuchus* spp. und *Leidyosuchus canadensis* als Stammgruppe der Crocodylia neu interpretiert. Die neue Topologie gibt Aufschluss über die Evolution der Osmoregulation bei Crocodylia und ihren nahen Verwandten, indem sie auf eine plesiomorphe Salzwassertoleranz bei *Deinosuchus* und der Kronengruppe sowie auf einen sekundären Verlust bereits bei den Stammgruppenvertretern der Alligatoriden schließen lässt. Die Divergenz der Alligatoroidea fiel mit dem extremen Hochstand des Meeresspiegels in der mittleren Kreidezeit zusammen, und die Verbreitung von *Deinosuchus* über das westliche Innere Amerikas lässt sich am besten über eine marine Ausbreitung erklären. Die phylogenetische Analyse der Körperlänge unter Verwendung eines Proxys für die Kopfbreite zeigt phyletischen Zwergwuchs zu Beginn der Alligatoroid-Evolution und bietet außerdem eine vernünftige Schätzung der Gesamtlänge für das vollständigste Exemplar von *Deinosuchus riograndensis*. Es wird angenommen, dass Gigantismus bei Krokodyliformes mit

hochproduktiven, extensiven aquatischen Ökosystemen in der Gegenwart und in der Vergangenheit zusammenhängt.

Das zweite und dritte Kapitel befassen sich mit der komplexen inner-Gruppen Taxonomie von *Diplocynodon*. Die Diagnosen der derzeit anerkannten *Diplocynodon*-Arten enthalten häufig gemeinsame und/oder nicht reproduzierbare Merkmale, die eine spezifische Abgrenzung erschweren. Auf der Grundlage der Überprüfung der derzeit bekannten Arten wird die erste taxonomische Revision der Gattung seit ihrer Aufnahme in moderne phylogenetische Arbeiten vorgelegt. Zusätzlich wird ein Bestimmungsschlüssel zur Verfügung gestellt, der Forscher bei der Identifizierung der gültigen Arten unterstützt. Darüber hinaus gibt die vorliegende Arbeit einen quantitativen Überblick über den Stand des gesamten Fossilnachweises von *Diplocynodon* (auf der Grundlage von zwei frei zugänglichen Datenbanken) und diskutiert den "Waste-basket"-Status des Taxons im Hinblick auf eine bessere taxonomische Praxis. Innerhalb von *Diplocynodon* hat die eozäne Art *Diplocynodon darwini* Ludwig, 1877 die größte Stichprobe im Paläogen, die aus Dutzenden von vollständigen, gut erhaltenen Exemplaren besteht. Trotzdem steht eine detaillierte osteologische Beschreibung der Art noch aus. Das Taxon wird hier erstmals anhand von Typusexemplaren, die vor 150 Jahren gesammelt wurden, und einer Fülle von hervorragend erhaltenem Material aus den Konservat-Lagerstätten Messel und Geiseltal neu beschrieben. Es werden Einblicke in die intraspezifische Variation des Taxons, einschließlich der ontogenetischen Variation in zeitlich begrenzten Populationen, gegeben. Die komplexe inner-Gruppen Taxonomie von *Diplocynodon* wird durch einen Überblick über bereits veröffentlichte und neu gefundene Phylogenien weiter erforscht und diskutiert.

ABSTRACT ESTESO (ITALIANO)

Le popolazioni di coccodrilli esistenti abitano quasi esclusivamente le regioni tropicali, distribuite sulla maggior parte delle terre emerse continentali. L'Europa continentale moderna rappresenta tuttavia una notevole eccezione, poiché non si trovano crocodiliformi in questa regione del mondo, in grande contrasto con la storia biogeografica passata del gruppo. Il Cenozoico iniziale, in particolare, mostra una fauna di crocodiliformi eccezionalmente diversificata, dominata principalmente da alligatoroidi. La disparità morfologica, la complessa biogeografia o anche la giovane età stratigrafica delle forme più primitive sono state difficili da conciliare con le relazioni filogenetiche dedotte con gli alligatoroidi, un gruppo d'acqua dolce e di piccole dimensioni nel Paleogene. Il genere europeo di possibili alligatoroidi *Diplocynodon* è riconosciuto come il più comune e meglio campionato crocodiliforme nel Paleogene europeo, come dimostrato dall'ampio record fossile distribuito in diverse località del Cenozoico. Il record suggerisce un'eccezionale sopravvivenza del genere dal tardo Paleocene al Miocene medio, complicando l'indagine completa della sistematica e della tassonomia del genere, e indicando la necessità di una revisione completa del genere.

La tesi presenta una filogenesi ampliata con una maggiore coerenza spazio-temporale che reinterpreta *Diplocynodon* spp. (qui strettamente imparentato con *Borealosuchus* del Nordamerica), nonché i nordamericani *Deinosuchus* spp. e *Leidyosuchus canadensis* come stem-group Crocodylia. La nuova topologia chiarisce l'evoluzione dell'osmoregolazione in Crocodylia e nei suoi parenti stretti, deducendo una tolleranza plesiomorfa all'acqua salata per *Deinosuchus* e il crown-group e una perdita secondaria già negli alligatoroidi basali. La divergenza degli Alligatoroidea ha coinciso con i massimi livelli marini della metà del Cretaceo e la distribuzione di *Deinosuchus* attraverso la via marittima interna occidentale americana può essere meglio spiegata dalla dispersione marina. L'analisi filogenetica della taglia corporea utilizzando un proxy della larghezza del cranio rivela un nanismo basale nelle prime fasi dell'evoluzione degli alligatoroidi e una stima ragionevole della taglia totale per l'esemplare più completo di *Deinosuchus riograndensis*. Si suggerisce che il gigantismo nei crocodiliformi sia correlato a ecosistemi acquatici estesi, altamente produttivi nel presente e nel passato.

Il secondo e il terzo capitolo affrontano la complessa tassonomia del gruppo di *Diplocynodon*. Le diagnosi delle specie di *Diplocynodon* attualmente accettate includono comunemente caratteri condivisi e/o irriproducibili, ostacolando delimitazioni specifiche. Sulla base della revisione di tutte le specie attualmente conosciute, viene presentata la prima revisione tassonomica del gruppo dopo la sua inclusione nei moderni lavori filogenetici. Viene inoltre fornita una chiave di identificazione per assistere i ricercatori nell'identificazione delle specie valide. Inoltre, il presente lavoro esamina quantitativamente lo stato dell'intera record fossile di *Diplocynodon* (sulla base di due database disponibili online) e discute lo stato di waste-basket taxon, e suggerendo migliori pratiche tassonomiche. All'interno di *Diplocynodon*, la specie eocenica *Diplocynodon darwini* (Ludwig, 1877) è rappresentata dal più grande campione del periodo paleogenico in termini di numero di individui, costituito da decine di esemplari completi ben conservati, ma manca ancora una descrizione osteologica dettagliata. Il taxon viene qui ridescritto per la prima volta sulla base di esemplari tipo raccolti 150 anni fa e di abbondante materiale ottimamente conservato proveniente dal Messel e dal Geiseltal Konservat-Lagerstätten. Vengono fornite informazioni sulla variazione intraspecifica del taxon, compresa la variazione ontogenetica in popolazioni temporalmente ristrette. La complessa tassonomia del gruppo *Diplocynodon* viene inoltre esplorata e discussa attraverso una revisione delle filogenesi precedentemente pubblicate e di quelle ottenute recentemente.

RESUME ETENDU (FRANÇAIS)

Les populations actuelles de crocodiliens habitent presque exclusivement les régions tropicales, réparties sur la plupart des masses continentales. L'Europe continentale moderne est toutefois une exception notable, car on ne trouve aucun crocodyliforme dans cette région du monde aujourd'hui, ce qui contraste fortement avec l'histoire biogéographique passée de ce groupe. Le début du Cénozoïque, en particulier, exhibe une faune crocodyliforme exceptionnellement diversifiée, dominée principalement par les alligatoroïdes. Les relations phylogénétiques des alligatoroïdes les plus primitifs avec les formes plus dérivées (généralement de petite taille et vivant en eau douce au Paléogène) ont souvent été difficiles à concilier, de part leurs disparité morphologique, la biogéographie complexe ou même l'âge stratigraphique. Le genre européen *Diplocynodon* est reconnu comme le crocodyliforme le plus commun et le mieux échantillonné du Paléogène sur le continent, illustré par le vaste registre fossile réparti sur de multiples localités tout au long du Cénozoïque. L'ensemble de ces données suggèrent une présence du genre exceptionnellement longue, de la fin du Paléocène au milieu du Miocène, ce qui rend l'étude complète de sa systématique et de sa taxonomie d'autant plus difficile mais nécessaire.

La thèse présente une phylogénie globale avec une cohérence spatio-temporelle accrue qui réinterprète *Diplocynodon* spp. (retrouvé étroitement apparenté au *Borealosuchus* nord-américain), *Deinosuchus* spp. et *Leidyosuchus canadensis* (tous deux nord-américains) comme appartenant au groupe souche des crocodyliens. La nouvelle topologie explique l'évolution de l'osmorégulation dans le groupe couronne Crocodylia et leurs proches parents, en déduisant une tolérance plésiomorphe à l'eau salée pour *Deinosuchus* et le groupe souche, ainsi qu'une perte secondaire de ce trait chez les alligatoridés basaux. Les estimations de la longueur totale du corps (corrigé phylogénétiquement) calculées à l'aide de la largeur du crâne révèlent un nanisme phylétique au début de l'histoire évolutive des alligatoroïdes, ainsi qu'une taille plus raisonnable pour *Deinosuchus riograndensis* sur la base d'un des spécimens les plus complets. Le gigantisme chez les crocodyliformes serait corrélé à des écosystèmes aquatiques riches et très productifs dans le présent et dans le passé.

Les deuxième et troisième chapitres abordent la taxonomie non résolue de *Diplocynodon*. Les diagnoses morphologiques des espèces de *Diplocynodon* actuellement acceptées comprennent souvent des caractères partagés et/ou impossibles à reproduire à l'observation, ce qui entrave donc les délimitations spécifiques. Sur la base de l'examen de toutes les espèces actuellement connues, la première révision taxonomique du groupe depuis son inclusion dans les travaux phylogénétiques modernes est présentée. Une clé d'identification pour aider les chercheurs à identifier les espèces évaluées comme valides est également fournie. En outre, le présent travail examine de manière quantitative et qualitative l'état de l'ensemble du registre fossile du *Diplocynodon* (sur la base de deux bases de données accessibles publiquement), et discute du statut de «waste-basket» du taxon en rapport à de meilleures pratiques taxonomiques. Au sein de *Diplocynodon*, l'espèce *Diplocynodon darwini* Ludwig, 1877 datant de l'Eocène possède le plus grand échantillon de la période Paléogène, constitué de dizaines de spécimens complets bien conservés, mais manque critiquement d'une description ostéologique détaillée. Le taxon est ici redécrit pour la première fois sur la base de spécimens types collectés il y a 150 ans et d'un matériel abondant découvert plus récemment et bien conservé provenant des Konservat-Lagerstätten de Messel et de Geiseltal en Allemagne. Des informations sur la variation intraspécifique du taxon sont fournies, y compris la variation ontogénétique de deux populations limitées dans le temps. La taxonomie complexe du groupe *Diplocynodon* est de plus explorée et discutée par le biais d'un examen des phylogénies publiées antérieurement et de phylogénies calculées dans cette étude.

GENERAL INTRODUCTION

In the aftermath of the Cretaceous/Paleogene mass extinction (Alvarez et al., 1980), global warming and cooling events give the tempo to the climate of the following geological period, namely the Paleogene (Zachos et al., 2008; Solórzano et al., 2020; Westerhold et al., 2020; CenCO2PIP, 2023). Flora and fauna paleobiodiversity studies of the latter period (frequently investigating the Paleocene-Eocene Thermal Maximum, PETM) agree on a general co-occurrence of global climatic fluctuations and ecosystems alterations, with the resulting impacts observed through the record of multiple extinctions and diversifications in distant taxonomic groups, ranging from plants, invertebrates and vertebrates (Hutchison, 1998; Mayr, 2022; Lyson et al., 2019; Yasuhara et al., 2022; Korasidis et al., 2022; Solé et al., 2022).

Crocodyliformes (*sensu* Benton & Clark, 1988) was no exception and experienced a significant turnover in the Cenozoic, initiated in the Late Cretaceous by the rise of the crown-group Crocodylia, “last common ancestor of *Gavialis gangeticus*, *Alligator mississippiensis*, and *Crocodylus niloticus* and all of its descendants” (*sensu* Brochu, 2003; Puértolas-Pascual et al., 2016). The latter group is indeed estimated to date back to ca. 100 Ma according to recent tip-dating studies employing different taxon and character sampling (morphology only, Turner et al., 2017; total-evidence, Lee & Lates, 2018; Darlim et al., 2022; see also Appendix 4.1), and included times of markedly higher regional diversity in the Paleogene compared to modern days (Mannion et al., 2015; de Celis et al., 2020; Scheyer et al., 2013; Solórzano et al., 2020).

Among crown lineages, Alligatoroidea (*sensu* Brochu, 2003) traditionally includes the oldest taxa (e.g., *Brachychampsa* spp., *Deinosuchus* spp., *Albertochampsa langstoni*, *Stangerochampsa mccabei*; Norell et al., 1994; Williamson, 1996; Wu, 1996; Brochu, 1999; Cossette & Brochu, 2020) and therefore sets a minimum age of the crown-group Crocodylia to ca. ~ 90 Ma in accordance with molecular studies (Oaks, 2011; Pan et al., 2021). The literal reading of the fossil record suggests that early alligatoroids rapidly dispersed out of North America after the K/Pg mass extinction, allowing the clade to reach a nearly global distribution by the end of the Paleogene (among others, Brochu, 1999;

Skutschas et al., 2014; Bronzati et al., 2015; Puértolas-Pascual, 2016; Iijima et al., 2016; Massonne et al., 2019; Rio & Mannion, 2021). Alligatoroidea became especially dominant in Europe by the late Eocene with the presence of the endemic genus *Diplocynodon* Pomel 1847, by far the most common crocodyliform and largely recognised as a monophyletic clade of early-branching alligatoroids based on the founding phylogenetic work of Brochu (1997, 1999) and all subsequent works expanding upon it (Martin, 2010; Martin et al., 2014; Macaluso et al., 2019; Massonne et al., 2019; Rio et al., 2020).

The taxonomic content of Alligatoroidea has however been subject to minor questioning following the extensive revisions and descriptions of new species in the last 25 years. More specifically, traditional stem-alligatorids such as *Deinosuchus* spp. and *Leidyosuchus canadensis* (Wu et al., 2001; Schwimmer, 2002; Cossette & Brochu, 2020) show contrasting morphologies with the oldest alligatoroids (e.g. *Brachychampsia* spp.; *Stangerochampsia mccabei*), which render the phylogenetic placement of the latter taxa increasingly unstable in recent phylogenies (Bona et al., 2018; Cossette & Brochu, 2018; Massonne et al., 2019; Walter et al., 2022).

In this context, *Diplocynodon* further complicates the picture, as a meaningful corpus of literature previously acknowledged shared morphologies with the stem-crocodylian *Borealosuchus* (Gilmore, 1910; Erickson, 1976; Brochu, 1997; Wu et al., 2001b and references therein), such as the presence of ventral armour made of bipartite osteoderms, the exclusion of the nasals from the external naris, or the similar occlusion pattern. This signal was however never recovered in phylogenetic analyses since the use of modern cladistics methods (Brochu, 1997, 1999; Martin et al., 2014; Rio et al., 2020; Rio & Mannion, 2021). Regarding the phylogenetic relationships of *Diplocynodon*, its early branching position within Alligatoroidea is moreover inconsistent with the relatively young stratigraphic distribution of the group in Europe, spanning from the late Paleocene to the Middle Miocene (Martin et al., 2014; Massonne & Böhme, 2022), as opposed to the strict Cretaceous age of all other early-branching alligatoroids (Wu et al., 2001; Schwimmer, 2002; Cossette & Brochu, 2020). The biogeographic origin of *Diplocynodon* is consequently puzzling, necessarily explained by a long ghost lineage of unsampled species extending back to the Late Cretaceous of North America (Brochu, 1999; Martin et al., 2014; Rio & Mannion, 2021). The first appearance date of *Diplocynodon* (*Diplocynodon*

remensis, Martin et al., 2014) however coincides with a substantial input of American immigrant species in European faunas in the Paleocene (West & Dawson, 1978; Smith et al., 2006; Mayr, 2009; Rose, 2012; Macaluso et al., 2022), suggesting that one or more dispersals occurred prior to the late Paleocene. Based on geographical and paleobiological evidence (Brikiatis, 2014; De Bast & Smith, 2017), these dispersals would have been possible through the De Geer route (between North America and Eurasia, via present day Scandinavia), open during the Late Cretaceous / early Paleocene (early Maastrichtian to middle Danian, 70.8 Ma to ca. 63 Ma). Alternatively, through the Thulean route, open during two short late Paleocene intervals (57 and 56 Ma), but not congruent with the first occurrence of *Diplocynodon* considering the slightly older age of the type locality of *D. remensis* (Cernay, France; late Thanetian, MP6, 58.14 to 57.92 Ma; Legendre and Lévêque, 1997). The ingroup palaeobiogeographical history of *Diplocynodon* in Europe is however hampered by largely unresolved relationships, as illustrated by the number of different topologies previously published (Buscalioni et al., 1992; Brochu, 1999; Piras & Buscalioni, 2006; Martin, 2010; Delfino & Smith, 2012; Massonne et al., 2019; Rio et al., 2020; Rio & Mannion, 2021).

The first chapter of the present thesis investigates the evolutionary relationships of long-established early-branching alligatoroids through an expanded molecular-informed morphological phylogeny, and further explore implications for the body-size evolution and osmoregulation in the crown-group Crocodylia. The second chapter of the thesis reconsiders the taxonomic validity of accepted *Diplocynodon* species. This work further assesses the current state of the fossil record of the taxon through a detailed survey of all occurrences reported in two open databases. The third and final chapter is a reappraisal of the species *Diplocynodon darwini*, for which a modern description is critically lacking, despite representing a unique chance to study intraspecific variation in a Paleogene taxon reported from two localities with abundant material. Intraspecific variation between Messel and Geiseltal populations is here reported, together with general insights into the ontogenetic trajectory observed in the sample. Insights into morphological variability of some character states shared across *Diplocynodon* species are also provided. The ingroup evolutionary relationships are further tested after the taxa scores in two different eusuchian character-taxon datasets.

CHAPTER 1: Expanded phylogeny elucidates *Deinosuchus* relationships, crocodylian osmoregulation and body-size evolution

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1. Introduction

The history of Alligatoroidea, the total (stem + crown) group of extant alligators and caimans (Alligatoridae), can be traced back to the Late Cretaceous of North America. Previous phylogenies of extinct taxa implicitly suggest that the early evolution of the group was already characterised by high morphological disparity and complex biogeographic histories, implying rapid rates of evolution (Brochu, 1999, 2003; Cossette & Brochu, 2020; Rio & Mannion, 2021). Several early alligatoroids from the Late Cretaceous (e.g., *Brachychampsia* spp., *Albertochampsia langstoni*, *Stangerochampsia mccabei*) overall fit an expected ancestral body-plan for the group and were characterised by a relatively small size, short and blunt snout, overbite dental occlusion, enlarged 4th maxillary tooth, molariform posterior dentition, and an initial distribution restricted to Laramidia, the western part of North America once bisected by the extensive epicontinental Western Interior Seaway (WIS; Brochu, 1999, 2001). A putative alligatoroid has been reported from the Atlantic coast but its age postdates the existence of the WIS (Cossette & Brochu, 2018). The absence of unambiguous alligatoroids in Appalachia, together with depositional environments (Erickson, 1972; Norell et al., 1994; Wu et al., 1996), imply a shared lack of saltwater tolerance with extant alligatorids (Taplin, 1988). In contrast, other species recovered as early diverging members of the group, like *Deinosuchus* spp. and *Diplocynodon* spp. resembled crocodyloids or stem-group crocodylians in having partly interfingering dental occlusion, an occlusal notch between the premaxilla and maxilla for the 4th dentary tooth, enlarged 4th and 5th maxillary teeth, narrower and longer snout, larger or even gigantic body-size, and transmarine distribution (Schwimmer, 2002; Rio &

Mannion, 2021). In addition to its extremely large body-size, the ‘terror-crocodile’ *Deinosuchus* (Erickson & Brochu, 1999) furthermore possessed highly derived morphological specializations (Cossette & Brochu, 2020) and, together with *Diplocynodon*, have also utilised coastal marine habitats (Wheatley, 2010; Venczel & Codrea, 2022; Kocsis et al., 2023). Moreover, the earliest alligatoroid record (~ 82 Ma) already includes both of these highly divergent morphotypes (*Deinosuchus* and *Brachychampsa sealeyi*; Williamson, 1996; Mohler et al., 2021), potentially implying a significantly earlier origin of the group. Most molecular divergence age estimates, however, do not suggest an earlier age than ~ 90 Ma (Oaks, 2011; Pan et al., 2021). *Diplocynodon* further complicates the picture with its early branching position within the group that is in turn conflicting with an endemic European distribution and comparatively late first appearance date (late Paleocene; Brochu, 1999; Rio & Mannion, 2021; Martin et al., 2014). Morphology, stratigraphic age, biogeography, and physiology are therefore markedly difficult to reconcile with alligatoroid phylogeny.

We present an expanded molecular-informed morphological phylogeny and find that character states previously diagnosing Alligatoroidea have a broader taxonomic distribution recovering both *Deinosuchus* and *Diplocynodon* as stem-crocodylians. The novel topology explains the geographic distribution of *Deinosuchus* with inferred salt tolerance, resolves the biogeographic history of *Diplocynodon*, and implies body-size reduction at the root of Alligatoroidea. In light of the resulting simpler biogeographic pattern, we hypothesise that the basal split of crown-group crocodylians, involving caiman and alligator ancestors, was triggered by extreme mid-Cretaceous sea level rise.

2. Material and Methods

2.1 Phylogenetic analysis

We expanded and combined previous morphological taxon-character datasets (Cossette & Brochu, 2020; Massonne et al., 2019; Stocker et al., 2021; Walter et al., 2022; Shan et al., 2021; Salas-Gismondi et al., 2015; Bona et al., 2018; Cossette, 2021) that are themselves expanded on previous works (Brochu, 1999, 2004, 2011; Brochu & Storrs, 2012). Our character/taxon dataset consists of 219 discrete morphological characters and 128 taxa, including taxa absent from other recent global datasets (e.g.

Deinosuchus spp., *Orientalosuchina*, *Diplocynodon remensis*, and *Borealosuchus griffithi*). Character definitions and scorings were managed in Mesquite version 3.7 (Maddison & Maddison, 2023). Multistate characters forming a morphocline were treated as ordered. Ordering, however, does not impact the position of *Diplocynodon*, *Leidyosuchus* or *Deinosuchus*. In total, 19 new taxa were added, 20 additional characters, and over 50 character scores were updated relative to the parent dataset (Massonne et al., 2019). For details of the dataset and analysis see Appendix 1.

The maximum parsimony analysis was performed in TNT 1.6 (Goloboff & Morales, 2023) using a manually implemented molecular scaffold (Darlim et al., 2022) based on the topology recovered by Oaks (Oaks, 2011): the scaffold constrains extant species relationships on the basis of molecular topology and allows fossil taxa to be placed within this topology based on morphological characters. Enforcing constraints enables the recovery of Longirostres, the consensual clade uniting *Gavialis gangeticus*, *Tomistoma schlegelii* and *Crocodylus niloticus* in accordance with molecular (Janke et al., 2005; Oaks, 2011; Lee & Yates, 2018) and some recent morphological topologies (Rio & Mannion, 2021). The parent datasets here combined and expanded, however, are unable to recover this clade and yet only few previous studies employed a molecular scaffold (Massonne et al., 2019; Walter et al., 2022; Darlim et al., 2022). It has been recently demonstrated that molecular scaffolds represent an appropriate alternative of total-evidence approaches for fossil crocodylian phylogenetic inference (Darlim et al., 2022). Nevertheless, the scaffold has apparently no impact on the phylogenetic position of *Deinosuchus*, *Diplocynodon* or *Leidyosuchus* in our analyses.

A first round of New Technology Search was performed as advised for large datasets (Goloboff et al., 2008), enabling all search algorithms (Sectorial search, XSS enabled; Ratchet; Drift; Tree fusing) and stabilising the consensus 5 times. A second round of New Technology Search was then conducted, but using the trees saved from RAM, disabling Sectorial searches. The consensus tree was obtained from trees recovered by the second round of calculation. Figs. 1 and 2 were created using the R package *strap* developed by Bell and Lloyd (Bell & Lloyd, 2015), using 1 Ma as minimum branch length, and using taxon ages from (Darlim et al., 2022) and sources reported in Appendix 1.3.

2.2 Phylogenetic body-size analysis

The estimation of body sizes of extinct species was undertaken using a Bayesian phylogenetic approach and the application of regressions based on head width (HW) and total body length (TL) measurements from extant crocodylians (O'Brien et al., 2019; Paiva et al., 2022). We expanded previous regression datasets (O'Brien et al., 2019; Paiva et al., 2022) by adding the extant *Osteolaemus osborni* and thus including a total of 25 species and 207 specimens. Head width, measured as the distance between the extremes of the quadrates, was collected using ImageJ (Schindelin et al., 2012) for 91 fossil and 16 extant taxa in our phylogenetic analysis (Supplementary Data 2.3, Table S1). For topological structure, we used the consensus tree obtained in the present study (Figs. 1-2; Fig. S1), including time calibration. This involved adding age information for all tips sourced from Darlim et al. (2022) and other references (Appendix 1.3). The calibration employed 5 million years as minimum branch lengths (*mbl* method; Laurin, 2004) in the *timePaleoPhy()* function of the *paleotree* package (Bapst, 2012) in R 4.3.1 (R Core Team, 2023).

Total body length was estimated through the BayesModelS method (Nunn & Zhu, 2014) for phylogenetic predictions, which adopts a Brownian motion model and employs a Monte-Carlo Markov-Chain (MCMC; Garland & Ives, 2000; Nunn & Zhu, 2014; O'Brien et al., 2019; Paiva et al., 2022). The phylogenetic signal values utilised by BayesModelS method were extracted from the *phytools* package (Revell, 2012) through *phylosig()* function. The entire protocol, data sources, along with additional details are available in Supplementary Data 2 (Appendix 1, Figshare repository), including packages such as *car* (Fox & Weisberg, 2018), *MASS* (Venables & Ripley, 2002), *caper* (Orme, 2018), *evomap* (Smaers & Mongle, 2014), and *rms* (Harell, 2017). A parsimony reconstruction of ancestral states was used to plot the discretised continuous values of mean total length in Mesquite (Maddison & Maddison, 2023) on the strict consensus tree (see Appendix 1, section 2). Temporal and taxic distribution of body size were visualised using R scripts using *ggplot2*, *deephime* and *jpeg* packages.

2.3 Figures

All figures were produced using the free image editor GIMP (<https://www.gimp.org/>) and free vector graphics editor Inkscape (<https://www.inkscape.org>). The silhouette used for *Deinosuchus* in Figure 1, 2 and 3 was created based on the artwork of Andrey Atuchin under the Creative Common BY-SA 4.0 license (<https://creativecommons.org/licenses/by-sa/4.0/>). Remaining silhouettes used to illustrate clades and taxa in Figures 1 to 4 were sourced from PhyloPic (<https://www.phylopic.org/>) and are in the Public Domain except for *Gryposuchus* (<https://www.phylopic.org/images/d4225b65-a520-42ae-b3ab-8725778a8403/gryposuchus-pachakamue>); *Paleosuchus* (<https://www.phylopic.org/images/9289a813-73ad-4644-b738-d9be619d8219/paleosuchus>), and *Purussaurus* (<https://www.phylopic.org/images/b7fedb04-759e-4f1a-b8bb-d0faefc64e75/purussaurus-neivensis>) by Armin Reindl and are accessible for reuse under the Creative Commons BY-NC 3.0 license (<https://creativecommons.org/licenses/by-nc/3.0/deed.en>); and *Euthecodon*, by Smokeybjb (<https://www.phylopic.org/images/a1e916c4-e020-4657-932b-d74ec6c08e0a/euthecodon-brumpti>); *Crocodylus anthropophagus* by Nobu Tamura (vectorised by Julian Bayona, <https://www.phylopic.org/images/c60b0e39-1437-4bb4-8940-f6da3d943adf/crocodylinae-anthropophagus>); *Stomatosuchus* by Stanton F. Fink (vectorised by Julian Bayona, <https://www.phylopic.org/images/f7d45c6d-e506-4826-8ffe-3f75d588d378/stomatosuchus-inermis>); *Phosphatosaurus* by Nobu Tamura (vectorised by Julian Bayona, <https://www.phylopic.org/images/13ff6eb0-a671-44d8-8a51-8b9f95d49403/dyrosaurus-phosphaticus>) accessible for reuse under the Creative Commons BY-SA 3.0 Unported license (<https://creativecommons.org/licenses/by-sa/3.0/>). Crocodylian skull silhouettes in Figures 1 and 3 are original creations. Map in Figure 4 was modified after (Scotese, 2008). All other elements presented in Figures 1 to 4 are original creations.

3. Results

3.1 *Phylogenetic analysis*

Our maximum parsimony analysis recovered 506 most parsimonious trees (strict consensus tree reported in Figure 1, 2 and Supplementary Figure 1). The most unstable taxa (*Eocaiman* spp. and *Necrosuchus ionensis*) were pruned from the strict consensus tree to increase resolution (see Supplementary Figure 1 for their respective placement). Alligatoroidea is formed by Orientalosuchina and its sister-group Alligatoridae (total group of caimans and alligators). Globidonta, the stem-based lineage comprising *Alligator mississippiensis* and all crocodylians more closely related to it than to *Diplocynodon ratelii*¹, is here redundant with Alligatoroidea because *Diplocynodon* is recovered as a non-alligatoroid stem-crocodylian. In contrast to previous phylogenies (Brochu, 1999; and all subsequent expansions), *Leidyosuchus canadensis*, *Deinosuchus* spp., and *Diplocynodon* spp. form the stem-lineage of crown-group crocodyliforms (Figure 1). *Diplocynodon* spp. is recovered as a monophyletic clade, nested in a polytomic *Borealosuchus* group from North America. This polytomy is caused by the occasional recovery of *Borealosuchus griffithi* as a sister taxon to *Diplocynodon* spp. in some trees, sharing a hypapophyseal keel present up to the 12th vertebra and a greatly reduced quadratojugal spine. Unordering multistate characters has minimal impact on the global topology: some trees recover *Borealosuchus* and *Diplocynodon* as separate clades, with *Diplocynodon remensis* placed outside *Diplocynodon* spp., one node stemward from *Borealosuchus*.

The strict consensus tree recovers a basal polytomy within Alligatoridae formed by Alligatorinae, Caimaninae (including *Bottosaurus harlani*), and the North American Late Cretaceous taxa *Brachychampsia* spp., *Stangerochampsia mccabei*, and *Albertochampsia langstoni*. The latter have two alternative positions either in Alligatorinae or along stem-Alligatoridae.

3.2 *Phylogenetic body-size estimation*

In light of the novel topology, with *Deinosuchus* spp., *Leidyosuchus canadensis*, and *Diplocynodon* spp. removed from Alligatoroidea, all early representatives of this clade were relatively small-sized and we

therefore wanted to test whether the origin of alligatoroids was characterised by phyletic dwarfing. In addition, we wanted to test the impact of the phylogenetic correction and the current topology on body-size estimates of *Deinosuchus* spp. relative to previous studies. Previous works addressing *Deinosuchus* body-length did not employ phylogenetic correction and instead included it in a regression of distantly related extant taxa (*Crocodylus porosus*, *Alligator mississippiensis*; Erickson & Brochu, 1999) with likely different body proportions (Brochu, 2001). Phylogenetic body-size estimates provide results that take into account the known or reconstructed proportions of close extant relatives (O'Brien et al., 2019). We here used the same individual of *D. riograndensis* as previous non-phylogenetic work (TMM43620-1 (Erickson & Brochu, 1999; Schwimmer, 2002; see Appendix 1 section 2, and Appendix 1 section 3 for the list of sources) but a skull width proxy (O'Brien et al., 2019) instead of skull/mandible length making the comparison only partly appropriate. However, skull width proxy has been argued to be more reliable as it is less influenced by differences in body proportions caused by a long snout, a trait present in species of *Deinosuchus* (O'Brien et al., 2019; Cossette & Brochu, 2020). Mean values of estimated body-length together with lowest and highest quantiles are provided in Appendix 1, and a parsimony ancestral state reconstruction of size bins is shown in Figure 3. We here divide body-sizes according to the following categories based on extant species: total length (TL) estimations of ca. 1.5 m and lower can be considered small size, representing the general body-size of some extinct species and exceptionally small individuals of extant species. Medium size category includes TL estimations between 1.5 and 4.0 m, and comprises all extant species. Large size category includes TL estimations between 4.0 and 7 m and includes large to maximal body length of extant species (e.g. *Crocodylus porosus*, *Gavialis gangeticus*; Whitaker & Whitaker, 2008). TL estimations above 7 m are considered gigantic and are only known in extinct species (Brochu & Storrs, 2012; Aureliano et al., 2015). The divergence of Alligatoroidea was coupled with size reduction with an ancestral body-length of 150–200 cm compared to 250–300 cm of the outgroup. Most Paleogene alligatoroids of North America retained a medium to small size or went through further shrinking including some taxa that are inferred to be relatively more terrestrial (Rauhe, 1995). Larger size independently evolved in the lineage containing extant *Alligator mississippiensis* and its extinct Miocene relatives, as well as extant *Melanosuchus niger* and a clade of South American Miocene caimanines, involving independent gigantism in *Purussaurus*

spp. and *Mourasuchus amazonensis* according to the present topology (Figure 3). Species of the stem-crocodylian *Deinosuchus* acquired giant sizes although our estimates give shorter, and possibly more realistic, total body length compared to previous work (Erickson & Brochu, 1999). The detailed results of the analysis are available in Supplementary Data 2.3.

4. Discussion

4.1 *Stem-crocodylian affinities of Deinosuchus can explain transmarine distribution through saltwater tolerance*

Expansions and modifications implemented in the present morphological taxon-character matrix included the merging of published data subsets, addition of characters and character states, rigorous redefinitions of select characters, homology reassessments and update of select character state scores, addition of taxa, and the inclusion of a molecular scaffold in the phylogenetic analysis (see Appendix 1.1 and 1.2). Our maximum parsimony analysis resulted in a topology where several taxa previously considered to represent stem-alligatorids (i.e., all studies descending from that of Brochu (1999), e.g. Whitaker & Whitaker, 2008; Brochu & Storrs, 2012; Martin et al., 2014; O'Brien et al., 2019; Massonne et al., 2019; Cossette & Brochu, 2020; Rio & Mannion, 2021; Stocker et al., 2021), such as *Deinosuchus* spp., *Leidyosuchus canadensis*, and *Diplocynodon* spp., are reinterpreted as stem-group crocodylians, regardless of the addition of the molecular scaffold (Figure 1). The placement of these taxa along stem-crocodylians is more consistent with their plesiomorphic morphology relative to other alligatoroids (Brochu, 1999), their stratigraphic and geographic distribution, and the fact that *Diplocynodon* shares a number of remarkable derived traits with the stem-crocodylian *Borealosuchus*. We detail our arguments below. Some of our results are congruent with recent published analyses using different datasets: some but not all analyses of Groh et al. (2020) employing quantitative characters recovered *Diplocynodon* spp. and *Leidyosuchus canadensis* as stem-crocodylians (Groh et al., 2020) and Rio and Mannion (2021) recovered a paraphyletic *Diplocynodon* sister to the lineage of Longirostres also using quantitative characters in some of their analyses. Muscioni et al. (2023), based on a more similar dataset to that of

the present study, found *Diplocynodon*, *Leidyosuchus canadensis*, as well as *Deinosuchus riograndensis* in a polytomy with Crocodylia.

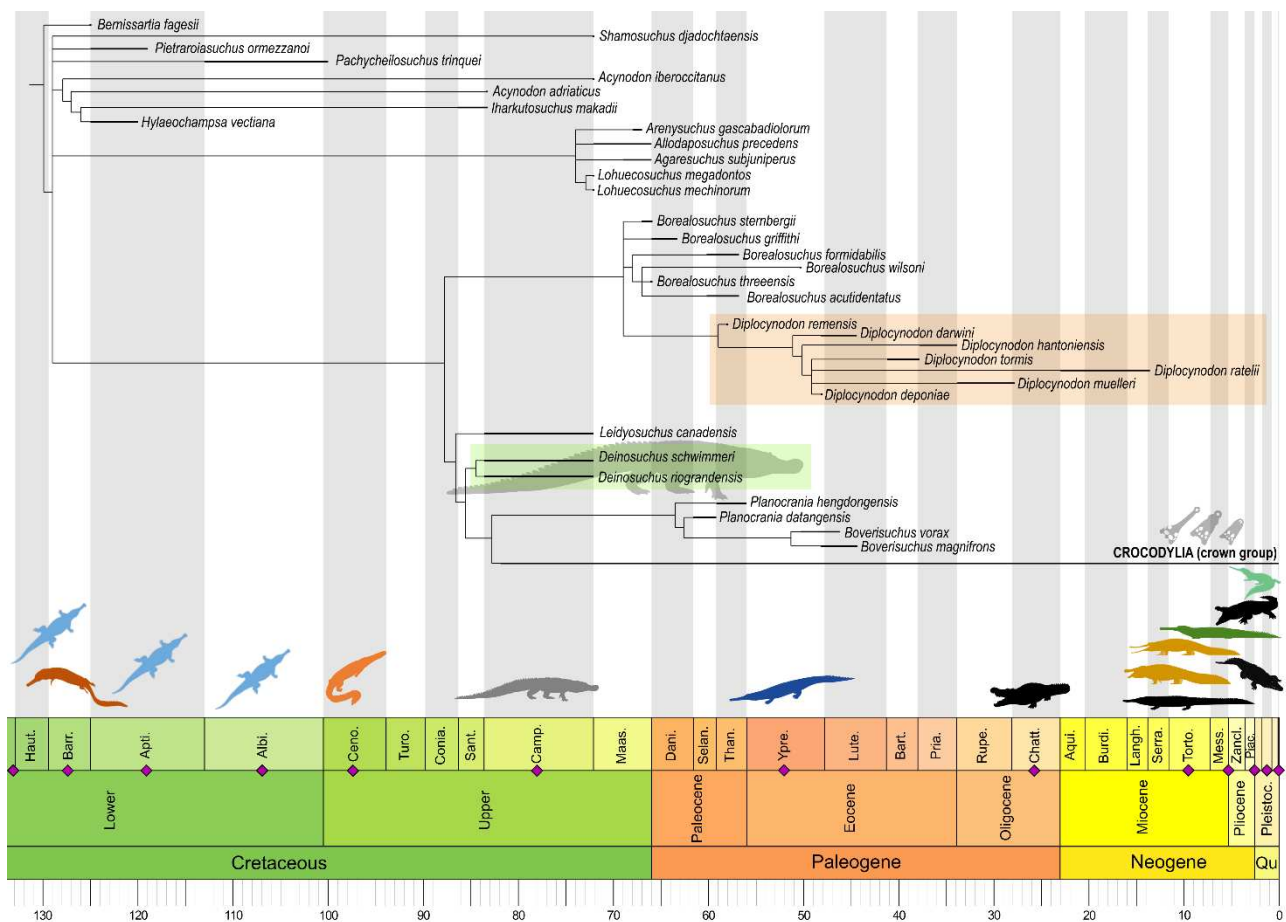


Figure 1: Reduced time calibrated strict consensus tree of the maximum parsimony analysis showing the position of *Deinosuchus* spp., *Leidyosuchus canadensis*, and *Diplocynodon* spp. as stem-crocodylians. *Borealosuchus griffithi* has two alternative positions, either as sister to *Diplocynodon* spp. or an early diverging placement within *Borealosuchus* spp. (Supplementary Data 1 “Walter et al_[TNT]”). Purple diamonds and silhouettes correspond to known occurrences of very large to giant (≥ 7) crocodyliforms. Each of the illustrated taxa is associated with high-productivity wetland or marine habitats (see Appendix 1.3 Table S1 for a list of taxa and sources). Ages are in Ma.

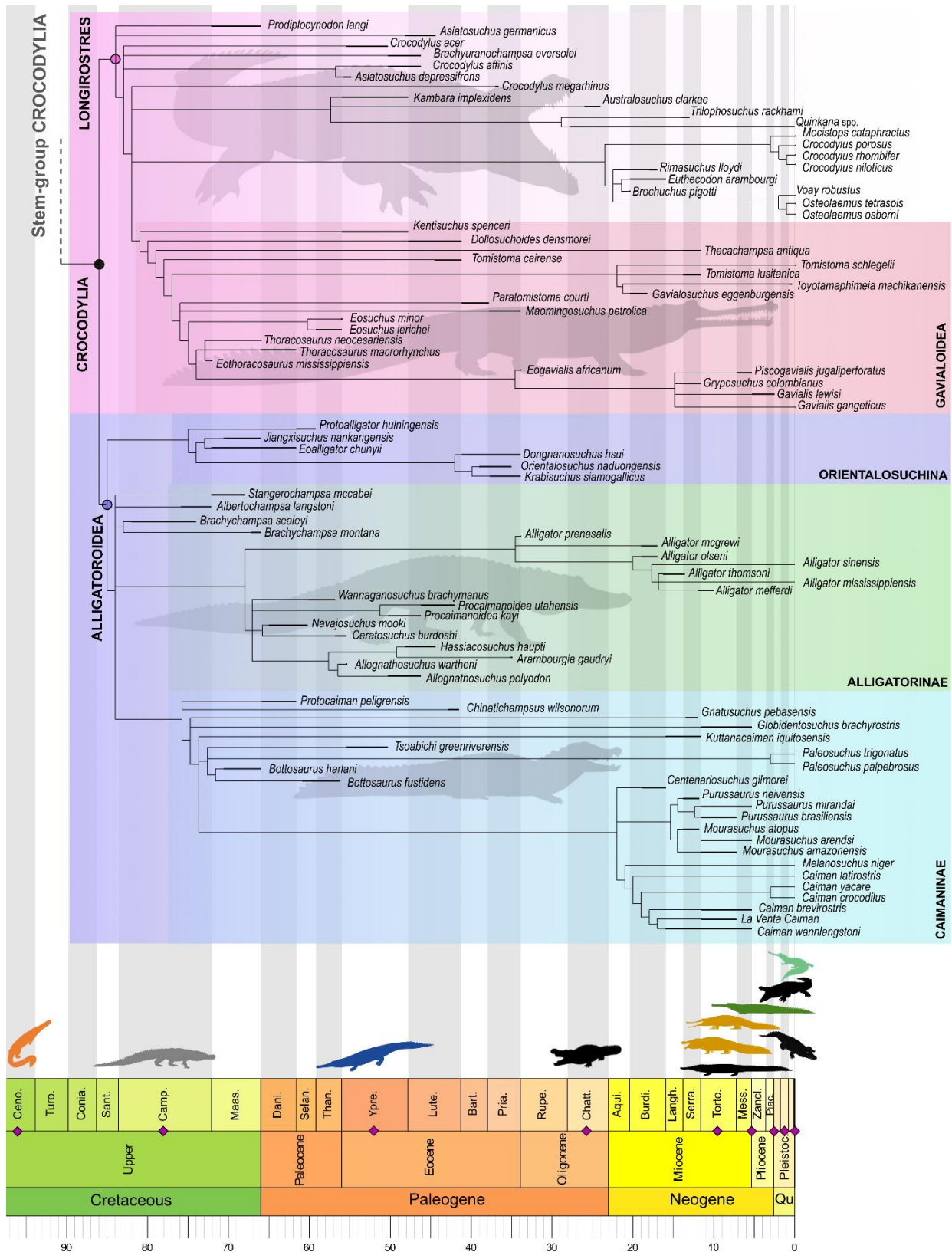


Figure 2: Reduced time calibrated strict consensus tree of maximum parsimony analysis showing the phylogeny of Crocodylia (i.e. crown-group) including Alligatoroidea. Purple diamonds and silhouettes correspond to known occurrences of very large to giant (≥ 7) crocodyliforms. Each of the illustrated taxa is associated with high-productivity wetland or marine habitats (see Appendix 1.3 Table S1 for a list of taxa and sources). Ages are in Ma.

Species of *Deinosuchus* from the Late Cretaceous (Campanian) coastlines of the North American Western Interior Seaway (WIS) and Atlantic have been considered among the largest crocodyliforms of all time with a body length previously estimated around 10 m (Cossette & Brochu, 2020; Erickson & Brochu, 1999; Colbert et al., 1954; Farlow et al., 2005). Bite mark evidence suggests their diet even included large dinosaurs (Schwimmer, 2002; Riveira-Sylva et al., 2009; Schwimmer & Harell, 2010). The first phylogeny including *Deinosuchus* (Brochu, 1999) found this taxon as an early diverging member of total-group Alligatoridae. All subsequent works, including a recent comprehensive revision of *Deinosuchus* (Cossette & Brochu, 2018), confirmed this placement despite marked morphological contrast relative to contemporaneous early alligatoroids, such as *Brachychampsia* (Williamson, 1996; Mohler et al., 2021). These differences include gigantic size, several traits associated with a secondarily elongated snout (Cossette & Brochu, 2020), subequal 3rd and 4th dentary fangs in confluent alveoli, or the largest maxillary teeth being the 4th and 5th, which variously represent plesiomorphies and homoplasies. Moreover *Deinosuchus* had a transmarine distribution unlike Cretaceous alligatoroids during the existence of the WIS (Brochu, 1999; Cossette & Brochu, 2018; Cossette & Brochu, 2020)

The phylogeny herein, on the other hand, finds *Deinosuchus schwimmeri* and *D. riograndensis* outside Alligatoroidea, along the stem-lineage of crown-group crocodyliforms (Crocodylia). In other words, *Deinosuchus* was neither a ‘greater alligator’ (Shiltuizen, 1999), or a ‘terror crocodile’ (Erickson & Brochu, 1999). Our expanded dataset is overlapping in taxon and character sample with previous studies including *D. schwimmeri* and *D. riograndensis* (Brochu, 1999; Brochu & Storrs, 2012; Massonne et al., 2019) and our character state scorings follow the latest work updating this taxon (Cossette & Brochu, 2020). The more stemward position in our study is largely due to the addition of two key Paleocene taxa to the dataset, *Diplocynodon remensis* and *Borealosuchus griffithi*, which resulted in the placement of *Diplocynodon* spp., *Deinosuchus* spp. and *Leidyosuchus canadensis* as stem-crocodylians in our analysis. These three taxa share the above listed differences from true early alligatoroids (except large body size) and their stem-crocodylian placement is retained even with the removal of the molecular scaffold from our analysis. *Deinosuchus* is excluded from Crocodylia by

lacking the following traits among others: an incisive foramen that abuts the toothrow; a single largest maxillary alveolus that is the 5th, and a frontoparietal suture that makes a modest entry into the supratemporal fenestrae. Some previous alligatoroid synapomorphies are now optimised as crocodylian plesiomorphies (Appendix 1.2). This novel stem-crocodylian position of *Deinosuchus* spp. is consistent with its early stratigraphic age (early Campanian), plesiomorphic morphology, and would also imply less homoplasies (Cossette & Brochu, 2020; e.g. character 71:0 was convergent with *Borealosuchus* but here optimised as a plesiomorphy for Crocodylia). Species of *Deinosuchus* nevertheless still share convergent characters with long-snouted taxa (Cossette & Brochu, 2020) even in the current topology. Scoring *Deinosuchus riograndensis* in a different dataset (Rio & Mannion, 2021) resulted in a relatively deeply nested position within Alligatoroidea, but we nevertheless find this highly doubtful due to the particularly poor stratigraphic fit of this topology and the ambiguous synapomorphies uniting Alligatoroidea, some of which are present only in a few of the ingroup taxa whereas others are present in many outgroup taxa as well (Appendix 1.2).

Deinosuchus as a stem-crocodylian is furthermore more consistent with its biogeographic distribution on both sides of the Western Interior Seaway (WIS) in contrast to early members of true early alligatoroids restricted to the West until the retreat of the seaway (Cossette & Brochu, 2018). Cossette & Brochu (2020) recently proposed that species of *Deinosuchus* were allopatric with *D. riograndensis* distributed along the western coast of the WIS (Laramidia), whereas *D. schwimmeri* along the eastern and Atlantic coasts (Appalachia). The authors suggested that speciation in the clade occurred through vicariance, during the opening phase of the WIS, separating *Deinosuchus* ancestral populations. The main rationale behind this was due to the supposed alligatoroid affinity of *Deinosuchus* with extant relatives lacking lingual salt glands, which would render them incapable of osmoregulation and prolonged saltwater exposure required for crossing the extensive WIS (Schwimmer, 2002; Jackson et al., 1996; Grigg et al., 1998; Elsey, 2005; Lehmann et al., 2024; Roberts & Kirschbaum, 1995). The herein proposed stem-crocodylian position, however, no longer infers lack of osmoregulation and may explain the distribution of *Deinosuchus* through dispersal across the WIS. Saltwater tolerance is inferred to be plesiomorphic for Longirostres (e.g. Rio & Mannion, 2021; Vélez-Juarbe et al., 2007) and may

well have been plesiomorphic for Crocodylia as many stem-group taxa close to the crown appear to be euryhaline (Wheatley, 2005). These include marine thoracosauroids (recovered as stem-crocodylians in tip-dated phylogenies; Lee & Yates, 2018), potentially *Diplocynodon*, occasionally recovered from marginal marine settings (Venczel & Codrea, 2022; Kocsis et al., 2023), and *Deinosuchus* itself, which is mostly recorded from estuarine or nearshore habitats such as coastal plains, deltas or platform contexts (Schwimmer, 2002). Moreover, stable isotope analysis of carbon and oxygen from eastern *Deinosuchus* tooth enamel samples suggest consumption of seawater or marine prey (Wheatley, 2005), the latter also supported by bite mark evidence of predation on nearshore marine turtles (Schwimmer, 2002). The simultaneous disappearance of *Deinosuchus* from the fossil record (supposed extinction) with the draining of megawetlands along the WIS and Atlantic coasts (including complete retreat of the former) later during the Cretaceous is furthermore consistent with a lifestyle linked to coastal habitats (Markwick, 1998; Dennis et al., 2013). *Borealosuchus* may serve as an additional example for salt-tolerant stem-crocodylians as it is known to co-occur with *Deinosuchus* in the Moorville Chalk of Alabama, a marginal marine setting (McCormack, 2019). Taking this data together, our parsimony ancestral state reconstruction, including data from this study, implies that the presence of saltwater tolerance (osmoregulation) may have been plesiomorphic for Crocodylia (Figure 4) and simply retained in species of *Deinosuchus*. This does not mean that osmoregulation was necessarily achieved through the presence of lingual salt glands. Saltwater tolerance, possibly including lingual salt glands, were subsequently lost in alligatoroids and *Gavialis* (Taplin & Grigg, 1989). A recent review suggested that salt tolerance may have been present in early alligatoroids (Stout, 2024) as previous phylogenies left it ambiguous whether salt glands (with no known osteological correlates) were already lost in stem- or in crown-group alligatoroids only (Brochu, 1999). The topology of the present study, however, implies the loss of effective osmoregulation (possibly including lingual salt glands) in the stem-lineage as all early true alligatoroids in the new phylogeny come from freshwater deposits (Erickson, 1972; Norell & Clark, 1994; Wu, 1996; Figure 4).

Morphological differences in western *Deinosuchus riograndensis* and eastern *D. schwimmeri* are relatively minor except for body size with known specimens of the western taxon being considerably

larger (Cossette & Brochu, 2020). If speciation took place, dispersal is more consistent with the novel phylogeny than vicariance. Isolation would have been maintained through the episodic nature of the dispersal due to the significant width of the seaway. A literal reading of the fossil record would imply an east to west dispersal as eastern records are so far somewhat older (Schwimmer, 2002), but this simply may be a sampling bias in the fossil record of *Deinosuchus*.

4.2 Body-size estimation of *Deinosuchus* and evolution of gigantism in crocodyliforms

Previous work estimated the total body-length of *Deinosuchus* spp. between ca. 8 and 12 m (up to 12 m, Schwimmer, 2002; 7.67 and 10.640 m, Farlow et al., 2005; and 7.73 to 8.13 m, Iijima et al., 2016). Total body-length has been shown to more strongly correlate with head-width than with cranial length given the variability of rostral proportions among crocodylians (Paiva et al., 2022). Because *Deinosuchus* has a relatively long snout (Cossette & Brochu, 2020), previous approaches (Schwimmer, 2002; Erickson & Brochu, 1999) may have overestimated the total length of this taxon, as they based their regression on shorter-snouted taxa, *Alligator mississippiensis* and *Crocodylus* spp. Our method of estimation differs from that of previous studies in employing a skull width proxy (O'Brien et al., 2019) instead of femur (Farlow et al., 2005), mandible (Schwimmer, 2002; Erickson & Brochu, 1999) or vertebra (Schwimmer, 2002; Iijima et al., 2016) and furthermore includes a phylogenetic correction to bypass the use of a unique extant proxy (e.g., *Alligator mississippiensis*, *Crocodylus porosus*) as body size proportions show strong phylogenetic structuring in crocodylians (O'Brien et al., 2019). The phylogenetic approach, however, is still only sampling living crocodylians, a fraction of past morphological diversity, and body proportions of extinct taxa, particularly those (but not only) outside the clade may have significantly differed (including *Deinosuchus*). This implies that, following O'Brien et al. (2019), outer quartile estimates should be considered for taxa showing “sufficient biological evidence to presume that body size should be meaningfully greater or lesser than the mean estimate (e.g., terrestrial versus fully aquatic denizens, tail, or head size atypically large or small in a given taxon)”. Concerning the present estimate, we consider the 97.5 percentile estimate (7.66 m total length for *Deinosuchus riograndensis* and 6.37 m for *Deinosuchus schwimmeri*; see Appendix 1.6) more

realistic than the mean (5.80 m for *Deinosuchus riograndensis* and 4.83 m for *Deinosuchus schwimmeri*). Our reasoning is that the 97.5 percentile estimates lie between the conservative mean of our estimates and previous non-phylogenetic estimations using cranial length. Our estimate of *D. riograndensis* is based on the skull of the same individual as in Schwimmer (2002; 9.8 m) and Erickson and Brochu (1999; 8.43 to 9.10 m) who, however, both used the length of the lower jaw of the specimen. Furthermore, previous applications of phylogenetic body-size estimations systematically found lower mean estimates compared to non-phylogenetic methods (O'Brien et al., 2019; Paiva et al., 2022; Engelman, 2023). The maximal size of *D. riograndensis* was, nevertheless, likely larger than even our 97.5 percentile estimates as evidenced by the larger size of the holotype specimen (AMNH 3073) compared to the specimen used in our study (TMM 43620-1).

Very large to gigantic body size (here defined as ≥ 7 m total length) has repeatedly evolved during the history of crocodyliforms and represents a wide range of taxa across the phylogenetic tree known from the Cretaceous to the present Britton et al., 2012; Godoy et al., 2019; Martin et al., 2019; Gearty & Payne, 2020; Figures 1 and 2). Previous work has underlined the importance of aquatic to semi-aquatic lifestyle (Godoy et al., 2019) and temperature (Lakin et al., 2020; Stockdale & Benton, 2021) in driving large body-size in crocodyliforms, but the triggers of extreme sizes across clades have not been explicitly addressed. We propose that *Deinosuchus* exemplifies an ecological pattern that has been universally characteristic of giant crocodyliforms and their ecosystems. Species of *Deinosuchus* were inhabitants of a marginal mega-wetland along the WIS and the Atlantic east coast, sustaining other extremely large megafauna species during highly favourable mean annual temperatures for growth (Schwimmer, 2002; Markwick, 1998). Other species of giant crocodyliforms (e.g. *Rhamphosuchus*, *Phosphatosaurus*, *Sarcosuchus*, *Crocodylus porosus*; for a complete list, see Appendix 1.3 Table S1) are/were likewise associated with extraordinarily productive and spatially extensive warm marine or wetland ecosystems including other megafauna. A proposed relationship of extreme body-size and ecosystem productivity is well in accordance with a global analysis of phanerozoic animals, excluding crocodyliforms, which found that the critical factor for gigantism is an unusually highly structured ecosystem in which productivity imposes only exceptionally low limits to sustain extraordinary body-

size (Vermeij, 2016). Favourably constant warm temperatures (Markwick, 1998), an evolutionary shift to rapid growth rates early in ontogeny (Britton et al., 2012), and elevated long-term ecosystem productivity can be therefore considered key for the evolution of gigantism in crocodyliforms. The existence of very large, ~ 7 m long crocodylians in the present and Pleistocene icehouse conditions (*Crocodylus porosus*, Britton et al., 2012; *C. thorbjarnarsoni*, Brochu & Storrs, 2012; *Crocodylus* sp., Delfino & de Vos, 2014) suggests that, contrary to what the literal reading of the fossil record implies, a world with enormous crocodyliforms may have been rather the norm than the exception in the last ~130 million years.

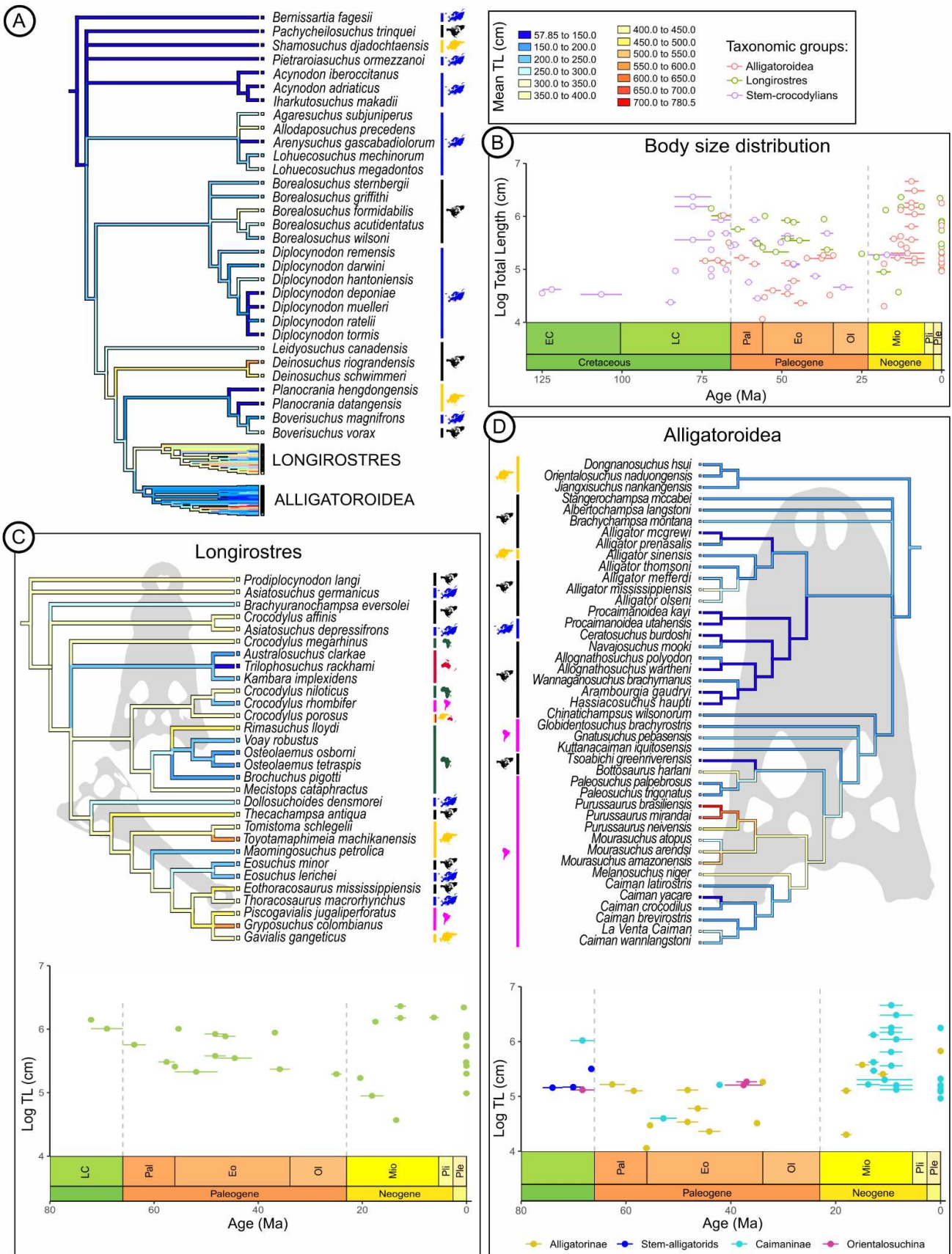


Figure 3: Parsimony ancestral state reconstruction of the phylogenetic mean total length estimations (Appendix 1.6) plotted on the strict consensus tree using equal branch length. A: stem- and crown-group Crocodylia; B: body size distribution of all taxa against geological time; C: Longirostres and body size distribution of the group through time; D: Alligatoroidea and body size distribution of the group through time. Ages are in Ma.

4.3 Systematics of *Diplocynodon* and implications for Euramerican paleobiogeography

Another novel aspect of the phylogeny presented in our study is the placement of the European Cenozoic *Diplocynodon* outside Crocodylia in a monophyletic group with species of North American *Borealosuchus* (Figure 1; *B. griffithi* has two alternative positions within the clade). This novel result is largely the impact of the addition of the geologically earliest known species of *Diplocynodon*, *D. remensis* (late Paleocene) as well as the early Paleocene *Borealosuchus griffithi* to our dataset. Pre-cladistic work has long acknowledged the high morphological similarities between *Diplocynodon* and *Borealosuchus* (Gilmore, 1910; Mook, 1960; Erickson, 1976; Rauhe & Rossmann, 1995) but this signal was never recovered in phylogenetic analyses (e.g. Brochu, 1999; Rio & Mannion, 2021; Martin et al., 2014; Brochu & Storrs, 2012; Massonne et al., 2019; Walter et al., 2022; Brochu, 1997; Wu et al., 2001; Rio et al., 2020). Several plesiomorphies of *Diplocynodon* are shared with *Borealosuchus* and *Deinosuchus* but are absent in typical alligatoroids (e.g., long snout, confluent 3rd and 4th dentary alveoli, 4th and 5th maxillary alveoli equal in size; notch between premaxilla and maxilla in adults). A key character previously placing *Diplocynodon* in Alligatoroidea is the presence of a premaxillary-maxillary pit (instead of a notch) for the reception of the dentary fang early in ontogeny. The notch seen in adult *Diplocynodon* (the inferred plesiomorphic condition for Crocodylia) is secondary, developed later in ontogeny due to abrading occlusion (Brochu, 1999). However, the early ontogenetic pit is not confirmed for all species of *Diplocynodon* and more importantly, the condition remains unknown for *Borealosuchus* spp. and other stem-crocodylians (Brochu, 1997, 1999). The taxonomic distribution of the early ontogenetic premaxillary-maxillary pit is therefore ambiguous and might diagnose a more inclusive clade. On the other hand, some of the shared traits between *Diplocynodon* and *Borealosuchus* are derived and include the presence of ventral armour made of bipartite osteoderms (otherwise only known in *Tsoabichi greenriverensis* and extant caimanines; Brochu, 2010), the exclusion of the nasals from the external naris, unequal anterior processes of the surangular, and the presence of occlusion pits between the 7th and 8th maxillary alveoli. Indeed, our phylogeny optimises these three character states as synapomorphies uniting the clade *Diplocynodon* + *Borealosuchus*.

This topology has far better stratigraphic fit for species of *Diplocynodon* and *Borealosuchus* compared to previous phylogenies: for the first time, we recover the oldest species (i.e. the late Paleocene *D. remensis* and the Late Cretaceous *B. sternbergii*) of each clade as also the earliest branching taxa. Although the early Paleocene *Borealosuchus griffithi* has an unresolved position in our phylogeny, several of our most parsimonious trees place this species as the sister taxon of *Diplocynodon* spp. Under this particular topology, *Borealosuchus* is paraphyletic and the ghost lineage of nearly 20 Myrs inferred by previous phylogenies (with *Diplocynodon* spp. as early branching alligatoroid) are reduced to ca. 6 Myrs. Notably, *Diplocynodon remensis* and *Borealosuchus griffithi* both share the derived trait of a shallow recess on the medial wall of the premaxillary-maxillary notch (Martin et al., 2014), a character yet to be included in a phylogeny and explored for other species of *Diplocynodon* and *Borealosuchus*. A (*Borealosuchus* spp. (*B. griffithi* + *Diplocynodon* spp.)) clade is implying a single dispersal from North America to Europe during the Paleocene. The earliest known occurrence of *Diplocynodon* in the late Paleocene of Europe (*Diplocynodon remensis*, Martin et al., 2014) may underestimate the timing of the dispersal since a high number of North American species immigrated via Greenland and Scandinavia to Europe during the early and middle Paleocene using the De Geer route (West & Dawson, 1978; Smith et al., 2006; Mayr, 2009; Boyer et al., 2012; Rose, 2012; de Bast & Smith, 2017; Macaluso et al., 2022; Legendre & Lévêque, 1997; Briakitis, 2014). In light of the herein recovered stem-crocodylian status of *Diplocynodon*, a dispersal through a marine route cannot be excluded. A comprehensive revision of Paleogene *Borealosuchus* may contribute to testing or further refining these hypotheses.

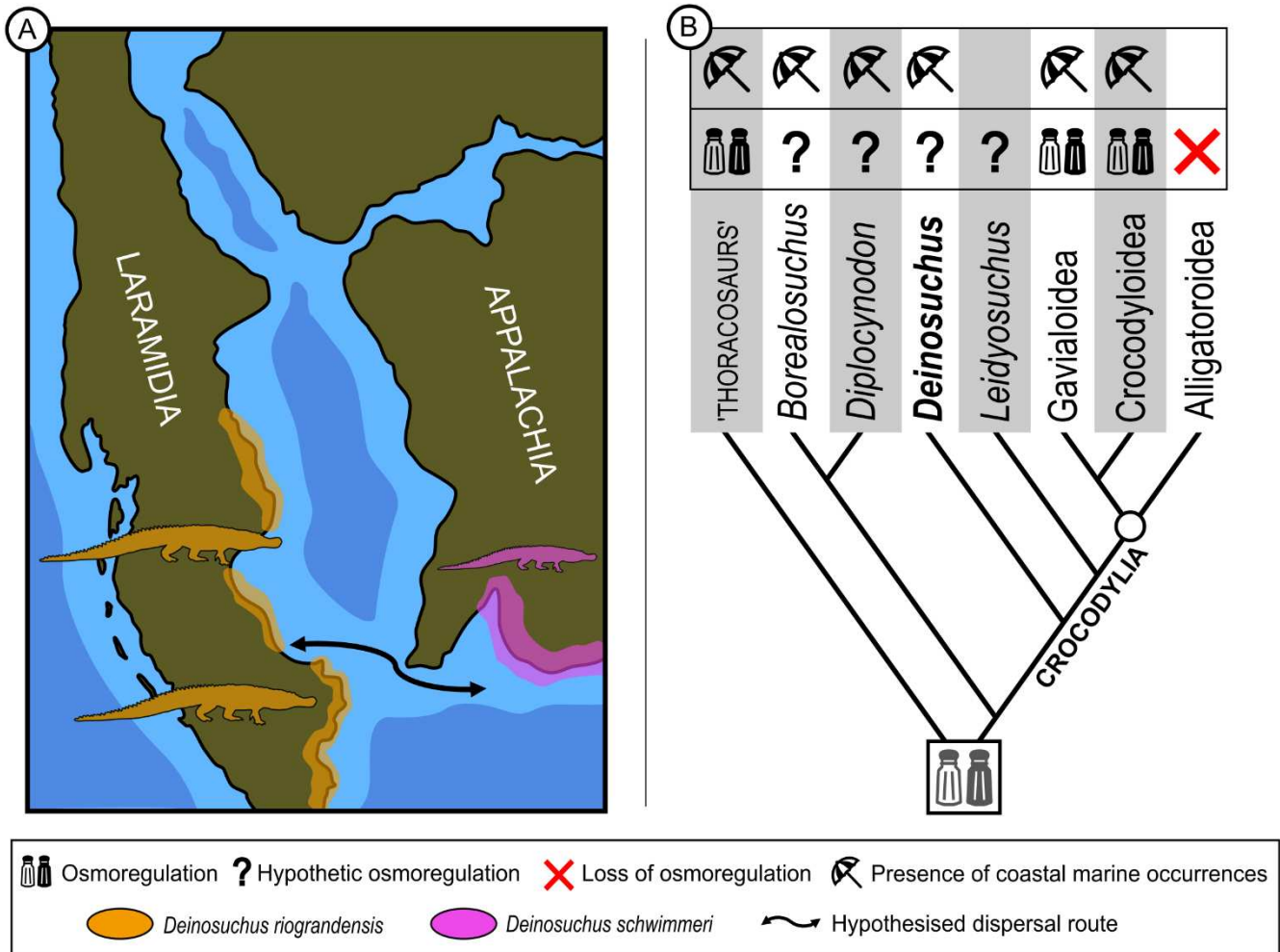


Figure 4. A: Distribution of *Deinosuchus riograndensis* and *D. schwimmeri*³ during the Campanian around the Western Interior Seaway (WIS). B: parsimony ancestral state reconstruction (equal branch length) of osmoregulation in Crocodylia and close relatives using presence/absence of salt glands, stable isotopes, and coastal marine occurrences as proxies [Schwimmer, 2002; Wheatley, 2010; Venczel & Codrea, 2022; Kocsis et al., 2023; Mohler et al., 2021; Jackson et al., 1996; Grigg et al., 1998; Elsey, 2005; Lehmann et al., 2024; Roberts & Kirschbaum, 1995; Vélez-Juarbe et al., 2007; Markwick, 1998; McCormack, 2019; Burke et al., 2024]. The topology is from the present study except for 'thoracosaurus' for which we follow a more appropriate tip-dated work [Lee & Yates, 2018]. The analysis suggests potential plesiomorphic saltwater-tolerance for *Deinosuchus* and Crocodylia with early loss in Alligatoroidea. The distribution of *Deinosuchus* may be explained by dispersal across the WIS. Map is redrawn from [Scotese, 2008], early to late Campanian. Distribution of *Deinosuchus* spp. follows [Cossette & Brochu, 2020; Schwimmer, 2002; Mohler et al., 2021] and references therein.

4.4 Implications for crocodyliform extinction across the Eocene/Oligocene cooling

Our topology has implications for phylogenetic patterning of high crocodyliform extinction rates across the cooling climate of the Eocene/Oligocene transition in North America and Europe (Markwick, 1998). Previous phylogenies implied that all crocodyliform survivors in terrestrial ecosystems were alligatoroids, including *Diplocynodon* (e.g. Brochu, 1999; Brochu, 2004; Kotsakis et al., 2004; Delfino & Smith, 2012; de Celis et al., 2020; Seghetti et al., 2022). In contrast, the topology herein suggests a survival pattern less structured by phylogeny: in Europe, the stem-crocodylian *Diplocynodon* spp., whereas in North America, the alligatorine lineage leading to *Alligator* spp. crossed the transition (Walter et al., 2022; Brochu, 2010). In contrast, the herein proposed sister-taxon of *Diplocynodon*, the North American *Borealosuchus* did not survive into the Oligocene (with the last occurrence known from the middle Eocene; *Borealosuchus wilsoni* (Rio & Mannion, 2021, Brochu, 1997). This divergent survival pattern may be best explained by independent cold adaptation in *Diplocynodon* and the lineage leading to *Alligator*. It has been previously proposed that following global cooling, shrinking habitats led to increased competition between large and small-bodied crocodylians and selective extinction of small-sized taxa (Godoy et al., 2019). An alternative explanation consistent with our body-size analysis, at least for alligatoroids, is that small-sized lineages evolved large body-sizes during the Neogene without selective extinction of small taxa.

4.5 Early alligatoroid evolution

The most important difference relative to previous datasets is the sampling of the key taxa *Diplocynodon remensis*, *Borealosuchus griffithi*, and *Deinosuchus* spp. in the present work and these additions are largely responsible for the changes in topology. In contrast to previous global phylogenies (Brochu, 1999; Cossette & Brochu, 2020; Rio & Mannion, 2021; O'Brien et al., 2019; Brochu & Storrs, 2012; Massonne et al., 2019; Stocker et al., 2021; Walter et al., 2022, Brochu, 2011; Shan et al., 2021), the analysis herein advocates a less inclusive alligatoroid clade (Figure 2). Under this topology, previously recovered synapomorphies for Alligatoroidea, including *Deinosuchus* (e.g. foramen aëreum set in from the margin of the retroarticular process, occlusion of anterior dentary teeth lingual to maxillary teeth,

quadratojugal spine located between the posterior and superior angles of the infratemporal fenestra; see Cossette and Brochu, 2020) are reoptimized to diagnose a more inclusive clade. The earliest representatives of Alligatoroidea are herein restricted to only a few taxa from the Late Cretaceous of North America (*Brachychampsa* spp., *Stangerochampsa mccabei*, and *Albertochampsa langstoni*; Norell et al., 1994; Wu et al., 1996, Williamson, 1996), here recovered either as representatives of stem Alligatoridae or the early branching Alligatorinae (total group of *Alligator* spp.). Both alternatives would make the name Globidonta (Brochu, 1999) redundant with Alligatoroidea. This restricted taxonomic composition has a better stratigraphic fit owing to the removal of the stratigraphically old and morphologically specialised *Deinosuchus*. It also implies less homoplasy and eliminates the phenetic contrast with taxa previously inferred as early branching alligatoroids. In turn, taxa replaced as stem-crocodylians are arranged in a topology with a better stratigraphic fit, such as *Diplocynodon* and *Borealosuchus* (see above).

Almost all Cretaceous alligatoroids, under the novel topology, share a relatively reduced body-size compared to other non-alligatoroid crocodylians, suggesting phyletic dwarfism (Gould & McFadden, 2004) early during the evolution of the group (Figure 3). An exception is *Brachychampsa montana*, which retains a body-size comparable to the ancestral condition of Crocodylia. *Bottosaurus harlani* is another large-sized early putative alligatoroid (Cossette & Brochu, 2018) but its affinity with the group has been questioned (Walter et al., 2022). Additionally, all share a typical short and blunt snout, full overbite dental occlusion, a caniniform 4th maxillary tooth, crushing posterior dentition, a North American Laramidian distribution, and freshwater habitat. The only exceptions in our topology are representatives of Late Cretaceous–Paleogene Orientalosuchina that are here recovered as the earliest diverging alligatoroids and are characterised by plesiomorphies including a 5th maxillary caniniform tooth, a notch between the premaxilla-maxilla for the reception of the 4th dentary tooth, as well as a strictly Asian distribution (Massonne et al., 2019; Shan et al., 2021; Martin & Lauprasert, 2011; Wang et al., 2016; Li et al., 2019). The global phylogenetic relationships of Orientalosuchina, however, has been unstable and studies variously placed them in stem-group Alligatoridae (Massonne et al., 2019; Walter et al., 2022; Shan et al., 2021; Wu et al., 2023), Crocodyloidea (Wang et al., 2016; Li et al.,

2019; Wu et al., 2023; Wu et al., 2018), Caimaninae (Walter et al., 2022, under equal weighting), and Australian Mekosuchinae (Ristevski et al., 2023). The alligatoroid position of Orientalosuchina in our phylogeny is not well supported since most synapomorphies uniting the two groups are unknown in most orientalosuchines and the outgroup (Appendix 1.2 for the list of alligatoroid synapomorphies and trees). Additionally, their endemic Asian distribution is in contrast with that of all other early alligatoroids and would imply an early dispersal to Asia during the Late Cretaceous, a route otherwise poorly supported (Massonne et al., 2019).

Except for Orientalosuchina, the simplified paleobiogeographic pattern inferred by our topology is consistent with a vicariant divergence between Alligatoroidea and its sister-clade, Longirostres (Crocodylidae + Gavialidae; Oaks, 2011). Most early and living representatives of Longirostres have an Asian origin and/or distribution (Rio & Mannion, 2021), whereas all definite early alligatoroids are North American. The age of this divergence has been estimated into the early Late Cretaceous (ca. 90–100 Mya; Oaks, 2011; Pan et al., 2021; Lee & Yates, 2018; Darlim et al., 2022) coinciding with a period of extreme sea level increase culminating in the highest sea level during the entire Mesozoic and Cenozoic eras (90–94 Mya, Turonian; Olde et al., 2015). Exceptionally high sea level may have isolated North American and Asian ancestral stem-crocodylians by posing a wide marine barrier, even for saltwater tolerant species, across Beringia. In contrast, warm climate would have instead favoured high latitude faunal connections during the Turonian (Cretaceous thermal maximum; Moriya, 2011) and is therefore unlikely to have driven divergence. Based on our topology, we can infer that alligatoroids, as a freshwater clade in the interior of the continent, secondarily lost lingual salt glands and associated osmoregulation ability early during their evolution. Our parsimony body-size analysis recovers a minimum of 20% reduction in total body length (TL) at the root of Alligatoroidea, involving a shrinkage from 200–250 cm to 150–200 cm. This reduction reaches up to 40% (from 200–250 cm to < 150 cm) when early alligatorines such as *Ceratosuchus burdoshi* are considered (Figure 3). Low body-size disparity and shrinking early in the evolution of the group is a novel finding of this study as previous body-size analyses employed different topologies (i.e. not accommodating molecular topologies in the phylogenetic framework, placing *Diplocynodon* and *Leidyosuchus* as early alligatoroids, and excluding

Deinosuchus from the sample; Gearty & Payne, 2020; Godoy & Turner, 2020; Godoy et al., 2019). Small body size was broadly retained during the Paleogene and gigantic forms only evolved in the Neogene among caimanines (*Purussaurus* and *Mourasuchus* from South America). In addition, large size (3–4 m) independently evolved in the lineage of extant *Alligator mississippiensis*. Godoy et al. (2019) proposed that Cenozoic Crocodylia body-size progressively increased in response to selective extinction of smaller-bodied taxa due to global cooling-induced habitat loss and associated increased competition. However, as we demonstrate here, in alligatoroids at least, there were no large-bodied taxa before the Neogene and instead, small-bodied taxa may have simply evolved into large-bodied ones. In line with this, Miller-Camp & Brochu (2018) suggested that small-sized Paleogene specialists with crushing dentition evolved into larger-sized generalists in the Neogene, although we note that a specialised morphology may not be necessarily associated with narrow niche (Darlim et al., 2023). Under our topology, we detect a minor body-size increase in *Alligator* following the Eocene/Oligocene extinction of all other North American crocodylians (Hutchison, 1992; de Celis et al., 2020).

CHAPTER 2: Assessing the waste-basket status of *Diplocynodon* through quantitative and taxonomic analysis of fossil occurrences

To be submitted as: Walter J. D., Macaluso L., Rabi M., Martin J. & Delfino M. Assessing the waste-basket status of *Diplocynodon* through quantitative and taxonomic analysis of fossil occurrences.

1. Introduction

The European fossil record of Eusuchia during the early Cenozoic greenhouse shows an exceptionally diverse fauna, including large generalist forms such as *Asiatosuchus* spp., short-snouted alligatorines (*Allognathosuchus* and *Hassiacosuchus*), two unrelated terrestrial hypercarnivores, and a mid-sized generalist, *Diplocynodon* (Hastings & Hellmund, 2017; Rio & Mannion, 2021). This high diversity is in contrast with the period immediately preceding the global cooling of the Eocene/Oligocene (33.9 Ma; de Celis et al., 2020) transition, by which time European crocodyliformes already experienced a severe diversity decline (Martin, 2010; Mannion et al., 2015). *Diplocynodon* however maintained a continuous presence in Europe from the late Paleocene to the Middle Miocene, offering a rich and widespread record (Berg, 1966; Buscalioni et al., 1992; Martin et al., 2014; Rio et al., 2020; Rio & Mannion, 2021). The extinction of *Diplocynodon* was previously hypothesised as a result of the global cooling occurring in the Middle Miocene, shortly after dispersal of the taxon from central to south Europe (Böhme, 2003). The recent research focus on the group allowed the revision of previously described species and to test the phylogenetic relationships of *Diplocynodon*, largely recognising a monophyletic clade of early-branching alligatoroids (Brochu, 1999; Martin, 2010; Martin et al., 2014; Macaluso et al., 2019; Rio et al., 2020; Rio & Mannion, 2021) or stem-group crocodylians (see discussion in Martin et al., 2014; Walter et al., 2025). The successive revisions and erections of species have however overlooked the genus diagnosis, therefore setting lengthy combinations of morphological characters to discriminate taxa. As a result, previous studies suggest that species-level taxonomy of *Diplocynodon* is not well-established, and highly incongruent stratigraphic fits are commonly recovered in phylogenies (Martin, 2010; Delfino & Smith, 2012; Martin et al., 2014; Rio & Mannion, 2021). Knowledge of speciation

mechanisms in the clade is consequently impoverished: allopatry due to climate or tectonics-induced geographic isolation, or even sympatry as in the case proposed for *Diplocynodon darwini* Ludwig, 1877 and *Diplocynodon deponiae* Frey, Laemmert & Ries, 1987 from Messel (Delfino & Smith, 2012) may have taken place in the evolutionary history of the group.

Since Pomel (1847) erected the genus based on the crocodylian remains found in Saint-Gérard-le-Puy, Cenozoic crocodylian material was repeatedly attributed to *Diplocynodon*. As such, it might today be considered as a waste-basket taxon, given that it shares with other waste-basket taxa (Plotnick & Wagner 2006) an early date of first description and a stratigraphically extended fossil record. To test this possible status, we herein quantitatively and qualitatively review the nature of the occurrences and of the material attributed to *Diplocynodon* through a survey of the literature cited by two open online palaeontological databases.

Furthermore, the current study revisits the ingroup taxonomy of *Diplocynodon*, assessing whether the currently established species are morphologically distinct, and presents updated and concise diagnoses of the genus and of the valid species. A dichotomous key of the valid species was subsequently built to favour future straightforward identifications.

2. Material and Methods

We performed a complete material survey of *Diplocynodon* for the total number of occurrences found in two online databases, namely The Paleobiology Database (PBDB; <https://paleobiodb.org>) and fosFARbase (Böhme & Ilg, 2003). The database outputs for *Diplocynodon* were retained and checked to remove overlapping occurrences. The supporting literature cited for each of them was then cross checked to categorise the nature of the reference to *Diplocynodon* (*Diplocynodon* sp. or species level, either simply mentioned, described and/or figured, see below). Occurrences that could not be corroborated in the cited literature were deleted, as the information provided could not be verified. Second, the type of material for each occurrence was assessed by scoring the presence of different types

of specimen categories: articulated specimens, cranial and/or postcranial elements. The terminology used for the survey mainly follows Uhen et al. (2023) and are explained as follows:

- ‘occurrence’ refers to the presence of a taxon per locality;
- ‘evidence’ refers to a description (including osteological element) and/or figure(s) of the specimen(s)
- ‘cited/mentioned’ refers to a simple citation of a taxon without evidence (e.g. in a faunal list).

The complete list of occurrences, taxonomic identifications (including the updated attributions following the taxonomic revision presented in this study), calculations, references, and list of all specimens studied first hand is provided Appendix 1. The supplementary references list is reported in Appendix 2.3.

3. Results

The complete list of described species of *Diplocynodon* is reported in Table 1, and the revised validity and diagnostic characters are expanded in the following Systematic Palaeontology section. In total, 169 occurrences were qualified as usable after removal of overlapping and uninformed entries in both databases (see Figure 1 for a summary of the results). A majority of this sample actually includes concrete evidence of *Diplocynodon* occurrence (60.9%). Attributions at species level rank represent nearly half of the total number of occurrences (45%), of which only one third report one or more articulated specimens (32.8%). Most occurrences providing evidence report disarticulated material (88.3%), comprising teeth and osteoderms as their main components. Regarding the distribution of the material over geological ages, the record is underrepresented in the Paleocene (1.7%) and largely dominated by Miocene remains (59.8%).

4. SYSTEMATIC PALAEOLOGY

Crocodyliformes Hay, 1930 (*sensu* Benton & Clark, 1988)

Eusuchia Huxley, 1875 (*sensu* Brochu, 2003)

Crocodylia Gmelin, 1789 (*sensu* Brochu, 2003)

Diplocynodon Pomel, 1847

Emended diagnosis:

Diplocynodon is a medium-sized crocodyliform characterised by the unique combination of the following characters:

- the presence of paired canines both on the dentary (3rd + 4th teeth) and the maxillary (4th + 5th teeth);
- the 3rd and 4th dentary alveoli are confluent;
- the 3rd and 4th dentary alveoli occlude in a pit early in ontogeny;
- the ventral shield consists of bipartite osteoderms;
- the iliac blade is rounded and ventrodorsally deep.

Comments:

Pomel (1847: 383) names the genus *Diplocynodon* in a short note briefly describing the confluence of the 3rd and 4th dentary teeth: “[...] the third and fourth mandibular teeth, very close, very strong and nearly equal, protrude the upper jaw together in a cavity located at the junction between the maxillary and intermaxillary; the teeth are also less numerous than in extant species. We can call them *Diplocynodon*.” We hereby propose an emended diagnosis of *Diplocynodon* based on characters consistently recognised in founding taxonomical works, recent studies and personal observations. These morphological traits were previously included in nearly all *Diplocynodon* species diagnoses, complicating the interspecific identification. *Diplocynodon* is today only unambiguously found in the Cenozoic of Europe. Early studies attributed material from North America (*Diplocynodon stuckeri*;

Mook, 1960) or Asia (Efimov, 1988; Liu & Chen, 1993), but were later reattributed to other taxa or considered too fragmentary to be confidently referred to *Diplocynodon* (Brochu, 1999).

Species	Authorship	Historical synonymies	Possible synonyms	References	Age
<i>Diplocynodon remensis</i>	Martin et al., 2014	-	-	Martin et al., 2014	Thanetian
<i>Diplocynodon deponiae</i>	Frey et al., 1987	<i>Baryphracta deponiae</i>	-	Delfino & Smith, 2012	Lutetian
<i>Diplocynodon darwini</i>	Ludwig, 1877	<i>Alligator darwini</i>	-	Berg, 1966	Lutetian
		<i>Crocodylus ebertyi</i>	-		
		<i>Diplocynodon hallense</i>	-	Kuhn, 1938 Rauhe & Rossmann, 1995	
<i>Diplocynodon tormis</i>	Buscalioni et al., 1992	-	-	Buscalioni et al., 1992	Lutetian / Bartonian
<i>Diplocynodon elavericus</i>	Martin, 2010	-	-	Martin, 2010	Priabonian
<i>Diplocynodon hantoniensis</i>	Wood, 1846	<i>Alligator hantoniensis</i>	-	Rio et al., 2020	
		<i>Crocodylus hastingsiae</i>	-	Owen, 1848	
<i>Diplocynodon kochi</i>	Venczel & Codrea, 2022	-	-	Venczel & Codrea, 2022	Priabonian
<i>Diplocynodon gervaisi</i>	Gervais, 1859	-	-	Gervais, 1859	Rupelian
<i>Diplocynodon muelleri</i>	Kälin, 1936	<i>Hispanochampsia muelleri</i>	-	Piras & Buscalioni, 2006	Rupelian
		<i>Diplocynodon guerini</i>	-	Bataller, 1941	
		<i>Diplocynodon marini</i>	-	Bataller, 1941	
		-	<i>Diplocynodon monsvialensis</i> <i>Diplocynodon dalpiazii</i>	Macaluso et al., 2019	
<i>Diplocynodon levantanicum</i>	Huene & Nikoloff, 1963	-	-	Massonne & Böhme, 2022	Chattian
<i>Diplocynodon ratelii</i>	Pomel, 1847	<i>Crocodylus ratelii</i>	-	Pomel, 1846	Aquitanian
<i>Diplocynodon ungeri</i>	Prangner, 1855	<i>Enneodon ungeri</i>	-	Martin & Gross, 2011	Langhian
		<i>Diplocynodon styriacus</i>	-	Thenius, 1955	
		<i>Diplocynodon steineri</i>	-	Thenius, 1955	
<i>Diplocynodon buetikonensis</i>	von Meyer, 1845	<i>Crocodylus bütikonensis</i>	-	Berg, 1966	Tortonian

Table 1: List of valid taxa ordered according to their age (from the oldest to the youngest) including authorship, historical synonymies, possible synonyms, and essential references.

Ingroup taxonomy

Valid taxa (ordered alphabetically)

Diplocynodon darwini (Ludwig, 1877)

(Plate 2)

Type material:

Table I–XVI in Ludwig (1877)

Type locality:

Grube Messel (Darmstadt, Germany).

Geological stage and age:

Middle Eocene, early Lutetian (MP 11), 47 Ma.

Diagnosis:

Diplocynodon darwini belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above).

It differs from all other *Diplocynodon* species by the combination of the following characters:

- presence of a linear sulcus on the prefrontal, along the anteromedial margin of the orbit;
- lack of osteoderms coverage on posterior section of the tail (i.e. the posterior two-thirds);
- the orbital margin flush with the circumscribing bones surface.

This species is further characterised by:

- a retention of the pterygoid-ectopterygoid flexure (shared with *D. deponiae* and *D. hantoniensis*).

Comments:

Diplocynodon darwini was erected by Ludwig (1877) on the basis of disarticulated material from the locality of Messel. It was originally subdivided in two separate species, *Alligator darwini* and *Crocodylus ebertyi*, based on subtle variation in dental ornamentation. Personal observation of multiple

specimens not available at the time of the species erection did not reveal such discrimination: available specimens shared similar dentition, cranial and postcranial skeletal organisation. We thus hereby agree with Rauhe & Rossmann (1995) and later works in considering both taxa to belong to a single species. Our investigation also involved specimens of *Diplocynodon hallense* (Kuhn, 1938), housed in the collections of the Geiseltalmuseum (Halle, Germany). We hereby agree with Berg (1966) in invalidating *D. hallense*, as no evident morphologies distinguish the Geiseltal population from the Messel population at species level. Comparison of the two populations however revealed intraspecific variation (including ontogenetic) in *D. darwini*, and that may also occur in congeneric species. These include: 1) length of mandibular symphysis (reaching the 3rd and up to the posterior end of the 4th dentary alveolus), size of the medial jugal foramen, presence of a premaxillary-maxillary notch, or confluence of the 4th and 5th maxillary alveoli.

While *Diplocynodon darwini* is currently recognised from the localities of Messel and Geiseltal, its distribution may have been more widespread: unstudied material currently attributed to *Crocodylia* indet. or *Diplocynodon* sp. was recovered from various Eocene localities in Europe (e.g. Dormaal, Maransart or Eckfeld). This material, if pertaining to *Diplocynodon darwini*, would extend the time range and geographical distribution of the species.

Diplocynodon deponiae (Frey, Laemmert & Riess, 1987)

(Plate 1B)

Type material:

SMF ME 899 (holotype), a complete skeleton exposed in left lateral and ventral views.

Type locality:

Messel Pit (Darmstadt, Germany).

Geological stage and age:

Middle Eocene, early Lutetian (MP 11), 47 Ma.

Diagnosis:

Diplocynodon deponiae belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- a relatively small body-size (ca. 1 m in total length);
- a complete armour coverage extending on limbs, body and tail;
- choanae placed approximately in the middle of the pterygoids;
- a significant overhang of the supratemporal fenestrae by dermal bones of the skull roof;
- external naris circumscribed by a thin ridge.

This species is further characterised by:

- a retention of the pterygoid-ectopterygoid flexure throughout ontogeny (shared with *D. darwini* and *D. hantoniensis*);
- very blunt posterior dentary and maxillary teeth (shared with *D. hantoniensis*).

Comments:

The species was first erected by Frey, Laemmert & Riess (1987) under the genus and species name *Baryphracta deponiae*. It was later recombined into *Diplocynodon deponiae* by Delfino & Smith (2012) based on newly prepared specimens housed in the Institut Royal des Sciences Naturelles de Belgique in Brussels. We amended the previous diagnosis of Delfino & Smith (2012) to discard characters shared among all species where known, and further specify characters shared with *D. hantoniensis* and *D. darwini* but no other species.

Diplocynodon deponiae differs noticeably phenotypically from its congeneric species, bearing several characters found in combination in extant dwarf crocodylian species at maturity: a reduced total length, supratemporal fenestrae closed or nearly closed, and an extensive armour coverage (Clarac et al., 2024). These characters were previously described by Delfino & Smith (2012) and are confirmed in the present study after first-hand study of several specimens (JDW pers. obs.). Found solely in the locality of Messel (Germany), *Diplocynodon deponiae* may well represent a dwarf species of *Diplocynodon*. The species may have evolved derived characters related to dwarfism to maximise niche partitioning with

Diplocynodon darwini and/or other large crocodylians such as *Asiatosuchus* found in the same locality (Morlo et al., 2004; Smith et al., 2024).

Diplocynodon hantoniensis (Wood, 1846)

(Plate 1G)

Type material:

NHMUK OR 25166 (holotype), a complete snout.

Type locality:

Hordwell Cliff (Hampshire, United–Kingdom).

Geological stage and age:

Upper Eocene, early Priabonian (MP 17), 37 Ma.

Diagnosis:

Diplocynodon hantoniensis belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- premaxillary surface posterolateral to external naris with a deep notch;
- short anterior ectopterygoid process, which forms the medial wall of the posteriormost maxillary alveolus, before veering medially to the suborbital fenestra;
- broad preorbital ridge on the lacrimal.

This species is further characterised by:

- a retention of the pterygoid–ectopterygoid flexure throughout ontogeny (shared with *D. darwini* and *D. deponiae*);
- very blunt (“globular” in Rio et al., 2020) posterior dentary and maxillary teeth (shared with *D. deponiae*).

Comments:

The validity of *Diplocynodon hantoniensis* was reassessed and confirmed by Rio et al. (2020), who redescribed and referred additional material in their recent revision of the species, including several complete skulls and disarticulated skull elements, postcranial material consisting of vertebrae and limb bones, and osteoderms. The diagnosis of *Diplocynodon hantoniensis* by Rio et al. (2020) was slightly modified here to specify characters shared with *D. deponiae* and *D. darwini* but not with the other species.

The general proportions of known specimens of *Diplocynodon hantoniensis* make it one of the largest species in the group, potentially explained by a better preservation in volume and higher degree of maturity of the individuals. A nearly complete skull of comparable size and shape from the Oligocene of Dordogne (France) was described and referred to *Diplocynodon* cf. *hantoniensis* by Vignaud et al. (1996). However, following comments of Rio et al. (2020) and after first-hand observation of a cast of the specimen (JDW pers. obs.), we advise a referral to *Diplocynodon* sp. pending restudy of the specimen.

Diplocynodon kochi Venczel & Codrea, 2022

(Plate 1H)

Type material:

UBB V.1453 (holotype), a nearly complete skull.

Type locality:

Cluj-Mănăştur former limestone quarry, Cluj-Napoca (Transylvania, Romania).

Geological stage and age:

Upper Eocene, early Priabonian (MP 17), 37 Ma.

Diagnosis:

Diplocynodon kochi belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- lateral carotid foramen opens dorsal to basisphenoid at maturity;
- posterior series of maxillary (12th–16th) and dentary (14th–19th) teeth and alveoli are mediolaterally compressed;
- the 1st, 2nd and 3rd premaxillary alveoli are placed closer to each other than to the 4th and 5th.

Comments:

Additional material was referred to *Diplocynodon kochi* by Venczel (2023), including postcranial elements, previously unknown for the species and not preserved in the holotype. The assignment of this undiagnostic material (e.g. UBB V 1005, 1006: femurs; and 1007: a vertebra) to the latter species relies on their co-occurrence in the same stratigraphic unit.

We amended the diagnosis of *Diplocynodon kochi* in light of new insights in intraspecific variation of *Diplocynodon* spp. and detailed comparison with published revisions of other species. Characters diagnostic at generic level were removed from the diagnosis.

Previous autapomorphies were also amended: enlarged and procumbent 1st dentary teeth are also present in *D. darwini*, *D. hantoniensis* and *D. ratelii*, therefore not autapomorphic for *D. kochi*. Additionally, the recess on the parietal medial wall does not appear any different from the condition seen in most *Diplocynodon* species which bear an open supratemporal fenestra where the parietal forms a medial shelf and is slightly concave on its lateral wall. The 'recess' described in *D. kochi* is rather likely the effect of the modest overhang of the parietal over the anteromedial corner of the supratemporal fenestra coupled with dorsoventral compression of the braincase. Furthermore, the preorbital ridge described by Venczel & Codrea (2022) rather appears like a step between the dorsal level of the lacrimal and the dorsal level of the anterolateral corner of the orbit due to dorsoventral compression on this part of the skull. Virtually all crocodylians bear a variably pronounced preorbital ornamentation on the lacrimal, usually linear and running along the lacrimal dorsal surface. The condition in *Diplocynodon* spp. is very modest to absent. One character state is here newly added to the diagnosis, as it differs from the condition

seen in all other congeneric species: the 1st, 2nd and 3rd premaxillary teeth are placed closer to each other than to the 4th and 5th.

Diplocynodon levantinum Huene & Nikoloff, 1963

Type material:

NMNHS 31-1 (lectotype), cast of a right dentary fragment.

Type locality:

Nadeshda (Dimitrovgrad, Bulgaria), Chattian (late Oligocene).

Geological stage and age:

Upper Oligocene, early Chattian (MP 27), 26 Ma.

Diagnosis:

Diplocynodon levantinum belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- a lingual foramen for the articular artery situated entirely on the surangular;
- a long suborbital fenestra reaching the level of the eighth maxillary alveolus;
- an occlusion pit in line with the tooth row posterior to the 14th dentary alveolus.

Comments:

Massonne & Böhme (2022) recently revised *Diplocynodon levantinum* based on new and previously published specimens by Huene & Nikoloff (1968). The authors proposed an updated late Oligocene age for the material and confirmed the species validity. We hereby amended the previous diagnosis of Massonne & Böhme (2022) by discarding characters shared among all species, where known, and retaining characters bearing a different condition from other *Diplocynodon* species.

Diplocynodon muelleri (Kälin, 1936)

(Plate 1D)

Type material:

NMB Spa 4 (holotype), NMB Spa 73 (paratype).

Type locality:

El Talladell (Lleida, Spain).

Geological stage and age:

Lower Oligocene, Rupelian (MP 23), 31–29 Ma.

Referred material:

Complete list provided by Piras & Buscalioni (2006).

Diagnosis:

Diplocynodon muelleri belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- splenial excluded from mandibular symphysis, and with anterior tip passing dorsal to Meckelian groove;
- orbital contour anteriorly notched;
- lateral edges of palatines with anterior projections into suborbital fenestrae.

Comments:

Piras & Buscalioni (2006) provided a new combination of the taxon *Hispanochampsa muelleri* Kälin 1936 into *Diplocynodon muelleri*: a handful of specimens from Spain were newly referred to the species and the species diagnosis was amended. The latest revision of the Oligocene crocodylians from Monteviale by Macaluso et al. (2019) attributed the local specimens to *Diplocynodon* cf. *muelleri*, as no significant differences could be put forward to justify the presence of a separate species in the Italian locality. The definitive attribution to *D. muelleri* was prevented by both the uncertain distinction

between the two Spanish species *D. muelleri* and *D. tormis* at that time, and by the longer extension of the mandibular symphysis of the Monteviale *Diplocynodon*, that would have eventually distinguished it from *D. muelleri*. In light of the first-hand variation observed in *D. darwini*, we argue for the intraspecific nature of the mandibular symphysis length in *Diplocynodon* species, that can vary from the level of the 3rd dentary alveolus to reaching the posterior edge of the 4th. This variation is actually known in crocodylians: the character coding for the length of the mandibular symphysis is actually used in various eusuchian morphological datasets (e.g. Brochu, 1999, and subsequent works; Rio & Mannion, 2021), and regard the variation described above as a single state for eusuchian taxa. We therefore refute the use of this character to separate *D. muelleri* from other *Diplocynodon* species. If the Monteviale material has to be referred to the same taxon as the Spanish material (referred to *D. muelleri*), then the taxon would take the name *Diplocynodon monsvialensis* comb. nov. based on nomenclature priority rules (ICZN, 1999).

However, crucial to this matter is the ambiguity of the diagnostic characters of the Spanish species retained in the present work:

- a. The dorsal projection of the anterior tip of the splenial relative to the Meckelian groove is only briefly mentioned by Piras & Buscalioni (2006), without reference to any precise specimen showing this condition. Our first-hand observation of NMB Spa 4 (holotype) did not allow us to confirm this condition, as the mandibular rami are strongly twisted and damaged on the relevant region. NMB Spa 73 (paratype) on the other hand preserves the right mandible with its medial surface, but the anterior tip of the splenial is broken off: the sutural mark however indicates exclusion from the mandibular symphysis, with the tip placed ventrally to the Meckelian groove. One cannot exclude that Piras & Buscalioni (2006) based their observations on specimens that are not figured and/or specifically referred, other than the types, making their interpretations irreproducible as to now. The condition in *Diplocynodon* from Monteviale is rather unclear, as most specimens either do not preserve the relevant region, or the splenial tip is largely obscured because of the mandibular occlusion. A thorough reassessment of this character in both specimen samples is in order to clarify the appropriate morphology.

- b. The orbital contour anteriorly notched is apparent in both *D. muelleri* and the Monteviale *Diplocynodon*, but this could be a taphonomic artefact caused by dorsoventral compression during diagenesis. As a matter of fact, the most severely compressed specimens of *D. darwini* from Messel and Geiseltal show a similar anteriorly notched orbital outline, contra less deformed skulls.
- c. Similarly to point (a), the anterior projections of the lateral edges of the palatines into the suborbital fenestrae are only mentioned in the diagnosis of the taxon. No specimens are referred by the authors to corroborate this condition. This character, defined by Brochu (1999; character 106), describes an evident and thin flange protruding in the anteromedial corner of the suborbital fenestra. This morphology cannot be assessed in the holotype of *D. muelleri*, but the right palatine (although distorted) seems to project slightly in the fenestra. Like other diagnostic characters, future research should focus on the reassessment of this morphology in both the material referred to *D. muelleri* and specimens from Monteviale.

Diplocynodon ratelii Pomel, 1847 (type species of the genus)

(Plate 1E-F)

Type material:

MHNN F BR 4020 (holotype), a fragmented skull.

Type locality:

Saint-Gérard-le-Puy (Allier, France).

Geological stage and age:

Lower Miocene, early Aquitanian (MN1), ca. 23–22 Ma.

Diagnosis:

Diplocynodon ratelii belongs to *Diplocynodon* by the combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the unique following character:

- the nasals contact the posterior margin of the external nares;
- the snout remains comparably narrow throughout ontogeny (shared with *D. ungeri*).

Comments:

Diplocynodon ratelii, type species of *Diplocynodon*, is recorded in several Miocene localities across Europe. Pomel (1846) originally referred material from Saint-Gérard-le-Puy to *Crocodylus ratelii*, mentioning the abundance of osteoderms. Reference to the species is actually absent in Pomel (1847) where the author erected the genus *Diplocynodon* in a brief note (see above comments on *Diplocynodon* spp.). Only later Pomel (1853:123) provides a more complete description of the species, referred to *D. ratelii* in the latter work: “1. *Diplocynodus ratelii*, Pom. Skull with a nearly straight shape up to the anterior third of the orbits, where it forms an obtuse and right angle beyond the skull region. The latter resembles the true crocodiles one much more than the one of caimans, because of the development of its temporal fossae, nearly as large as in the Nile species. The skull is, as a whole, less large posteriorly than in alligators, and less constricted anteriorly than in crocodiles. The head never exceeds 0.32 to 0.33 [meter], and the species is small”. Vaillant (1872) revised the latter material and gives a complete description of new specimens (referred to *Crocodylus gracilis*). *Crocodylus gracilis* is today considered a junior synonym of *Diplocynodon ratelii*, following more formal diagnoses from Berg (1966) and subsequent studies (e.g. Brochu, 1999; Brinkmann & Rauhe, 1998). Despite a fossil record that has become increasingly richer since the earliest works, a thorough redescription and update of the taxon diagnosis is critically lacking. Future studies on this matter should include the several recent finds from other European localities (Diaz-Araez et al., 2016; Luján et al., 2019; Chroust et al., 2021).

Diplocynodon remensis Martin, Smith, de Lapparent de Broin, Escuillié & Delfino, 2014

(Plate 1I)

Type material:

MHNF F BR 4020 (holotype), a fragmented skull.

Type locality:

Mont de Berru (Champagne, France).

Geological stage and age:

Upper Paleocene, late Thanetian (MP 6), 57 Ma.

Diagnosis:

Diplocynodon remensis belongs to *Diplocynodon* by the combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- presence of two parallel ridges creating a recess on the lateral wall of the premaxillary notch;
- splenial participation in the mandibular symphysis.

Comments:

The oldest taxon, *Diplocynodon remensis*, is the only species of *Diplocynodon* recognised from the Paleocene (Thanetian). The material referred by Martin et al. (2014) from the Mont de Berru locality consists of one complete and two partial skulls, along with numerous disarticulated remains (cranial and postcranial). We confirm the reproducibility of the taxon diagnosis here and did not alter it. Paleocene localities with vertebrate assemblages (e.g. Hainin, Belgium; Walbeck, Germany) are relatively rare in Europe and so far did not yield any additional and identifiable *Diplocynodon* remains.

Diplocynodon ungeri (Prangner, 1845)

(Plate 1A)

Type material:

UMJ 1774 (holotype), a partial rostrum.

Type locality:

Vordersdorf and Schöneegg (Styria, Austria).

Geological stage and age:

Middle Miocene, early Langhian (MN5), ca. 16–15 Ma.

Diagnosis:

Diplocynodon ungeri belongs to *Diplocynodon* by the combination of characters diagnosing the genus (presented above). It differs from all other *Diplocynodon* species by the combination of the following characters:

- the anterior process of the palatine is thin (laminar);
- the snout remains comparably narrow throughout ontogeny (shared with *D. ratelii*).

Comments:

Diplocynodon ungeri was erected by Martin & Gross (2011) as a new combination of specimens from the Miocene of Styria (Austria), previously referred to the previously described species *Enneodon ungeri*, *Diplocynodon (Crocodylus) styriacus* and *Diplocynodon (Crocodylus) steineri*. Additional material from France (Bézian, Ginsburg & Bulot, 1997) was referred to *Diplocynodon ungeri* by the authors, including a complete skull. The latter specimen however shows a significant contact between the anterior process of the nasals and the posterior region of the external nares, diagnostic character of *D. ratelii* and absent in *D. ungeri*. Given the clear presence of this character in the skull from Bézian, the specimen should rather be attributed to *D. ratelii*. Other Miocene localities in Europe yielded material attributed to *D. ungeri* (or indicated as *D. styriacus*), but on the basis of isolated elements not identifiable beyond the genus if not family level. Additional crocodylian remains were previously reported in the southeast of Europe (Gračanica, Bosnia; Vasilyan, 2020), geographically close to the region of Styria (Austria), but the initial identification needs further testing (D. Vasilyan pers. com.).

Invalid species of Diplocynodon

Diplocynodon buetikonensis von Meyer (1855)

Type material:

PIMUZ, a fragmented skull and mandible with osteoderms.

Type locality:

Lindenberg, Büttikon (Canton Aargau, Switzerland).

Geological stage and age:

Upper Miocene, Tortonian (MN 9–12), ca. 11.6–7.2 Ma.

Comments:

The holotype and only specimen referred to *Diplocynodon buetikonensis* was dated to the Tortonian (Late Miocene) according to Berg (1966). In the latter work, the author pointed out the uncertain presence of the diagnostic paired canines on the dentary of *Diplocynodon*. An additional noticeable difference is the occurrence of longer than wide dorsal osteoderms, feature that is absent in the taxon. The anterior part of the snout is very narrow, with a larger incisive foramen compared to other congeneric taxa. We consider the evidence too weak in order to refer the species to *Diplocynodon*.

Diplocynodon elavericus Martin, 2010

Type material:

Rhinopolis B3, a fragmented skull and mandible with osteoderms.

Type locality:

Domérat (Allier, France).

Geological stage and age:

Upper Eocene, middle Priabonian (MP 18–20), ca. 36–34 Ma.

Comments:

Diplocynodon elavericus is based on a fragmented skull, a mandible and few osteoderms. Elongated quadrate rami and a pterygoid–palatine suture located at the posterior angle of the suborbital fenestra

are presented as autapomorphies by Martin (2010). These characters however cannot be confidently recognised in the specimens Rhinopolis B3:

- the length of the quadrate rami does not differ from the condition seen in other mature *Diplocynodon* (e.g. *D. hantoniensis*, NHMUK OR 30392; or *D. remensis*, CE 0001);
- the palatine–pterygoid suture intersects the suborbital fenestra at the posteromedial medial margin in all other *Diplocynodon*, but the pterygoids appear severely fractured at this level, obscuring the actual extent of the pterygoids relative to the posterior margin of the fenestrae. Comparing the right and left suborbital fenestrae, one could interpret the suture to be placed at the posteromedial corner on the right side, whereas it can be interpreted more anteriorly on the left side.

No additional material is referred to *Diplocynodon elavericus*, but as noted by Martin (2010), *Diplocynodon* cf. *hantoniensis* (from the early Oligocene of Dordogne, France; Vignaud et al., 1996) is also similar in size and shape (see comments in the previous section on *D. hantoniensis*). Both *Diplocynodon* cf. *hantoniensis* and *Diplocynodon elavericus* however differ from *Diplocynodon hantoniensis* by the shape of the sutural contact between the ectopterygoid and maxilla, and the absence of circumscribing ridge around the supratemporal fenestrae and orbits. We therefore consider that, given the current state of the art, *Diplocynodon elavericus* cannot be confidently considered as a valid species of *Diplocynodon*. We advise reference to Rhinopolis B3 as *Diplocynodon* sp. pending future comparative studies and/or discovery of additional material.

Diplocynodon gervaisi Gervais, 1859

Type material:

Osteoderms, an isolated hemimandible and a fragmentary skull.

Type locality:

Ronzon (Haute-Loire, France).

Geological stage and age:

Lower Oligocene, early Rupelian (MP 21), 33.5 Ma.

Comments:

Diplocynodon gervaisi (or *Saurocainus gervaisii*) is mentioned and figured by Gervais (1859: plate 57, Fig. 4) without providing any description or diagnosis for the taxon, but citing Aymard (1856) as a reference. Berg (1966) summarised the situation and provided a short description of two specimens from the same locality, previously illustrated by Zittel (1885:697): a skull, curated in the paleontological collections of the University of Munich (Germany; plate 2, Fig. 11 in Berg, 1966), and a partial hemimandible (Rz 33) housed at the Natural History Museum of Basel, Switzerland. As a matter of fact, additional postcranial disarticulated specimens are curated at the Natural History Museum of Bern, Switzerland (L. Macaluso pers. obs.) In the absence of original diagnosis and description, *Diplocynodon gervaisi* is considered a nomen dubium and *Saurocainus gervaisii* a nomen nudum. The specimens referred to the species should be regarded as *Diplocynodon* sp. pending further description.

Diplocynodon kintyktshensis Efimov, 1988

Type material

A fragmentary skull roof and an isolated osteoderm.

Type locality:

No precise locality is given. The material was discovered in the Kintykche Formation cropping out in the northern Priaralie region (Kazakhstan).

Geological stage and age:

Middle Miocene (no further indications).

Comments:

The absence of an adequate diagnosis, figure and more detailed description of the material published by Efimov (1988) lead researchers to disregard *Diplocynodon kintyktshensis* as a valid species. We advise

referring to the specimens of this locality as *Crocodylia* indet. given the absence of diagnostic characters pertaining to *Diplocynodon*, as well as the apparent conservative morphology of the different elements. This conclusion was also drawn by Kurochkin et al. (2015).

Diplocynodon tormis Buscalioni, Sanz & Casanovas, 1992

Type material:

IPS 36361 (= IPS 9001, holotype), ST-7066 and ST-344 (paratypes).

Type locality:

Salamanca province (Duero basin, Spain).

Geological stage and age:

Middle-Upper Eocene, Bartonian (MP14-16), ca. 41–38 Ma.

Comments:

We herein consider *Diplocynodon tormis* as invalid after the direct revision of the referred and figured material by Buscalioni, Sanz & Casanovas (1992). This is motivated by the following observations:

- 1) The diagnosis of *Diplocynodon tormis* is based on the paratypes STUS 344 and ST 7066, as the holotype does not preserve the posterior region of the skull; the paratypes and described material however do not differ in their morphologies from other *Diplocynodon* species.
- 2) First-hand study of the holotype of *Diplocynodon tormis* (IPS 36361) revealed that diagnostic features of *Diplocynodon* are undoubtedly different or absent from the latter specimen, such as the absence of a double pairs of canines, 4th and 5th dentary alveoli not being confluent, and an unknown condition for ventral osteoderms (paired or “bipartite” in *Diplocynodon*, but not preserved in the specimen here).
- 3) further differences between IPS 36361 and all other *Diplocynodon* species are evident: a frontoparietal suture that does not enter the supratemporal fenestrae, the posterior dentary and maxillary teeth are severely compressed mediolaterally and bear well-defined striations, and an

inconsistent ornamentation of the parietal between IPS 36361 and STUS 344 (and other species).

- 4) the dermoccipital projects backwardly, as described by Buscalioni & Sanz (1992) for STUS 344, but the occipital condyle is not obscured in dorsal view (as previously defined in the diagnosis); this can be verified in Figure 1B of Serrano-Martinez et al. (2019), while the condyle is cropped in Figure 1E.

We advise referring to all previously referred specimens as *Diplocynodon* sp. pending new comparative study of the material.

5. Discussion

5.1 *The most common crocodylian in the Cenozoic of Europe*

With 446 total entries (128 entries in PBDB and 318 in fosFARbase, counting overlapping occurrences, i.e. presence of a taxon per locality), *Diplocynodon* is one of the most frequently occurring crocodylian in the Cenozoic of Europe. In comparison, the larger crocodylian *Asiatosuchus* is only recorded 62 times (32 entries in PBDB and 30 in fosFARbase), or 90 times for *Tomistoma* spp. (29 entries in PBDB and 61 in fosFARbase). Notably, only *Crocodylus* spp. shows a higher count than *Diplocynodon* with a combined count of 515 occurrences (385 entries in PBDB and 130 in fosFARbase), with ~50% of these occurrences being younger than the Middle Miocene, and nearly all certainly not represent the genus as currently defined (Delfino et al., 2007; Delfino et al., 2020). The dominating record of *Diplocynodon* is firstly a quantitative consequence of its unmatched survivorship (in Eusuchia) throughout the Cenozoic, as more material could statistically be fossilised, but also a result of the qualitative appreciation of the specimens that lead to the waste-basket status of the taxon discussed later.

Our global review of *Diplocynodon* spp. occurrences was carried out with 169 occurrences fulfilling the criteria for the material survey (overlaps between both databases as well as entries unsupported by the literature were discarded), which represents 37.9% of the original total occurrences count. The results show that 39.1% of the latter 169 occurrences are solely based on a simple citation of

the genus in the literature (i.e. material is neither described nor figured; Figure 1A). This corpus of literature consists of faunal lists for localities or specialised articles focusing on other vertebrate groups that only mention the presence of *Diplocynodon* without stating the type of material, and/or why it is attributed to the taxon.

Occurrences supported by evidence are based on articulated and disarticulated material in the literature. Articulated material is reported in 34% of the supported occurrences, and 10.7% including multiple articulated specimens (Fig. 1A). On the other hand, disarticulated material is reported in 88.3% of these occurrences with evidence. Frequent in the case of crocodylians, isolated teeth are the most commonly recovered elements when it comes to reports including disarticulated material (70.3%). Old teeth are regularly shed and replaced during the animal's life (polyphyodonty), therefore statistically more likely to be discovered in the sediments, in addition to their higher resistance to alteration processes (Frey & Monninger, 2010). It is moreover worth noticing that one fifth of the reports of *Diplocynodon* disarticulated material are based on teeth alone (20.9%). Besides teeth, osteoderms are also highly represented in the sample, being present in 50.5% of occurrences reporting disarticulated material, and can be diagnostic if belonging to the ventral armour (characterised by a bipartite structure in *Diplocynodon*). Most reports of osteoderms however critically lack a specification of the type elements, including their count, in their descriptions and/or figures.

Regarding the taxonomic identification, *Diplocynodon* sp. represents 55% of the total number of occurrences, but nearly half of these occurrences lack evidence and are only based on simple citations (52.7%; Figure 1B). The remaining *Diplocynodon* sp. identifications are in majority based on medium-size disarticulated material (93.9%). It appears evident from our survey that *Diplocynodon* has been commonly used as a 'wastebasket taxon' that can include any indeterminate specimen bearing a generalist morphology. Less than half of the occurrences report material referred at species rank, among which 22.3% lack descriptions and figures, therefore rendering any identification irreproducible. Species occurrences citing informative literature are largely based on disarticulated material (53.9%), before relying on material including one articulated specimen (19.7%) or more abundant articulated remains (13.1%).

As such, most published studies attribute fragmentary, disarticulated crocodylian material to *Diplocynodon*, only in rare cases relying on diagnostic characters (in the latter cases a separate species is usually erected). It is necessary to stress-out here the importance of cautious taxonomic attribution, as a biased taxonomy can have a direct negative impact on larger scale diversity studies, through a series of escalating interpretations. First, attributing non-diagnostic and conservative material to the species level artificially encourages additional attribution of non-diagnostic material by the way of comparative anatomy, since vaguely similar elements can be included. When repeated enough times for a majority of the species, this cycle prevents an accurate reconstruction of the phylogenetic relationships in the group because of the high overlapping morphological variation of each character in the taxa. The genus definition therefore becomes a combination of morphological traits that encompass all species, but that may not be strictly applicable case by case. Second, this phenomenon introduces an abundance bias in the fossil record, making a particular taxon more common than the others, while this was not necessarily true from an ecological point of view. Third, it can mislead taxonomical research priorities, because there are virtually less chances for new information to be gained from specimens attributed to an abundant form. To remedy to the issues inherent to this practice, we advise consistent referral to the higher Linnean classification category in the case of tentative attribution of morphologically conservative material, such as teeth or osteoderms for crocodylians (unless specifically distinct such as bipartite osteoderms in *Diplocynodon*). At the cost of sample size, palaeobiogeographical reconstructions for a given taxon should be done using only the better supported occurrences that include valid evidence.

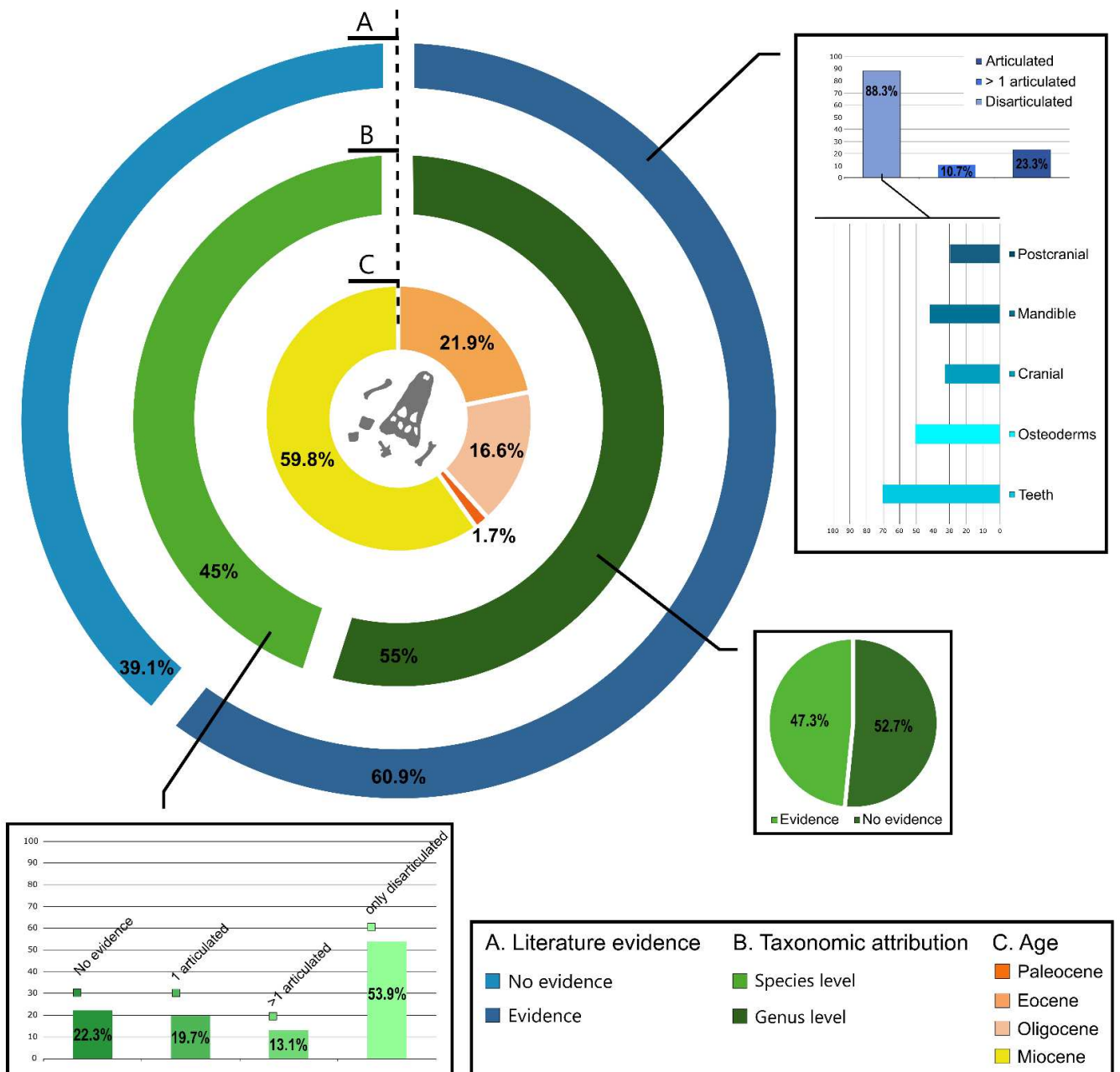


Figure 1: Combined graphics of *Diplocynodon* occurrences distribution in the Cenozoic. A, evidence ratios in the supporting literature. B, taxonomic attributions. C, age distribution.

5.2 Revised taxonomic diagnoses and diversity

As far as the valid species are concerned, the present paper provides a complete revision of their diagnoses. According to recommended taxonomic practices, an effective diagnosis would need to be as concise as possible in order to allow straightforward identifications of specimens at hand (among others Mayr, 1969; Dubois et al., 2021; Borkent, 2021). The literature concerning *Diplocynodon* reveals that taxonomic studies of the taxon either erect new species or refrain to refer the material (even if well-preserved and/or abundant) to an already published species, preferring an open nomenclature (Bengston, 1988; and see Appendix 2). Indeed, there are no report of studies that definitely attribute newly described material to an already published species, if not from a comparable geological age and area (the only exception being *D. darwini* reported from Messel and Geiseltal Lagerstätten). This phenomenon might be largely caused by previous convoluted and redundant diagnoses that rendered species-level identifications difficult to make, hampering paleobiogeographic and evolutionary relationships assumptions. The revised diagnoses are herein summarised in a comprehensive dichotomous key, to facilitate the identifications of *Diplocynodon* remains (Figure 2). As a general trend, many features listed in previous diagnoses were characters common to most (if not all) *Diplocynodon* species, or part of intraspecific variation. These characters are herein implemented in the revised diagnosis of the genus, where they better pertain.

The possible phylogenetic affinities of *Diplocynodon* and *Borealosuchus* pointed out by Walter et al. (2025; see Chapter 1) raises the additional question of the presence of the latter genus in Europe and the former in North America. Incomplete specimens bearing characters shared by both groups are classically assigned to each genus on the basis of their geographical origin (i.e. *Diplocynodon* for Eurasia and *Borealosuchus* for North America). May the two taxa be closely related, the recurrent practice of geography-based attributions introduces a bias in the fossil record that leads to circular reasoning in paleobiogeographical interpretations. A thorough reappraisal of the morphology and taxonomy of *Borealosuchus* is critical in this context in order to allow future straightforward identifications of both taxa in North America and Europe.

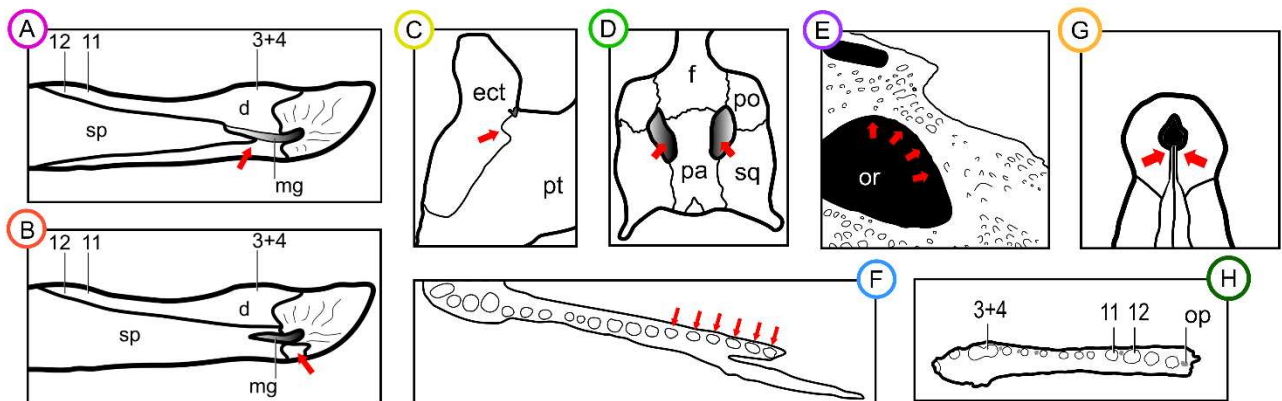
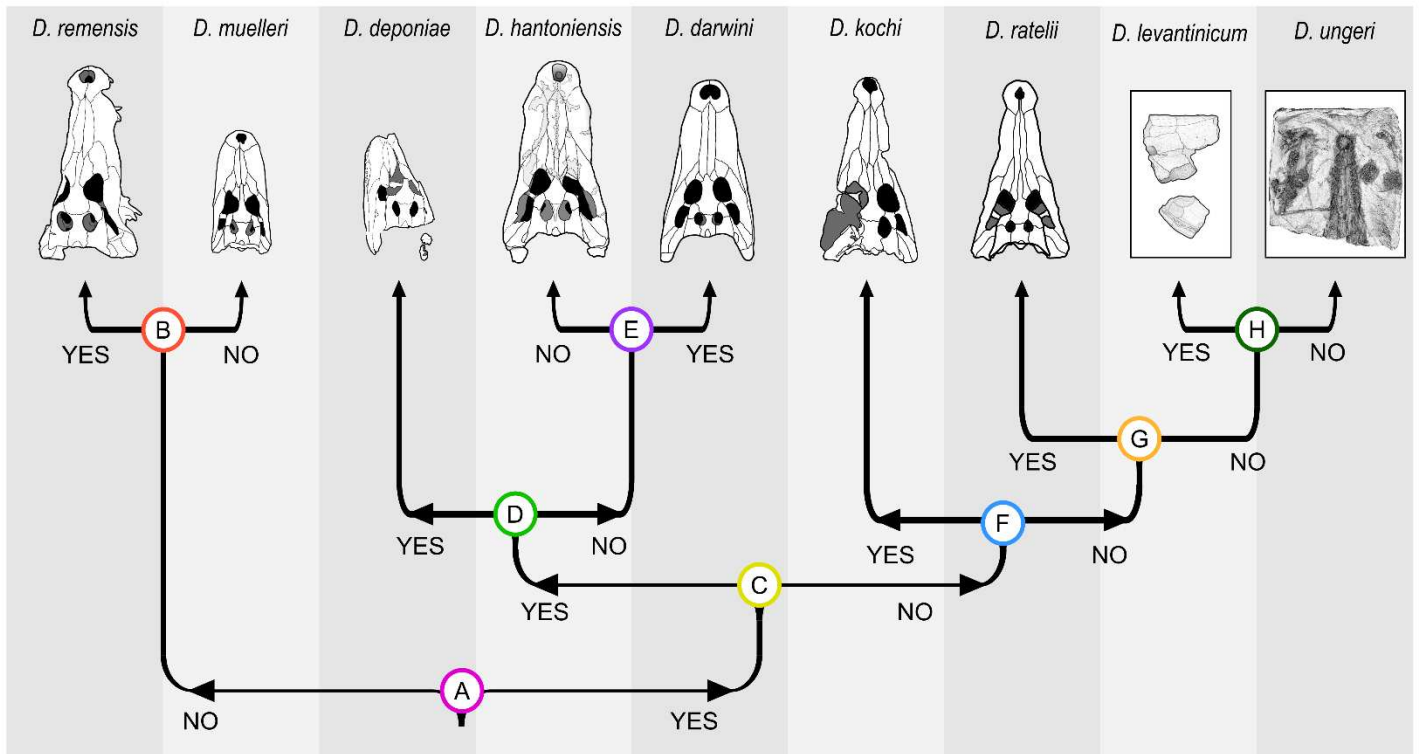


Figure 2: Dichotomous key for *Diplocynodon* (species order does not represent ingroup phylogenetic relationships). A, exclusion of the splenial from the mandible symphysis with its anterior tip passing ventral to the Meckelian groove; B, presence of a splenial symphysis; C, retention of the ectopterygoid-ptyergoid flexure at maturity; D, dermal bones of skull roof overhang the rim of supratemporal fenestra at maturity; E, absence of upturned orbital margins; F, posterior dentary teeth (caudal to 14th) are laterally compressed; G, nasals protrusion in the posterior margin of the external nares; H, presence of an occlusion pit posterior to the 14th dentary alveolus.

The taxonomic revision of *Diplocynodon* spp. conducted herein invalidates the species *Diplocynodon elavericus* and *Diplocynodon tormis* (to be added to the list of Paleogene invalid taxa; see Table 1). The characters proposed for the diagnosis of the former species currently do not allow to confidently distinguish it from the larger specimens of the other congeneric species. Concerning *D.*

tormis, its description is mainly based on the holotype, whose morphology significantly diverges from the diagnostic characters of the genus (see above for the list of diagnostic characters).

Our revision therefore concludes on nine valid species in the Paleogene out of the eleven previously proposed: *D. darwini*, *D. deponiae*, *D. hantoniensis*, *D. kochi*, *D. levantinum*, *D. muelleri*, *D. ratelii*, *D. remensis* and *D. ungeri*.

The Eocene epoch shows the highest diversity with four species (Figure 3), including the unique case of co-occurrence of two *Diplocynodon* taxa in a restricted geographical area (*Diplocynodon darwini* and *Diplocynodon deponiae* in the Lutetian age locality of Messel). It is one of the rare examples of syntopic extinct species (Scheyer et al., 2013; Wilson & Parker, 2023), which may well have been achieved by the dwarfism and acquisition of a derived posterior dentition in *Diplocynodon deponiae*, and the latter can reflect the occupation of a specialised ecological niche as in the case of *Acynodon adriaticus* (Delfino et al., 2008), *Gnatusuchus pebasensis* (Salas-Gismondi et al., 2015) or *Alligator munensis* (Darlim et al., 2023).

In the Oligocene, several occurrences argue for the presence of *Diplocynodon* aside from *D. levantinum* and *D. muelleri* (see Appendix 2.1). Brinkmann & Rauhe (1998) published a nearly complete specimen from Oligocene horizons of Céreste (southern France) that they attributed to *Diplocynodon* cf. *ratelii*. This attribution is rather uncertain given the incomplete description and figures of the specimen, in addition to the absence of a catalogue number. *Diplocynodon ratelii*, the type species of *Diplocynodon*, was erected by Pomel (1847) on the basis of Miocene specimens from Saint-Gérand-le-Puy (Allier, France), and most of the material attributed to the taxon was found in strata of approximately the same age (Diaz Araez et al., 2017; Chroust et al., 2021). A thorough study of potentially well-preserved *Diplocynodon* specimens (currently unpublished) from France (JDW pers. obs.) may eventually confirm the presence of *Diplocynodon ratelii* in the Oligocene, or possibly extend

the paleobiogeographic range of the two valid species being currently recorded in this epoch (Figure 3; *D. muelleri*, Spain; *D. levantinum*, Bulgaria).

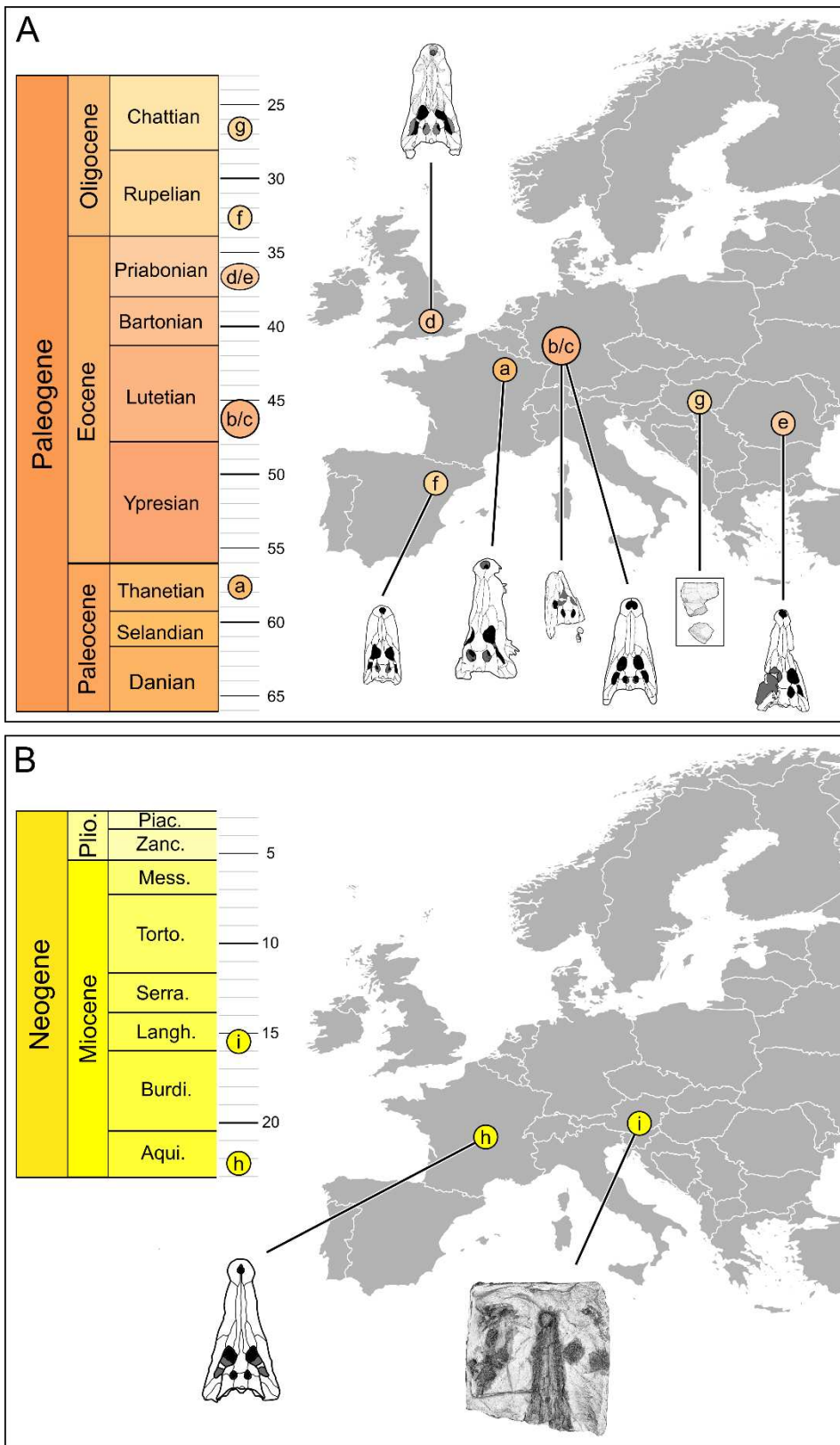


Figure 3: Spatiotemporal distribution of *Diplocynodon* in the Cenozoic. A, Paleogene: a. *Diplocynodon remensis* (after Martin et al., 2014); b. *Diplocynodon deponiae* (after Delfino & Smith, 2012); c. *Diplocynodon darwini* (after Ludwig, 1877); d. *Diplocynodon hantoniensis* (after Rio et al., 2020); e. *Diplocynodon kochi* (after Venczel & Codrea, 2022); f. *Diplocynodon muelleri* (after Piras & Buscalioni, 2006); g. *Diplocynodon levantinum* (after Massonne & Böhme, 2022). B, Neogene: h. *Diplocynodon ratelii*; i. *Diplocynodon ungeri* (after Martin & Gross, 2011).

The diversity of *Diplocynodon* in the Neogene is in contrast with the Paleogene peak, consisting of the two species, *D. ratelii* and *D. ungeri* from the Early and Middle Miocene respectively (Figure 3). According to the PBDB and fosFARbase databases, the number of Miocene occurrences however largely dominates the record (Figure 1C). The critical lack of a modern osteological description of *D. ratelii* however prevents attribution of isolated material to the species when new material is not found in correlated geological layers. Reappraisal of specimens with indeterminate and/or debatable taxonomic attribution has the potential of enhancing the study of morphological variation in greater details, and further investigate whether *D. ratelii* and *D. ungeri* were co-occurring geographically during a given time period. According to the current state of the fossil record, the extinction of *Diplocynodon* in the Early to Middle Miocene appears clear, as no valid attributions with identifiable evidence have ever been reported later than the Langhian.

Plate 1

Type material of valid *Diplocynodon* species. A. *Diplocynodon ungeri* (UMJ 1774, holotype); B. *Diplocynodon deponiae* (SMF-Me 899, holotype); C. *Diplocynodon levantanicum* (NMNHS 31-1; lectotype); D. *Diplocynodon muelleri* (NMB Spa 4, holotype); E/F. *Diplocynodon ratelii* (MNHN SG 539 / original illustration of the holotype by Pomel, 1847 – specimen); G. *Diplocynodon hantoniensis* (NHMUK OR 25166, holotype); H. *Diplocynodon kochi* (UBB V. 1453, holotype); I. *Diplocynodon remensis* (MNHN F BR 4020, holotype); scale

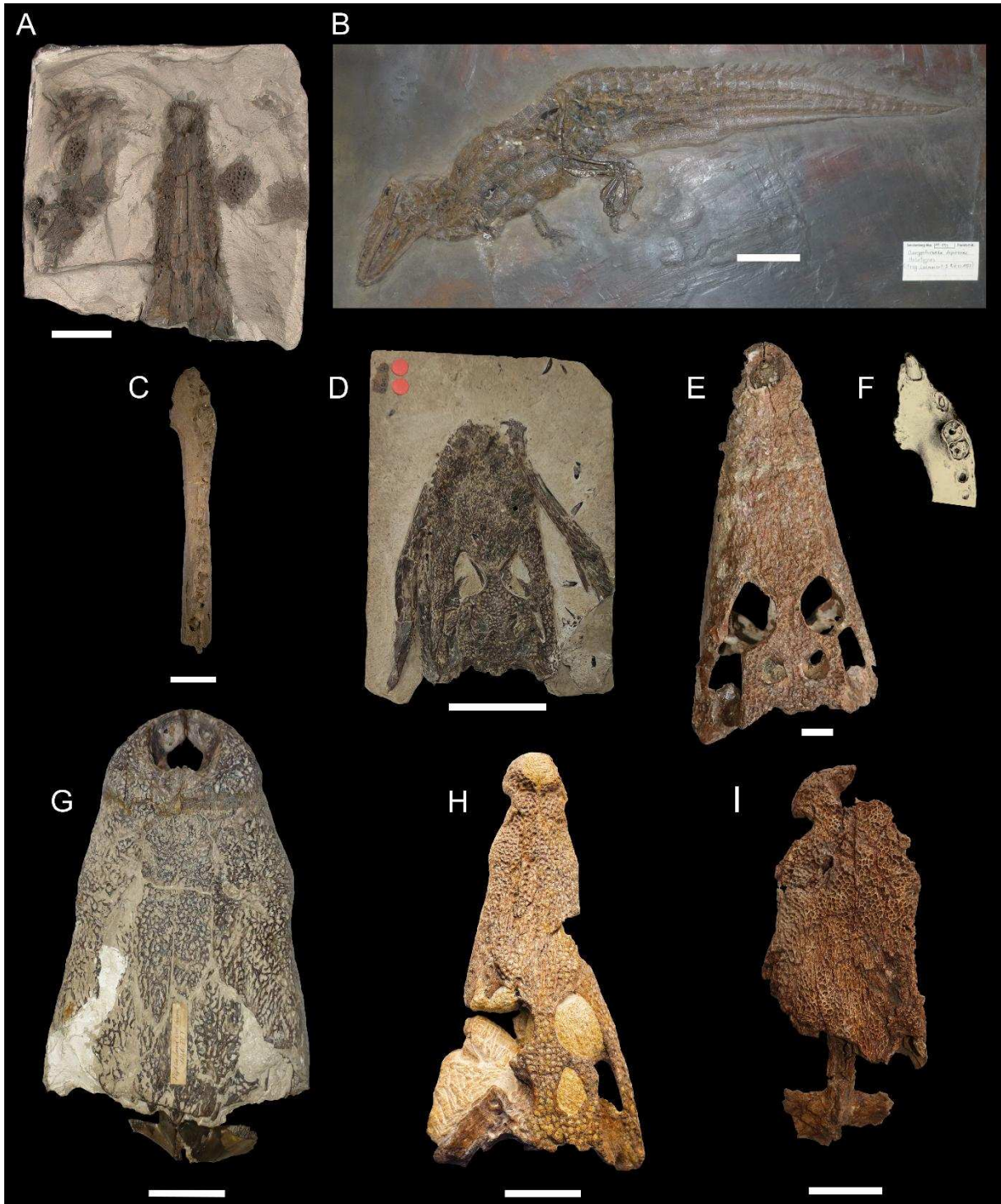
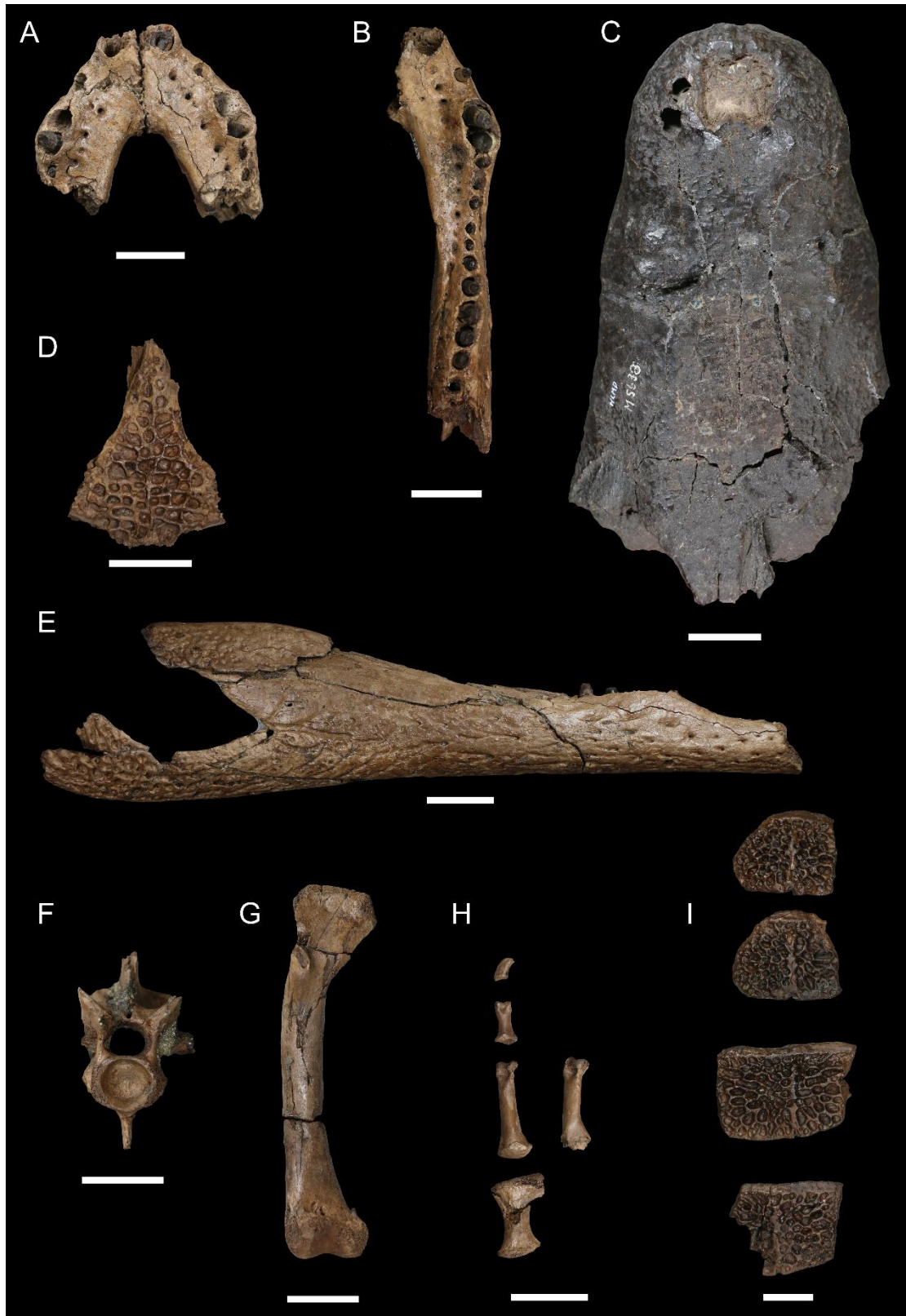


Plate 2

Selected type material of *Diplocynodon darwini*. A, HLMD-Me 5366; B, HLMD-Me 5360 (lectotype); C, HLMD-Me 5638; D, HLMD-Me 5348; E, HLMD-Me 5361; F, HLMD-Me 6004; G, HLMD-Me 5902; H, HLMD-Me 3033; I, HLMD-Me 6015; scale bars = 2 cm.



CHAPTER 3: Redescription of *Diplocynodon darwini* from the middle Eocene of Germany and evolutionary relationships in the group

1. Introduction

European crocodyliform faunas of the early Paleogene greenhouse were particularly diverse, including several members of the crown clades Longirostres and Alligatoroidea. Notably, the fossil record of the mid-sized generalist taxon *Diplocynodon* is particularly extensive (see Chapter 2 and references therein). The taxon was previously also reported from the Paleogene of North America (*Diplocynodon stuckeri* Mook 1960), before the specimen was synonymised with the ‘Northern Crocodile’ *Borealosuchus*, currently known from six species ranging from the Late Cretaceous to the middle Eocene of North America (Gilmore, 1910; Mook, 1959; Erickson, 1996; Brochu, 1997; Wu et al., 2001a; Brochu et al., 2012; Lindblad et al., 2022). Both genera indeed share notable characters that might pertain to a common ancestor, though most eusuchian phylogenies currently place *Diplocynodon* spp. as a monophyletic group of early-branching alligatoroids (Martin et al. 2014; Massonne et al., 2019; Groh et al., 2020; Rio & Mannion, 2021) but see Chapter 1 (Walter et al. 2025; Chapter 1) for an alternative topology. Recent studies have extensively tested and discussed the interrelationships of the group but failed at retrieving any topological consensus (Brochu, 1999; Martin, 2010; Brochu et al., 2012; Delfino & Smith, 2012; Martin et al., 2014; Rio et al., 2020; Rio & Mannion, 2021).

The continuous presence of *Diplocynodon* in Europe from the late Paleocene to the middle Miocene produced a rich fossil record, from which numerous species were erected and seven currently considered valid (see Chapter 2). The taxon disparity was studied relatively recently through a series of revisions (Piras & Buscalioni, 2006; Martin, 2010; Martin et al., 2011, 2014; Delfino & Smith, 2012; Rio et al., 2020), with however the notable exception of the middle Eocene species *Diplocynodon darwini* Ludwig, 1877 from the Konservat-Lagerstätte of Messel (Germany).

The paratropical Lake Messel was an open and warm environment hosting a rich biodiversity, today fossilised in the pit’s oil-shale layers (Schaal & Ziegler, 1988; Smith, 2021; Smith et al., 2024). Together

with plants (Wilde, 2018) and invertebrates (Wedmann, 2018), several well-preserved vertebrates were recovered from the sediments, such as mammals (Franzen et al., 2009, 2015), birds (Mayr, 2017), fishes (Micklich, 2012) and crocodyliformes (Brochu & Miller-Camp, 2018). The latter are notable vertebrates found at the Messel Pit as they show an exceptional diversity for a single fossil site, including the two alligatorines *Allognathosuchus* and *Hassiacosuchus*, two unrelated terrestrial forms *Bergisuchus* (sebecosuchian) and *Boverisuchus* (planocraniid), the large sized crocodyloid *Asiotosuchus*, and the above-mentioned *Diplocynodon* (Chapter 1 and 2; Smith et al., 2018). Two separate *Diplocynodon* species are known from Messel: the medium-sized *Diplocynodon darwini* Ludwig, 1877 and the short-sized and heavily armored *Diplocynodon deponiae* (Delfino & Smith, 2012). Originally described as two separate species, *Diplocynodon darwini* today embodies the previously erected *Alligator darwini* Ludwig, 1877 (in honour of Charles Darwin), *Crocodylus ebertsi* Ludwig, 1877 and *Diplocynodon hallense* Kuhn, 1938 from Geiseltal (Germany). The validity and taxonomical status of the species was previously corroborated by Berg (1966), Rauhe & Rossmann (1995) and Brochu (1999) (see also Walter et al., Chapter 2), but the taxon critically lacks a modern reappraisal.

The present work aims at redescribing the species *Diplocynodon darwini* and report intraspecific variation between two distinct populations. We additionally provide here insights into morphological variability shared across *Diplocynodon* species. We further investigate the ingroup evolutionary relationships of *Diplocynodon* after the revision of the taxa scores in a eusuchian character-taxon dataset.

2. Geological settings

2.1 Messel Pit Konservat-Lagerstätte

The Messel Pit fossil site is located in the Hesse (Germany) region, north-east to the town of Darmstadt. This ancient Eocene lake formed after the initial creation of a maar consequently to earlier phreatomagmatic eruptions (Schulz et al., 2002; Mezger et al., 2013). Continuous input of sediments and biotic material in the crater slowly filled the anoxic bottom of the structure, where oil/bituminous

shale layers developed in large volumes (Goth, 1990; Bauersachs et al., 2014; Moshayedi et al., 2020). A series of research drillings were performed between from 1993 to 2006 in order to precisely date the formation of the maar, rate, and duration of sedimentation (Mezger et al., 2013). The maar formation was dated to be around 48.2 Ma by Lenz & Wilde (2014; 2018), and independent evaluations of the laminated sediments provided an average sedimentation rate of 0.14 mm/yr (Mertz & Renne, 2005; Lenz & Wilde, 2014, 2018). The chronostratigraphy of the sediments was recently reassessed, indicating a deposition period between 48.06 Ma and 47.22 Ma with an average sedimentation rate of ~0.2 mm/yr (Kaboth-Bahr et al., 2024).

2.2 Geiseltal Konservät-Lagerstätte

The Geiseltal Lagerstätte is located in the Saxony-Anhalt (Germany) region, south to the town of Halle (Saale). The Geiseltal succession formed from marsh sediments and fluvial material (Krumbiegel et al., 1983) that deposited in dominant layers of siltstones and claystones of variable thickness, intruded by thinner lignite strata. The fossiliferous horizons are found in coal seams intercalated in the claystones and sandstones beds (Haubold, 1989). Six lignite seams are recognised in Geiseltal, chronologically named lower lower coal or ‘Untere Unterkohle’ (LLC), lower middle coal or ‘Untere Mittelkohle’ (LMC), upper middle coal or ‘Obere Mittelkohle’ (UMC), upper sandstone/siltstone deposits or ‘Oberes Hauptmittel’ (UHM), lower upper coal or ‘Untere Oberkohle’ (LUC) and middle upper coal or ‘Mittlere Oberkohle’ (MUC; Lincke, 1977; Falk et al., 2022). The relative dating of these units was previously made by mean of mammal biochronology (Haubold & Hellmund, 1998; Franzen, 2005) and concludes to a total discontinuous span of ~ 6 Myrs in the Lutetian (Falk et al., 2022 Fig. 2), but otherwise challenged by taxonomical ambiguity for some key mammal species that consequently render biochronological correlations uncertain (see Ring et al., 2020).

Institutional abbreviations

GMH: Geiseltal Museum of Martin-Luther-University Halle-Wittenberg, Halle (Saale), Germany;

HLMD: Hessisches Landesmuseum Darmstadt, Darmstadt, Germany;

SMF: Senckenberg Museum Frankfurt, Frankfurt, Germany.

SYSTEMATIC PALEONTOLOGY

DIPLOCYNODONTINAE Brochu, 1999

DIPLOCYNODON Pomel, 1847

Type species: *Diplocynodon ratelii*, Pomel 1847

Diagnosis:

Diplocynodon is a medium-sized crocodyliform characterised by the unique combination of the following characters:

- the presence of paired canines both on the dentary (3rd + 4th teeth) and the maxillary (4th + 5th teeth);
- the 3rd and 4th dentary alveoli are confluent;
- the 3rd and 4th dentary alveoli occlude in a pit early in ontogeny;
- the ventral shield consists of bipartite osteoderms;
- the iliac blade is rounded and ventrodorsally deep;

DIPLOCYNODON DARWINI Ludwig, 1877

Alligator darwini Ludwig, 1877

Diplocynodon darwini Berg, 1966

Diplocynodon darwini Brochu, 1999

Diplocynodon darwini Walter, [Chapter 2]

Type material:

HLMD-Me 5360 (lectotype); HLMD-Me 3014, 3015, 3012, 3014, 3015, 3016, 3018, 3019, 3020, 3022, 3023, 3024, 3025, 3027, 3031, 3033, 3037, 3111, 3112, 3118, 3119, 3120, 3121, 3122, 3125, 5348, 5349, 5361, 5365, 5366, 5367, 5368, 5369, 5370, 5371, 5374, 5712, 5714, 5875, 5886, 5890, 5892, 5893, 5895, 5896, 5902, 5903, 5905, 5907, 5908, 5909, 5910, 5911, 5912, 5919, 5925, 6001, 6002, 6003, 6004, 6005, 6006, 6007, 6008, 6011, 6012 (paralectotypes).

Synonyms:

Crocodylus ebertyi Ludwig, 1877; *Diplocynodon hallense* Kuhn, 1938

Referred material:

An exhaustive list of specimens cited in the text is provided here (complete list of all the specimens studied first-hand is provided in Appendix 4): GMH XXXVI-524-1966; HLMD-Me 233, HLMD-Me 236, HLMD-Me 4423, HLMD-Me 5317, HLMD-Me 5349, HLMD-Me 5364, HLMD-Me 5368, HLMD-Me 5369, HLMD-Me 5605, HLMD-Me 5875, LMD-Me 5890, HLMD-Me 5907; HLMD-Me 5919; HLMD-Me 6001, HLMD-Me 6002, HLMD-Me 6004, HLMD-Me 6005, HLMD-Me 6006, HLMD-Me 6007, HLMD-Me 6008, HLMD-Me 6012, HLMD-Me 6015, HLMD-Me 6018, HLMD-Me 6026, HLMD-Me 6044, HLMD-Me 7500, HLMD-Me 7571, HLMD-Me 10262, HLMD-Me 10496,

HLMD-Me 10876, HLMD-Me 13729, HLMD-Me 14600, HLMD-Me 14926, HLMD-Me 16990, HLMD-Me 20336; SMF-Me 213, SMF-Me 896, SMF-Me 898, SMF-Me 900, SMF-Me 1137, SMF-Me 1341, SMF-Me 2748, SMF-Me 3780 and SMF-Me 10876.

Diagnosis:

Diplocynodon darwini belongs to *Diplocynodon* by the unique combination of characters diagnosing the genus (presented above).

It differs from all other *Diplocynodon* species by the combination of the following characters (Appendix 3, Figure S3):

- presence of a linear sulcus on the prefrontal, along the anteromedial margin of the orbit
- lack of osteoderms coverage on posterior section of the tail (i.e. the posterior two-thirds)
- the orbital margin flush with the circumscribing bones surface

This species is further characterised by:

- a retention of the pterygoid-ectopterygoid flexure (shared with *D. deponiae* and *D. hantoniensis*)

Description

General preservation

The description presented here is largely based on the exceptionally complete and well-preserved juvenile to adult specimens from Messel HLMD-Me 233, HLMD-Me 236, HLMD-Me 5317, HLMD-Me 7500, HLMD-Me 10262, HLMD-Me 10496, HLMD-Me 13729, HLMD-Me 14600, HLMD-Me 16990, HLMD-Me 20336, SMF-Me 213, SMF-Me 896, SMF-Me 898, SMF-Me 900, SMF-Me 1137, SMF-Me 1341, SMF-Me 2748, SMF-Me 3780 and SMF-Me 10876. Figures 2, 3, 9 and Figures S1 and S2 in Appendix 3 illustrate complete specimens on slabs. Deformation is generally characterised by dorsoventral compression: typically, the dorsal surfaces of the skull table and the rostrum are approximately at the same level. This results in a slight increase of the width proportions of the elements.

Complete specimens from Geiseltal however show further rework, as shown by general disarticulation of the limbs and full torsion of axial elements. The majority of the specimens are prepared, allowing 2D first-hand observation (or 3D for disarticulated and some exceptional articulated specimens). More rare specimens are still partly embedded in matrix and therefore not informative for the present description.

Skull

General shape:

The complete sample of specimens consists of three ontogenetic stages: juveniles, sub-adults and adults. Adult skulls are profusely ornamented and morphologically comparable to most other *Diplocynodon* species. The skull table is planar and the lateral edges of the rostrum are broadly parallel, exhibiting a partial overbiting dentition. The supratemporal and suborbital fenestrae are moderately large, similar in proportions to the morphology shown by *D. hantoniensis*. The orbit medial margins are flush with the surrounding bones surface.

Premaxilla:

The premaxillae are preserved in most of the complete individuals. They enclose the naris dorsally and, in the case of the most mature specimens, appear as an evident circumscribing swelling. This is similar to *D. hantoniensis*, although the latter species bears notches located posterodorsally to the nares (Rio et al., 2020). The posterior edge of the external nares variably bears a reduced indentation that projects into the trapezoidal opening of adult individuals of *D. darwini*. The posterior process of each premaxilla separates the nasal from the maxilla for a short distance, and reaches posteriorly to the level of the 2nd to 3rd maxillary alveoli. The premaxilla-maxilla suture intersects the lateral edge of the rostrum at the level of notch receiving the 4+5th dentary teeth. The premaxillae are profusely ornamented on their dorsal surface.

In palatal view, the premaxilla-maxilla suture is nearly straight, starting laterally from the interalveolar space between the 5th premaxillary and 1st maxillary alveolus, and intersecting the inter-premaxillary

suture in a perpendicular line. Adult and juvenile specimens have five premaxillary teeth, among which the 3rd and 4th are equally the largest, comparable in size to the 3rd and 4th maxillary ones. The 2nd alveolus is positioned closer to the 3rd than to the 1st, consequently to the presence of a large reception pit for the 1st dentary tooth lateral to the 1st premaxillary alveolus. The incisive foramen is rather small and teardrop shaped. A series of foramina punctures the bone immediately lingual to the alveoli.

Maxillae:

The maxillae are large rostral bones, contacting nasals medially for most of their length. Posteromedially, they contact the prefrontals and lacrimals. There, the suture is linear, no posterior maxillary process intrudes into the lacrimal. The ornamentation is similar to the premaxillae, without canthi rostralii nor elevated anterior boss. An evident festoon forms dorsally at the level of the 4th and 5th alveolus, making the maxillae appear broader on the rostrum. Immediately posteriorly, the lateral edge of the rostrum is gently concave. In palatine view, the maxillae meet medially and form the anterior corner of the suborbital fenestrae. The specimen HLMD-Me 5364 was sectioned sagittally during preparation, allowing to confirm the absence of caecal recesses, otherwise autapomorphic of *Crocodylus*. Regarding the dentition, a maximum of 19 alveoli was noted in the most complete specimens (e.g. HLMD-Me 7500, Figure 2). The bone is usually carved into a notch anterior to the 1st alveolus by the dentary canines (3rd + 4th teeth). The 4th and 5th maxillary alveoli are comparable in size and the largest of the toothrow. The completeness of the septum between the latter two alveoli varies among individuals, occasionally making both alveoli confluent. The concavity of the toothrow is noticeable from the level of the 6th alveolus in ventral view, and the toothrow becomes straight again posterior to the 8th alveolus. The 6th, 7th and 8th alveoli are further separated from each other than observed for the rest of the toothrow: notable occlusion pits at this level result from a local in-line occlusion with dentary teeth. Some specimens show a nearly in-line occlusion up to the 10th maxillary alveoli, with occlusion pits overlapping the alveoli necks.

Nasal:

The nasal separates the premaxillae anteriorly and are excluded from the external nares. The anteriormost tip ends at or nearly at the level of the premaxilla-maxilla notch. The anteroventral tips of the nasals occasionally pierce and intrudes into the nares due to the dorsoventral compression of the rostrum. Posteriorly, the nasal successively contacts the lacrimal and prefrontal laterally. The frontal anterior process separates the nasals medially for a short distance. The dorsal surface of the nasals is smoother than the surrounding bones: ornamenting pits are shallow and lengthened, nearly absent.

Jugal:

The jugal forms the ventral margin of the orbit and contacts the quadratojugal posteroventrally. It contacts the maxilla anteriorly in a broad convex suture running up to the lacrimal medially. The jugal process of the postorbital bar insets from the lateral margin, forming a shallow sulcus at the base of the bar. Anterior to the latter process, the medial jugal foramen is preserved in most complete isolated specimens, but its size differs among specimens. This variation is consistent across ontogenetic stages, as both juvenile and adult individuals appear to possess a large, medium or small foramen. Furthermore, some specimens bear up to two foramina, the second being consistently small. A large medial jugal foramen is also observed in *D. remensis* (Martin et al., 2014), *D. ratelii* (JDW pers. obs.) and variably in *D. hantoniensis* (Rio et al., 2020). Both the number and size of the foramina are not consistently similar on the left and right side of the skull.

In palatal view, the jugal contacts the ectopterygoid anteromedially at the level of the postorbital bar. The lateral jugal surface bears a similar ornamentation to the maxilla and premaxilla externally, while the medial surface is smooth.

Lacrimal:

The lacrimal forms the anterior margin of the orbit. It is bordered along its entire length by the maxilla anterolaterally and the nasal medially. As in all *Diplocynodon* species, the lacrimal is longer than the prefrontal and contacts the nasal medially immediately anterior to the prefrontal (Figure 1, 2 and 3).

Canthi rostrali and preorbital ridges are absent from the dorsal surface. In adult individuals, the lacrimal bears a more pronounced ornamentation than in other adjacent bones, taking the shape of a pitted shallow boss resulting from the pneumatization of the bone by the lacrimal duct opening on the anterior wall of the orbit.

Prefrontal:

The prefrontal forms the anteromedial margin of the orbits, contacting the lacrimal anterolaterally and the frontal and nasals posteromedially and anteromedially respectively. Prefrontals do not contact each other, being separated by the frontal anterior process and by the posterior processes of the nasals. A noticeable groove runs along the orbital margin (Figure 1, 2 and 3). This groove stops immediately anterior to the prefrontal-frontal suture and does not cross the inter-orbital bar. Most crocodylians, including *Diplocynodon*, bear variable ornamental features on the prefrontal surface: these features often take part in the formation of an interorbital bridge which, in the most derived cases, create a complete “spectacle” (e.g. *Caiman crocodilus*). The morphology observed in *Diplocynodon darwini* instead does not bear comparable structure, and the groove is strictly restricted to the prefrontal and does not uplift the anteromedial edge of the orbit.

Frontal:

The frontal is a robust bone forming the interorbital bar and anteromedial area of the skull table. Anterior to the orbits, the frontal separates the nasals posterior tips by sending a thin “v” shaped process, and no “step” is present as opposed to *Diplocynodon hantoniensis*. Posteriorly, it forms the anteromedial corner of the supratemporal fenestrae by contacting the postorbital laterally and the parietal posteriorly through linear sutures. The ornamented surface is restricted to the skull table area, while the anterior process is usually devoid of grooves or pits (Figure 1 and 2). The lateral edges forming the orbital margins flush with the skull surface, or only slightly uplifted in the most mature specimens. There is no interorbital bridge or “spectacle” crossing transversely on the frontal in *Diplocynodon darwini*, as in most congeneric species with the exception of *Diplocynodon hantoniensis*. In the latter species, Rio et

al. (2020) noticed a minimal step occurring on the frontal of the least mature specimens. In ventral view, the interorbital section of the frontal is excavated to receive the anterodorsal region of the cerebrum. Few specimens, among which HLMD-Me 10262 (Figure 3) preserved palpebrals: a single reduced, ossification is preserved in each orbit, similar to *Alligator mississippiensis*.

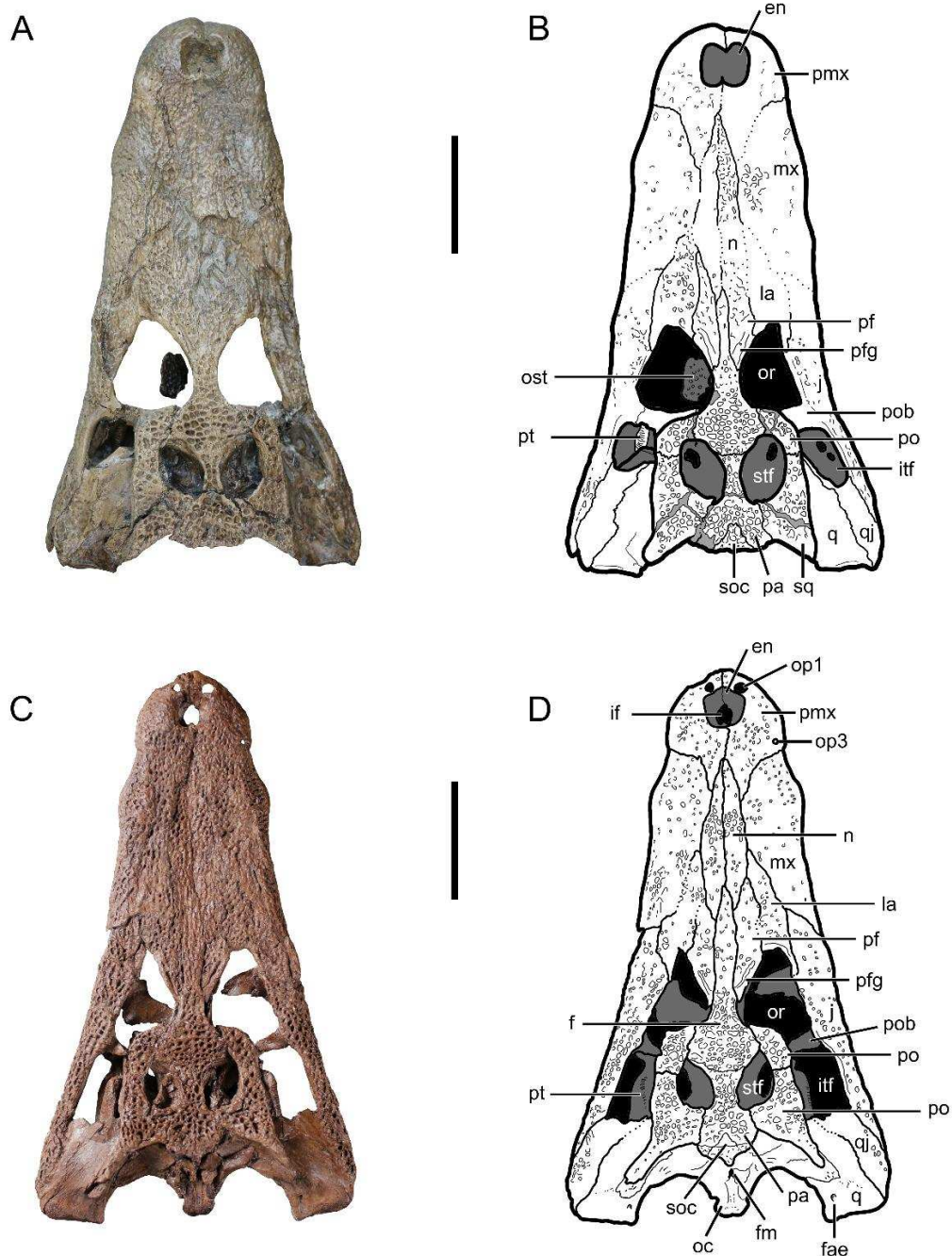


Figure 1: Skulls of *Diplocynodon darwini* (HLMD-Me 900, A-B, Messel; GMH XXXVI-524-1966, C-D, Geiseltal). Abbreviations: en, external naris; f, frontal; fae, foramen aërum; fm, foramen magnum; if, incisive foramen; itf, infratemporal fenestra; j, jugal; la, lacrimal; mx, maxilla; n, nasal; oc, occipital condyle; op1-3, occlusion pit for dentary tooth 1-3; or, orbit; ost, osteoderm; pa, parietal; pf, prefrontal; pfg, prefrontal groove; pmx, premaxilla; po, postorbital; pob, postorbital bar; pt, pterygoid; soc, supraoccipital; sq, squamosal; stf, supratemporal fenestra. Scale bars = 5 cm.

Postorbital:

The postorbital forms the anterolateral corner of the skull table, contacting the frontal medially, the squamosal posteriorly, and the jugal anteroventrally through the postorbital bar. The latter bar is rather thin and circular in cross-section, formed for most of its length by the postorbital which contacts the jugal process medially near its base. The ornamentation is well developed on the dorsal surface. One foramen pierces the anterior surface of the postorbital anterolateral corner in several specimens.

Parietal:

The parietal is a solid central bone of the skull table, contacting the frontal anteriorly along a mediolateral concavo-convex suture. The latter enters deeply into the supratemporal fenestrae laterally, before shifting anterolaterally on the medial wall of the supratemporal fossa, preventing any contact with the postorbital (Figure 1). The lateral edges of the parietal only minimally overhang the supratemporal fenestra and the medial wall of the fenestra is imperforate. The anteromedial corner of the supratemporal fenestrae are smoothly tapering anteriorly and flush with the skull surface. Most skulls preserving the posterior wall of the supratemporal fenestra display the parietal approaching the squamosal ventrally but not contacting it. Anteriorly, the parietal-laterosphenoid suture is horizontal. The dorsal surface of the parietal is planar and bears shallow pits and grooves.

Squamosal:

The squamosals form the posterolateral corners of the skull table, contacting the postorbital anteriorly and the parietal medially. There is no medial contact with the supraoccipital. The lateral edges of the squamosals are straight and parallel in mature specimens. Along the lateral surface of the bone, a subparallel dorsal and ventral rim bound the squamosal groove. Immediately ventral, the squamosal forms the dorsal and posterodorsal edge of the external auditory meatus. From this point, the squamosal contacts the quadrate along a dorsoventral linear suture. The squamosal prongs contact the paroccipital processes of the exoccipitals ventrally for a short distance. The squamosal dorsal surface is planar and

ornamented with pits and grooves of similar size than on the parietal and postorbital.

Supraoccipital:

The supraoccipital forms the medial posterior edge of the skull table and is enclosed by the parietal anteriorly and laterally. The bone is triangular in shape both in dorsal and posterior view, and is minimally exposed on the skull table in the largest specimens. The posterior edge of the supraoccipital is convex and slightly exceeds the posterior margin of the skull, giving the latter a slight concavo-convex outline in dorsal view. The posterior surface of the supraoccipital bears an evident sagittal crest erecting dorsally from the short dorsal overhang and fading ventrally into the posterior wall before reaching the sutural contact with the exoccipitals. Furthermore, the posterior wall surface of the supraoccipital bears two lateral processes that project slightly posteriorly, comparably to the sagittal crest. These processes are visible in dorsal view in some specimens, more specifically juveniles and subadult specimens (Figure 3B). Similar processes are also recovered in *Diplocynodon hantoniensis* (Rio et al., 2020). The ornamentation of the bone is often formed by two reduced and sagittally symmetrical grooves on the posteromedial region, surrounded by common shallow pits.

Quadrate:

The quadrate is the main bone of the ramus articulating with the lower jaw. Anteromedially, it sutures with the squamosal, preventing the exoccipital to be exposed laterally posterior to the external auditory meatus. At this level, the quadrate-squamosal suture flares dorsally along the straight posterior margin of the meatus. The quadratic ramus is rather long, as is the paroccipital process, which approaches the condyle. The quadrate foramen aëreum is located on the posteromedial part of the ramus, and is exposed on the dorsal surface of the latter. In posterior view, the quadrate condyle appears relatively large, with the dorsal and ventral edges being roughly parallel. Most specimens bear a medial hemicondyle that is slightly medioventrally directed, but the shape of the condyle may be subject to variation relative to the expansion of the medial notch (see character 118 and 119 in Rio & Mannion, 2021 for a discussion). A

thin anteroposteriorly directed crest is visible in ventral view, as the attachment surface for the posterior mandibular adductor muscle.

Quadratojugal:

The quadratojugal reaches the dorsal angle of the infratemporal fenestra and contacts the postorbital. The latter bone sends a short process ventrally into the quadratojugal. The quadratojugal forms the posterior angle of the infratemporal fenestra and sends a thin dorsal projection that contacts the postorbital, preventing contact between the quadrate and the postorbital. As in other *Diplocynodon* species, the spina quadratojugal is extremely reduced to completely absent. In rare specimens it takes the shape of a rounded knob placed at mid-height between the posteroventral and dorsal angles of the fenestra, comparable to *Leidyosuchus canadensis* (Wu, 2001). Anteriorly, the quadratojugal contacts the jugal along an anterodorsally directed linear suture. The posterolateral surface of the quadratic ramus is entirely hidden by the quadratojugal.

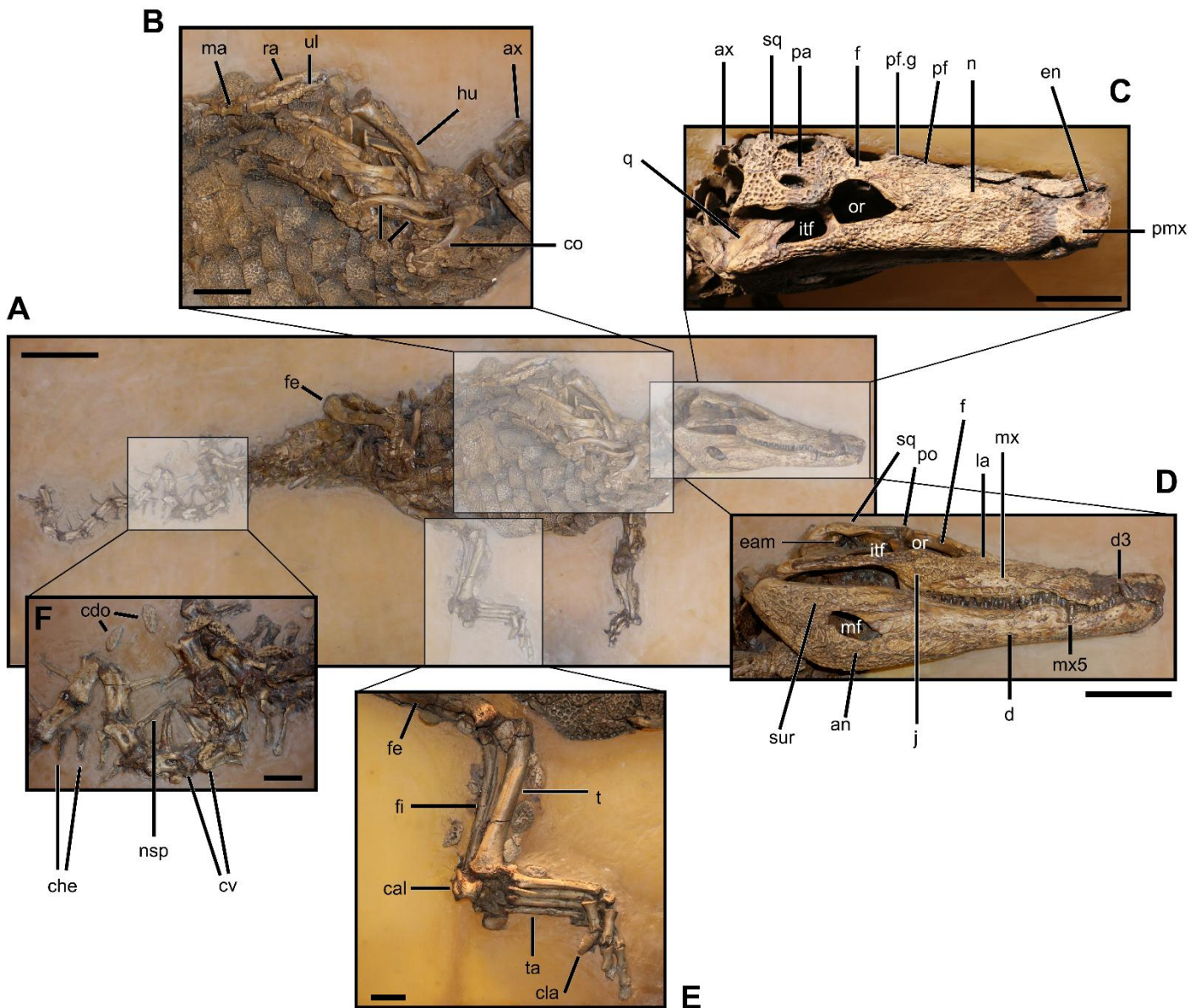


Figure 2: Articulated adult specimen of *Diplocynodon darwini*. A, HLMD-Me 7500 exposed ventrolaterally (scale bar = 10 cm); B, close-up view of thoracic region and pectoral girdle (scale bar = 5 cm). C-D, close-up view of the skull in dorsal and lateral views (scale bars = 5 cm); E, close-up view of the left hindlimb in medial view (scale bar = 2 cm); F, close-up view of the ultimate caudal vertebrae bearing osteoderms (scale bar = 2 cm). Abbreviations: an, angular; ax, axis; cal, calcaneum; cdo, caudal dorsal osteoderms; ch, choanae; che, chevrons; cla, claw; co, coracoid; cv, caudal vertebra; d, dentary; d3, dentary tooth 3; eam, external auditory meatus; en, external naris; f, frontal; fe, femur; fi, fibula; hu, humerus; itf, infratemporal fenestra; j, jugal; la, lacrimal; ma, metacarpals; mf, mandibular fenestra; mx, maxillary; mx5, maxillary tooth 3; n, nasal; nsp, neural spine; or, orbit; pa, parietal; pf, prefrontal; pf.g, prefrontal groove; pmx, premaxillary; po, postorbital; pt, pterygoid; q, quadrate; ra, radius; sq, squamosal; sur, surangular; t, tibia; ta, metatarsals; ul, ulna.

Palatine:

The palatines are long bones forming the medial border of the suborbital fenestrae. It contacts the pterygoid posteriorly along a mediolateral suture located at a short distance anterior to the posteromedial corner of the fenestra. Anteriorly, the palatine process projects up to the level of the 9th maxillary alveolus, and its tip is convex. There is a reduced lateral projection of the palatine along anteromedial margin of suborbital fenestra. The anterior process of the palatine however shows variation among the two populations: individuals from Messel locality bear a rounded bilobate suture with the maxilla, while Geiseltal specimens (where preserved) have a wider angled “V” shaped process. This process terminates slightly anterior to the suborbital fenestra, not further rostrally than 2 alveoli. The suborbital fenestra is devoid of palatine shelves, either anteromedially or posteromedially.

Ectopterygoid:

Only a few specimens preserve the ectopterygoid, even fewer in situ. The ectopterygoid approaches the medial wall of the last two maxillary alveoli, but does not contact the toothrow. The shape of the anterior suture is however unknown as the relevant area is not sufficiently well-preserved in any specimen. HLMD-Me 7571 and SMF-Me 898 were found with a sutural surface indicating a flexure in the ectopterygoid-ptyerygoid contact. This morphology is newly recognised in *Diplocynodon darwini*, and was recently acknowledged in two other *Diplocynodon* species, namely *Diplocynodon deponiae* and *Diplocynodon hantoniensis*. Posteriorly, the ectopterygoid stops before reaching the posterolateral tip of the pterygoid flange.

Pterygoid:

The pterygoid contacts the palatine anteriorly and the ectopterygoid anterolaterally. The bone is dorsoventrally long and forms the posterior and posterolateral margins of the suborbital fenestra. The pterygoid encloses entirely the choanae which is located further posteriorly from the level of the posterior margin of the suborbital fenestra. The lateral surface of the pterygoid is expanded dorsoventrally and rugous. The dorsal surface of the pterygoids could not be observed because of the absence of 3D specimens. The choanae, where preserved, are heart-shaped resulting from a short

invagination in its anterior margin and projects posteroventrally. The posterior margin of the choanae is positioned slightly anterior to the posterior margin of the pterygoid. The internal cavity of the choanae is septate and the septum remains recessed within the choanae is unknown. The anterior and lateral margins of the choanae are slightly upturned, but the degree varies among specimens, most presumably because of deformation. This morphology is also observed in *Diplocynodon deponiae* and *Diplocynodon hantoniensis*, but differs from the “neck” seen in osteolaemines which circumscribes the entire choanae. As in *Diplocynodon hantoniensis* and *Diplocynodon remensis*, thin crests directed anterolaterally are found lateral to the choanae.

Exoccipital:

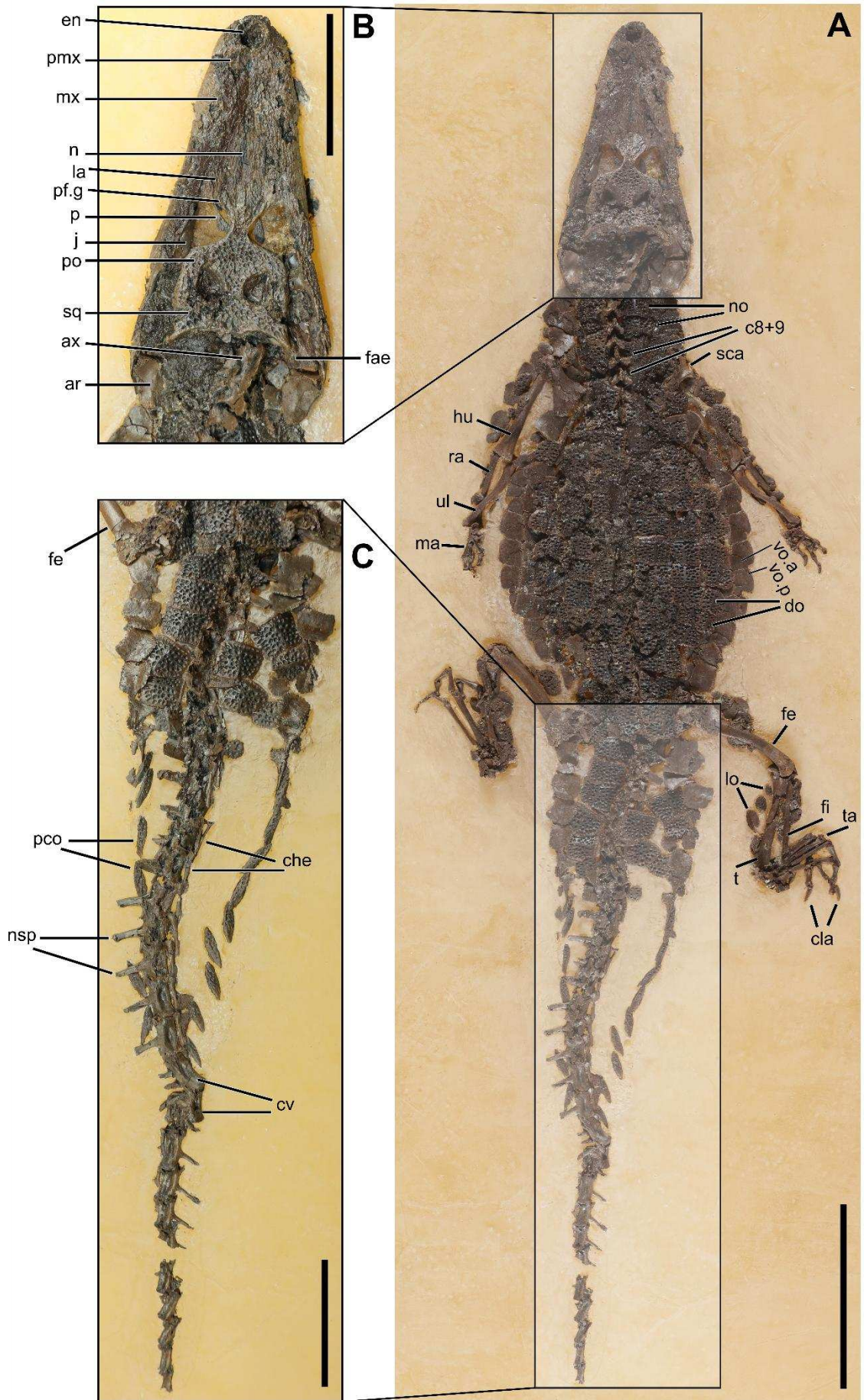
The exoccipital is exposed in posterior view and partially visible in dorsal view. The paroccipital process of the exoccipital sutures dorsally with the squamosal. Its lateral process is short and does not extend to the articular border of the quadrate condyle, without any projection in the paroccipital process. The exoccipital does not project far ventrally and does not contact the basioccipital tubera. The foramen magnum is oval in shape, bordered by the exoccipital dorsally and basioccipital ventrally. The ventrolateral surface of the exoccipital hosts several cranial foramina, the largest being the metotic foramen, located laterally at the level of the foramen magnum. The ventral portion of the exoccipital (otoccipital) is oriented vertically at maturity.

Basioccipital and basisphenoid:

Two isolated basicranium specimens were used to describe the following morphologies (HLMD-Me 5368, 5369). The basioccipital forms the ventral part of the skull in posterior view, immediately and ventral to the exoccipital. The exoccipital-basioccipital suture passes ventral to the lateral carotid foramen that is distinctly separated from the metotic foramen, located further ventrally. The lateral edges of the basioccipital are ventrally parallel and converge ventrally. A shallow concavity shapes the ventral margin of the basioccipital but is not comparable to the extreme state found in gavialoids. The

basioccipital tubera is slender and does not contact the exoccipital. Ventrally, the median eustachian foramen opens close to the basisphenoid-basioccipital suture. The lateral Eustachian canals open dorsolaterally to the median foramen. A short sagittal and thin crest runs dorsoventrally along the medial surface of the basioccipital ventral plate. The basisphenoid is exposed ventrally for a short distance in posterior view and hidden in ventral view. Most basicranium bones are consistently crushed in well-preserved specimens due to the common dorsoventral compression. The precise organisation between the basisphenoid and the surrounding bones could therefore not be observed and assessed.

Figure 3 (see below): Articulated sub-adult specimen of *Diplocynodon darwini*. A, HLMD-Me 10262 exposed dorsally (scale bar = 10 cm); B, close-up view of the skull in dorsal view (scale bar = 5 cm); C, close-up view of the ultimate caudal vertebrae bearing osteoderms (scale bar = 5 cm). Abbreviations: ar, articular; ax, axis; cal, calcaneum; ch, choanae; che, chevrons; cla, claws; co, coracoid; cv, caudal vertebra; d, dentary; d3, dentary tooth 3; eam, external auditory meatus; en, external naris; f, frontal; fae, foramen aërum; fe, femur; fi, fibula; hu, humerus; itf, infratemporal fenestra; j, jugal; la, lacrimal; ma, metacarpals; mf, mandibular fenestra; mx, maxillary; mx5, maxillary tooth 5; n, nasal; no, nuchal osteoderms; nsp, neural spine; or, orbit; pa, parietal; pco, posterior caudal osteoderms; pf, prefrontal; pf.g, prefrontal groove; pmx, premaxillary; po, postorbital; pt, pterygoid; q, quadrate; ra, radius; sca, scapula; sq, squamosal; sur, surangular; t, tibia; ta, metatarsals; ul, ulna.



Mandible

Dentary and dentition:

The dentary (Figure 4) forms most of the mandible length and hosts the complete toothrow. In lateral view, its dorsal surface is largely linear, with gentle concavity between the 4th and 10th alveoli. The dentary symphysis varies in length, but never reach further posteriorly than the level of the 4th alveolus. In medial view, the dorsal lobe of the symphyseal surface projects further posteriorly than the ventral counterpart.

The 1st dentary alveolus and tooth are generally projecting anterodorsally in *Diplocynodon darwini*, but the degree of projection can vary significantly, including strong procumbence in some specimens. As in all *Diplocynodon*, the 3rd and 4th alveoli are enlarged and confluent. This primitive morphology is shared with *Bernissartia fagesii*, *Borealosuchus* spp., *Leidyosuchus canadensis* and *Deinosuchus* spp. The alveoli are noticeably reduced in size immediately posterior to the 4th until the 11th and 12th which are similar in size to the 3rd and 4th. In lateral view, both pairs sit slightly higher than the rest of the toothrow.

Dentary and maxillary teeth occlude in a partial interlocking pattern. The 3rd and 4th dentary teeth form a pair of canines that occlude in a pit early in ontogeny, that later develops into a notch in adult specimens after carving the premaxilla-maxilla lateral surface. Posteriorly, the interalveolar space is enlarged between the 6th-7th, 7th-8th, and variably 8th-9th alveoli, for the in-line reception of the corresponding maxillary teeth. The dentary toothrow remains straight posterior to the 9th alveolus, and the respective teeth occlude lingually on the maxilla. All mandibular alveoli and teeth are circular in cross-section, with a very modest mediolateral compression for the ones posterior to the 12th alveolus. The first 13 dentary teeth are generally conical and acute, each bearing a distal and mesial carina. Posterior to the 13th dentary tooth, the teeth are slightly blunter and exhibit a ventral an easily identifiable constriction at the level of the crown-root contiguity.

Splénial:

The splénial runs along the medial surface of the dentary for most of its length. The dorsal edge of the bone is linear. The medial surface of the splénial is smooth and devoid of foramen for the cranial nerve V anteriorly. The splénial is excluded from the mandibular symphysis as in all *Diplocynodon* species except *Diplocynodon remensis*, in which the splénial participates in the symphysis. In *Diplocynodon darwini*, the anterior-most tip of the splénial is located ventral to the Meckelian groove. In the posterior region, the splénial contacts the angular and coronoid but does not separate the latter bones.

Coronoid: The coronoid is unfortunately lost in most specimens, or only fragmentary in some isolated mandibles. The coronoid contacts the splénial anteriorly: the sutural contact with the latter bone is perforated by the small foramen intermandibularis medius.

Angular:

The angular contacts the dentary anteriorly through a long ventral process reaching the mandible midlength, and the surangular dorsally from the posterior margin of the external mandibular fenestra up to the posterolateral tip of the retroarticular process (HLMD-Me 5349). The angular is ornamented by pits and shallow grooves on its lateral surface, but shows no eversion of the ventrolateral margin.

Surangular:

The surangular forms the posterodorsal corner of the jaw. It contacts the dentary anteriorly beyond the posterodorsal corner of the external mandibular fenestra, and the angular ventrally at the posterior margin of the latter fenestra. The latter suture intersects the articular medially, dorsal to its ventral tip. Medially, the surangular-articular suture is straight, running anteroposteriorly along the contact surface of both elements, and is perforated by the lingual foramen for the articular and alveolar nerve (HLMD-Me 5349). Laterodorsally, the surangular sends a short projection that nearly reaches the dorsal tip of

the lateral wall of the glenoid fossa. The surangular posterior process does not reach the posterior tip of the retroarticular process, and is instead pinched out. In dorsal view, two sub-equal processes extend anteriorly on either side of the surangular foramen. Similarly to the angular, the lateral surface of the surangular is ornamented with pits and grooves.

Articular:

The articular sutures with the surangular and angular laterally along all its length. Posterodorsally, the retroarticular process projects posterodorsally and level with or exceeds the dorsal height of the posterior edge of the articular fossa in lateral view. The foramen aërum opens dorsolaterally on the medial margin of the articular (or “inset”). As in *Diplocynodon hantoniensis*, a thin ridge erects from the foramen aërum neck and projects posteriorly for a short distance before fading into the smooth dorsal surface of the articular fossa.

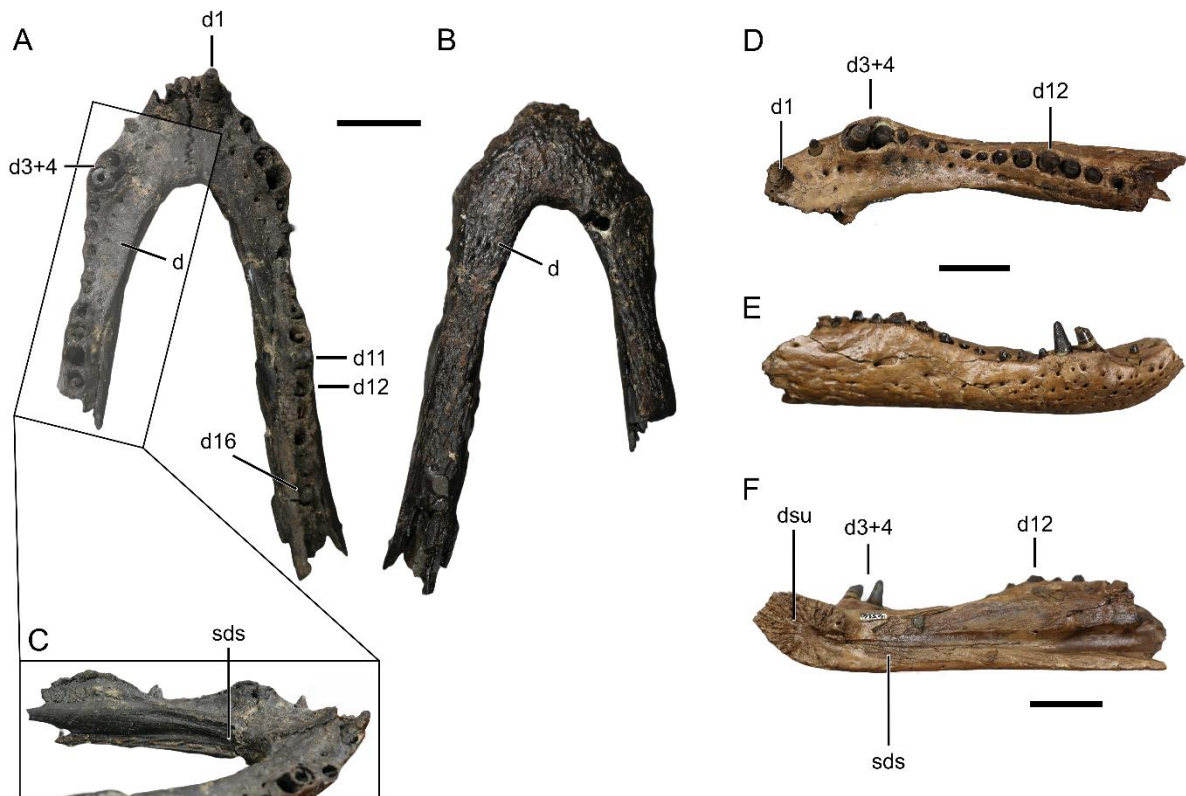


Figure 4: Lower jaw (HLMD-Me 4423; A-C) and right dentary (HLMD-Me 5360, lectotype; D-F) of *Diplocynodon darwini*. A, dorsal view; B, ventral view; C, dorsomedial view of the left dentary ramus; D, dorsal view; E, lateral view; F, medial view. Abbreviations: d, dentary; d1, d 3+4, d11, d12, d16, dentary alveolus position on the dentary; dsu, dentary symphysis surface; sds, splenial-dentary sutural surface. Scale bars = 2 cm.

Postcranial

Postcranial material of *Diplocynodon darwini* is well-preserved in complete and articulated specimens. Accurate observation of axial elements is however rendered difficult by the preservation of most complete specimens on slabs (in ventral or dorsal views), as well as the extensive osteoderm coverage. Description of the postcranial elements mostly rely on the multiple specimens exposed on slabs (Figure 2, 3, 6, 9 and Figures S1 and S2 in Appendix 3) and rare disarticulated bones (see Appendix 4 for a complete list of specimens).

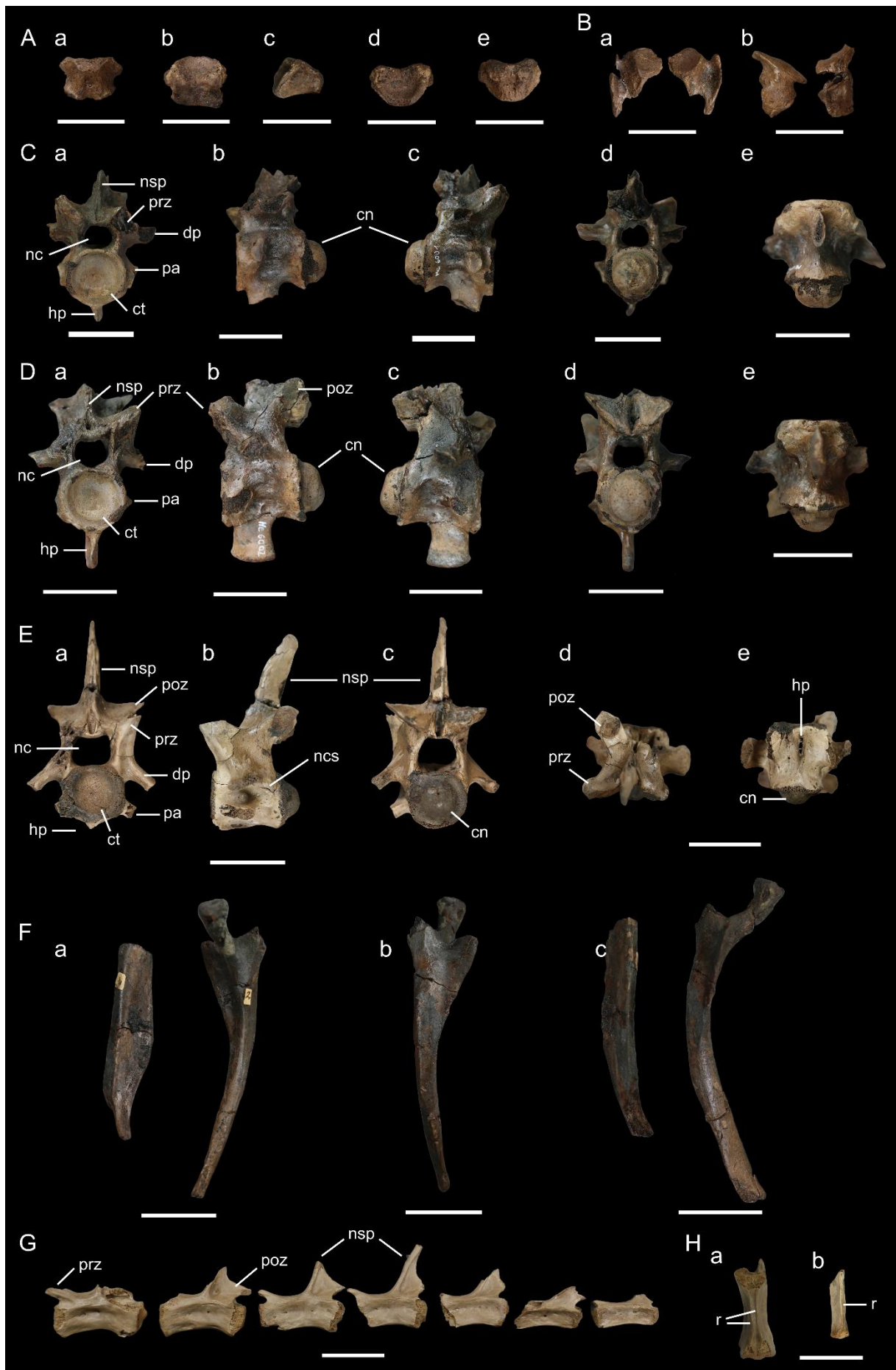


Figure 5: Disarticulated axial elements of *Diplocynodon darwini*. A, atlas intercentrum (HLMD-Me 5890); a, ventral view; b, dorsal view; c, left lateral view; d, anterior view; e, posterior view; B, atlantal ribs (HLMD-Me 5890); a, dorsal view; b, ventral view (lateral edge on top); C, cervical vertebrae (HLMD-Me 6001); a, anterior view; b, left lateral view; c, right lateral view; d, posterior view; e, ventral view; D, cervical vertebrae (HLMD-Me 6002); a, anterior view; b, left lateral view; c, right lateral view; d, posterior view; e, ventral view; E, posterior cervical vertebrae (HLMD-Me 6044); a, anterior view; b, left lateral view; c, posterior view; d, dorsal view; e, ventral view; F, anterior left dorsal ribs; a, anterior view; b, posterior view; c, medial view; G, series of 7 posterior caudal vertebrae; H, posterior caudal vertebrae presented in (G) in ventral view (note the width reduction); a, anterior vertebrae; b, posterior vertebrae. Abbreviations: cn, condyle; ct, cotyle; dp, diapophysis; hp, hypapophysis; nc, neural canal; ncs, neurocentral suture; nsp, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; r, ridge.

Proatlas, atlas and atlas intercentrum:

The proatlas and atlas were not observable in any complete individual, nor part of the disarticulated specimens. The atlas intercentrum is wedge-shaped (Figure 5A), condition shared with all non-alligatoroid crocodylians where preserved.

Axis:

The axis is preserved in 2 specimens illustrated here, HLMD-Me 7500 (Figure 2) and HLMD-Me 10262 (Figure 3). The neural spine is dorsoventrally high along its entire length, and its dorsal edge is horizontal up to its posterior tip. The position and morphology of the hypapophysis or axial ribs could not be determined in any of the specimens.

Cervical vertebrae:

Most cervical vertebrae were observable in dorsal or dorsolateral views (Figure 5C-E; HLMD-Me 6004/05/06/07/08, HLMD-Me 6026, HLMD-Me 6044). All isolated cervical vertebrae are prococleous and bear a prominent hypapophysis, when preserved. The respective position of each cervical can be assessed in complete specimens, but only in dorsal or ventral views. The neural spine of the 3rd cervical

vertebra is anteroposteriorly longer than the one of other cervicals, relatively to the centrum length. Posteriorly, the anterior extent of the hypapophysis of the 7th to 9th cervical vertebrae does not project further anteriorly than the ventral anterior margin of the centrum. The 8th and 9th cervicals are equal in length.

Dorsal vertebrae:

Dorsal vertebrae are preserved in most specimens, but are often covered by the dorsal shield, obscuring their exact location on the axial column. Most dorsal vertebrae have two medial foramina on the dorsal surface of the centrum, separated by a thin sagittal crest, visible through the neural canal. The neural spine is successively shifted posteriorly along the dorsal column: the 1st dorsal vertebra bears a neural spine located at mid-length in lateral view, while the last dorsal vertebra bears a neural spine located close to the posterior edge of the neural arch.

Sacral vertebrae:

As for all other crocodylians and eusuchians, *Diplocynodon darwini* has two sacral vertebrae. Their centrum is robust and slightly wider than other vertebrae. The wide ribs suture strongly to the lateral surface of the centrum. HLMD-Me 6012 are the only disarticulated sacral vertebrae available for three dimensional view, but are too poorly preserved to assess the respective extent of sacral ribs capitulum.

Caudal vertebrae:

The first caudal vertebra is biconvex in *Diplocynodon darwini* (HLMD-Me 10496), as in all extant crocodylians and most fossil eusuchians where known. All subsequent caudal vertebrae are procoelous. The centrum becomes progressively thinner mediolaterally along the tail and bear a shallow concavity on its lateral surface. This concavity becomes evident in the last vertebrae, making the ventral surface

of the centrum look constricted, and two thin ridges appear prominent on the ventrolateral surface of the centrum (HLMD-Me 6018; Figure 5G).

Transverse processes are present on caudal vertebrae until caudal vertebra 15. Articular surfaces for the chevrons are all fused in dorsal vertebrae posterior to the first caudal vertebra, visible in complete well-preserved specimens (HLMD-ME 10496, SMF Me 1137, SMF Me 1341, SMF Me 2748). The neural spine is located on the posterior part of the neural arch dorsal surface and projects posterodorsally. The postzygapophyses fuse into a single postzygapophysis in the posterior caudal vertebrae. This unique postzygapophysis is connected to the neural spine with a thin bony 'veil' (see Figure 5G).

Pectoral girdle:

Except from the most complete specimens, two scapulae (HLMD-Me 5905 and 5906) and three fragmentary isolated coracoids are preserved (HLMD-Me 5886, 5911 and 5912). The scapula and the coracoid are slender bones. The scapula bears a thin deltoid crest, but the blade itself is uniformly wide along its length. The articular facet of the coracoid is broad relative to the shaft width and ends in a pointed process anteriorly. The coracoid is pierced by a large foramen on its dorsomedial surface, anterior to the glenoid fossa (Figure 6Bb).

Forelimb:

The humerus is only slightly contorted, comparable to *D. hantoniensis* (Rio et al., 2020). The proximal margin of the deltopectoral crest emerges noticeably from the proximal end of the bone. Only a single scar for the attachment of the M. teres major and M. dorsalis scapulae was observed.

The ulna is relatively slender with a wide and rounded olecranon process. The proximal diaphysis is straight. The morphology of metacarpals in crocodylians is very conservative and do not, to our current knowledge, present any diagnostic differences across genera. The distal region of the forelimb comprises 5 digits among which number III being the longest (Figure 2, 3 and 6).

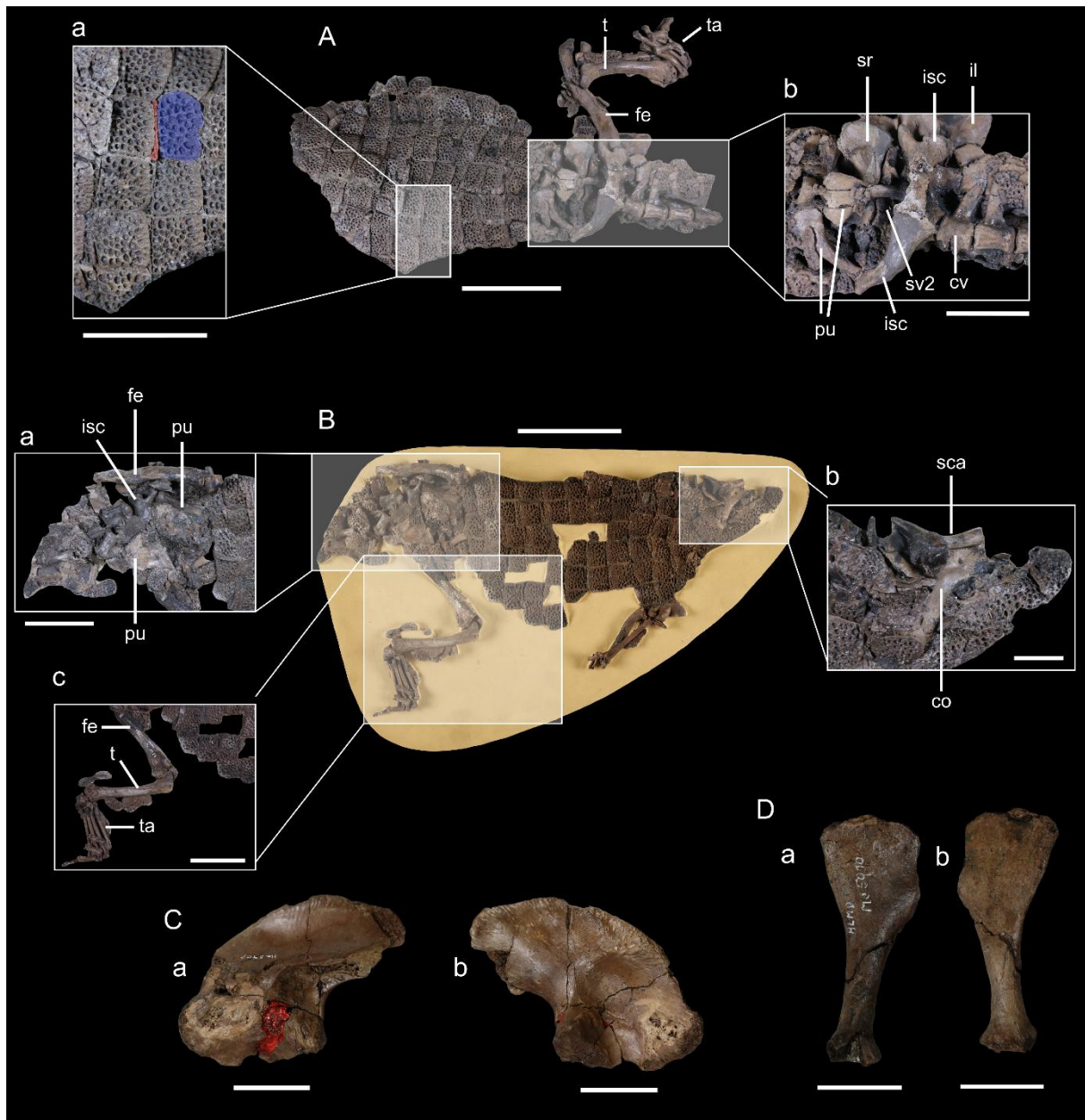


Figure 6: Articulated axial elements of *Diplocynodon darwini*. A, trunk region with pelvic girdle in ventral view (HLMD-Me 5605, scale bar = 10 cm); a, close-up view of the bipartite ventral osteoderms (anterior element in red, posterior element in blue, scale bar = 5 cm); b, close-up view of the pelvic girdle and first caudal vertebrae (scale bar = 5 cm); B, trunk region with pectoral and pelvic girdles in ventrolateral view (HLMD-Me 5605, scale bar = 10 cm); a, close-up view of the pelvic girdle and first caudal vertebrae (scale bar = 5 cm); b, close-up view of the pectoral girdle (scale bar = 2 cm); c, close-up view of the left hindlimb (scale bar = 5 cm); C, right ilium (HLMD-Me 5907, scale bar = 2 cm); a, dorsal view; b, medial view; D, left pubis (HLMD-Me 5910, scale bar = 2 cm); a, ventral view; b, dorsal view. Abbreviations: co, coracoid; cv, caudal vertebra; fe, femur; il, ilium; isc, ischium; pu, pubis; sr, sacral rib; sv2, sacral vertebra 2; t, tibia; ta, metatarsals.

Pelvic girdle:

The pelvic girdle is composed by the articulation of the ilium, ischium and pubis. The ilium preacetabular process is acute and pointed anteriorly. The dorsal margin of the latter bone is rounded and devoid of indentation. Diagnostic of *Diplocynodon*, the dorsoventral height of the postacetabular process is deep and projects posteriorly (HLMD-Me 5875; Figure 6C).

Hindlimb:

The hindlimb is generally longer than the forelimb (Figure 2, 3, 6 and 9). The femur has a reduced sulcus on its medial surface, ventral to the proximal epiphysis. The tibia and fibula are slightly curved bones and show no differences with the same bones described for other *Diplocynodon* species. As for metacarpals, the morphology of metatarsals in crocodylians is very conservative and do not, to our current knowledge, present any significant differences across genera.

Osteoderm coverage:

The dorsal shield is composed of six osteoderms in the nuchal region, and 6 middle transverse rows on the trunk at maturity. Midline dorsal osteoderms are rectangular in shape, bearing a well-defined but smooth median keel and an articular facet that is anterolaterally expanded (Figure 8A). Diagnostic of *Diplocynodon darwini*, caudal osteoderms only cover the anterior third of the tail (Figure 2, 3 and 9). No clear pattern was observed to explain the termination of the coverage, but it however seems that osteoderms are always absent posterior to ~ 1 to 3 vertebrae caudal to the ultimate vertebra bearing a transverse process. The caudal osteoderm coverage however does not evolve throughout ontogeny, as immature individuals already show a partially armoured tail (Figure 9). The ventral armor is made of bipartite osteoderms, diagnostic of the genus (Figure 3, 7, 8; Figure S1 in Appendix 3). The short anterior and squared posterior elements are connected through a straight mediolateral suture. The anterior element slides almost entirely under the anterior osteoderm (Figure 8D).

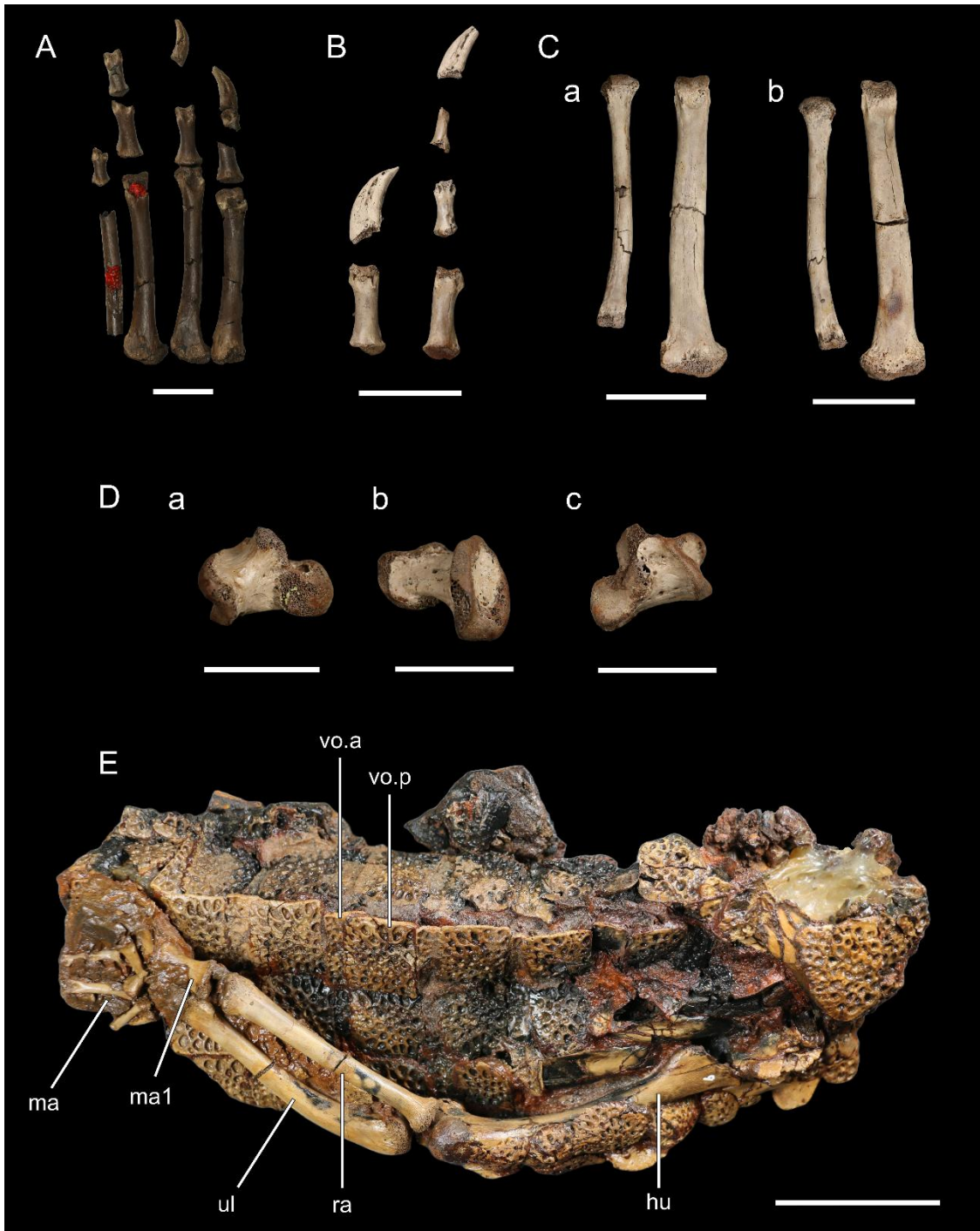


Figure 7: Disarticulated hindlimb elements and articulated forelimb of *Diplocynodon darwini*. A, right metatarsals and claws (HLMD-Me 5919, scale bar = 2 cm); B, ultimate left metatarsals (HLMD-Me 14926, scale bar = 2 cm); Ca-b, first left metatarsals (HLMD-Me 14926, scale bar = 2 cm); a, dorsal view; b, ventral view; Da-c, right calcaneum (HLMD-Me 14926, scale bar = 2 cm); a, ventral view (anterior part pointing to the left); b, dorsal view (anterior part pointing to the left); c, lateral view (anterior part pointing to the right). E, isolated articulated forelimb with anterior ventral osteoderms (HLMD-Me 14926b, scale bar = 5 cm). Abbreviations: hu, humerus; ma, metacarpal; ma1, metacarpal 1; ra, radius; ul, ulna; vo.a, anterior element of the ventral bipartite osteoderm; vo.p, posterior element of the ventral bipartite osteoderm.

Other

Gastroliths are often found among ventral osteoderms. In a large majority of cases, the gastroliths composition is dominated by smooth quartzite specimens white. One can hypothesise that the latter type of liths were intentionally selected for their hardness (as these represent the ultimate rock remains saved from erosion when reaching lowlands) and/or more easily distinguished in turbid environments by their colour.

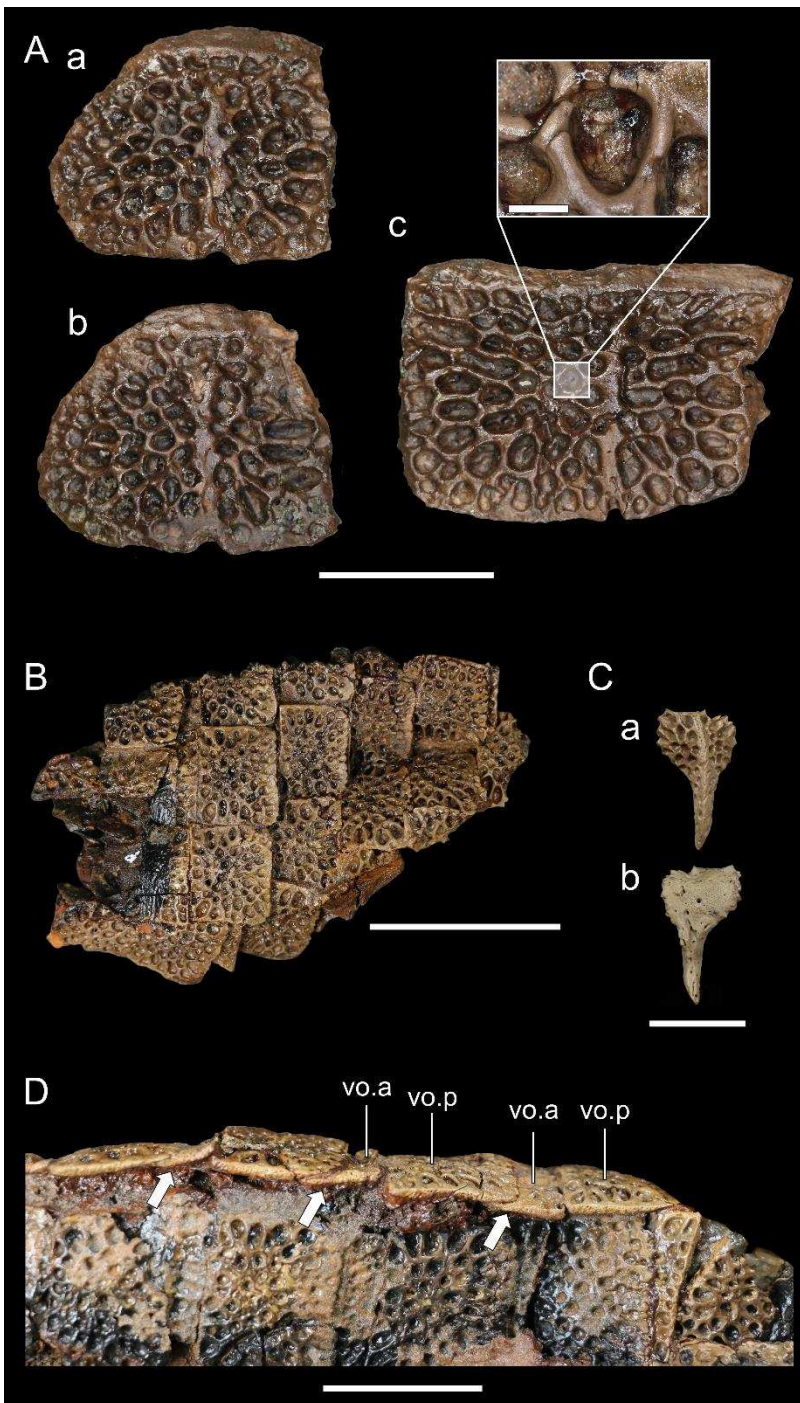


Figure 8: Disarticulated dorsal osteoderms and isolated section of ventral armor of *Diplocynodon darwini*. Aa-c, anterior dorsal osteoderms (HLMD-Me 6015, scale bar = 2 cm); a-b, left lateral dorsal osteoderms; c, anterior (right) medial dorsal osteoderm with a close-up of one of the pit (scale bar = 2 mm). B, isolated section of the ventral armor made of bipartite osteoderms (HLMD-Me 14926d, scale bar = 5 cm); Ca-b, posterior caudal dorsal osteoderm (HLMD-Me 6018, scale bar = 2 cm); a, dorsal view; b, ventral view; D, lateral view of the ventral osteoderms overlap organisation (arrows point at the anterior element covered by the successive posterior element, HLMD-Me 14926b, scale bar = 3 cm). Abbreviations: vo.a, anterior element of the ventral bipartite osteoderm; vo.p, posterior element of the ventral bipartite osteoderm.

Ontogeny

First-hand study of specimens from different ontogenetic classes (e.g. Figure 2, 3 and 9) allowed to identify a number of character states that evolve throughout ontogeny. These can be here used as a relative way to assess a given specimen's ontogenetic stage. These morphologies are as follows:

1. As recognised for other *Diplocynodon* species, the 4th dentary tooth occludes into a pit located between the premaxilla and maxilla early in ontogeny in *D. darwini*. In a majority of mature individuals, the canines eventually pierce through the dorsal surface of the bones and carve the original pit into an evident notch.
2. Juvenile specimens bear a thin crest circumscribing the external nares. This character is lost in mature specimens, where the dorsal surface of the narial opening is smooth. A narial crest is however known in adult specimens of *D. deponiae*, which may indicate a retention of the juvenile state in later ontogenetic states in this species.
3. The external nares opening projects dorsally early in ontogeny and progressively projects anterodorsally as the aperture changes shape (see point X).
4. The general skull shape evolves from an anteriorly tapering rostrum in juveniles to a stouter aspect in adults, with the maxilla lateral edges being parallel for most of their length. Posterior to the premaxillary-maxillary notch.
5. Morphological maturity in *Diplocynodon darwini* may have been acquired late in ontogeny. A majority of the cervical vertebrae studied in hand with a size comparable to adult elements showed a partially opened neurocentral suture, as also noted for *Diplocynodon hantoniensis* (Rio et al., 2020 fig. 14). Moreover, the scapula-coracoid complex is often preserved with the two constituting bones being disarticulated, which hints at a late closure of the synchondrosis.
6. The dentition of young individuals consists of sharp pointed teeth, nearly all equal in size. Throughout ontogeny, the canines become evidently developed, while the posterior teeth become increasingly blunt caudal to the 12th. The morphology however differs from *D. hantoniensis* and *D. deponiae* in which these teeth become more blunt (see Chapter 2).

7. In juveniles, the supraoccipital appears relatively larger, both in size and exposure on the dorsal surface of the skull. The supraoccipital may have a slower growth rate than surrounding bones during ontogeny, preserving its shape and size, slowly turning out to be modestly exposed in mature individuals.
8. The shape of the external nares evolves throughout ontogeny. The lateral sides of the external nares are broadly convex in the youngest individuals. The shape later evolves in a square in larger individuals identified as sub-adults. The external nares finally open and is flush with the premaxillae surface anteriorly. This gives the nares a trapezoidal shape in the largest individuals identified as adults.
9. Juvenile teeth are thinly striated (Figure 9), but this striation disappears throughout ontogeny as the enamel thickens.

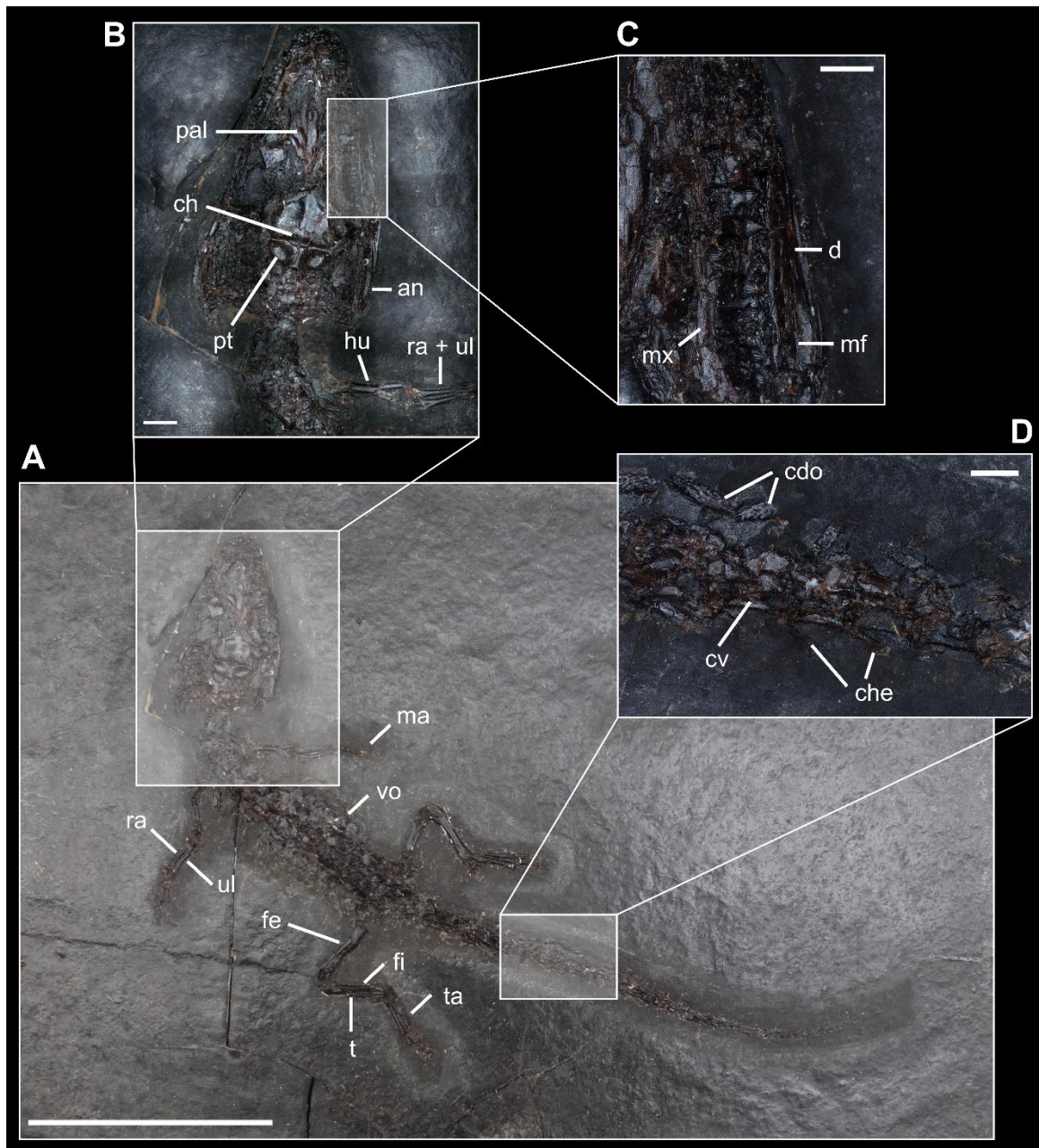


Figure 9: Articulated juvenile specimen of *Diplocynodon darwini*. A, HLMD-Me 5317 exposed dorsally (scale bar = 5 cm); B, close-up view of the skull region (the skull table and braincase were not preserved, scale bar = 4 mm); C, close-up view of the fragmentary right dentary and maxillary (scale bar = 2 mm); D, close-up view of the ultimate caudal vertebrae bearing osteoderms (scale bar = 2 mm). Abbreviations: an, angular; cdo, caudal dorsal osteoderms; ch, choanae; che, chevrons; cv, caudal vertebra; d, dentary; fe, femur; fi, fibula; hu, humerus; ma, metacarpals; mf, mandibular fenestra; mx, maxillary; pt, pterygoid; ra, radius; t, tibia; ul, ulna.

3. Phylogenetic analyses

3.1 Methods

The ingroup evolutionary relationships of *Diplocynodon* were tested using a modified version of two datasets:

- 1) Chabrol et al. (2024), expanded upon Rio & Mannion (2021); consisting of 26 continuous and 304 discrete morphological characters, among which 36 multistates characters are treated as ordered. Two versions of the dataset were used to run the analyses, one consisting of the quantitative characters treated continuously, and a second consisting of the quantitative characters treated discretely. Modifications of the dataset consists of changes previously implemented by Walter et al. (2025, Supplementary information; see Appendix 1) in Rio & Mannion (2021), and rescoreing *Diplocynodon darwini* and other valid *Diplocynodon* species already present in the dataset (following Chapter 2).
- 2) Walter et al. (2025; [Chapter1]), expanded upon Massonne et al. (2019); consisting of 219 discrete morphological characters, among which 11 multistates characters are treated as ordered. Modifications of the dataset consists of changes in the scoring of *Diplocynodon darwini* and other valid *Diplocynodon* species for corresponding characters modified in Chabrol et al. (2024).

The six most completely known and valid *Diplocynodon* species (see Chapter 2) served as operational taxonomic units (OTUs) to run two separate sets of parsimony phylogenetic analyses, using *Bernissartia fagesii* as an outgroup. The analyses were performed in TNT 1.6 (Goloboff & Catalano, 2008) under equal weighting and extended implied weighting (EIW3; k-value = 3), following Ezcurra et al. (2024, Table 2) for the choice of the k value. Given the reduced number of OTUs (7), the Traditional Search algorithm was used to obtain starting trees (Goloboff et al., 2008), with a number of replications set to 1000. A second round of search was run using only the starting trees (saved from RAM) in order to retrieve the final most parsimonious trees (MPTs). Figures 10-12 present the different consensus trees obtained from MPTs of each analysis set. The complete list of modifications and data files ([.tnt] for TNT 1.6) are provided in Appendix 3.

4. Results

The phylogenetic analyses yielded different results depending on the dataset and algorithms employed.

Parsimony analysis of the modified Walter et al. (2025) under EW recovered 4 MPT (tree length 88).

The strict consensus tree is largely unresolved, recovering a polytomy between four branches: the sister taxa *Diplocynodon darwini* + *Diplocynodon hantoniensis*, the sister taxa *Diplocynodon deponiae* + *Diplocynodon muelleri*, *Diplocynodon ratelii*, and *Diplocynodon remensis* (Figure 10Aa). A majority of the trees however recover *Diplocynodon ratelii* as the sister taxon to *Diplocynodon deponiae* + *Diplocynodon muelleri*, as well as *Diplocynodon remensis* being the earliest branching species (Figure 10Ab). The analysis under EIW recovered the same results from 4 MPTs of tree length 1.75, with the same topologies calculated by the strict and majority consensus trees (Figure 10Ba, b).

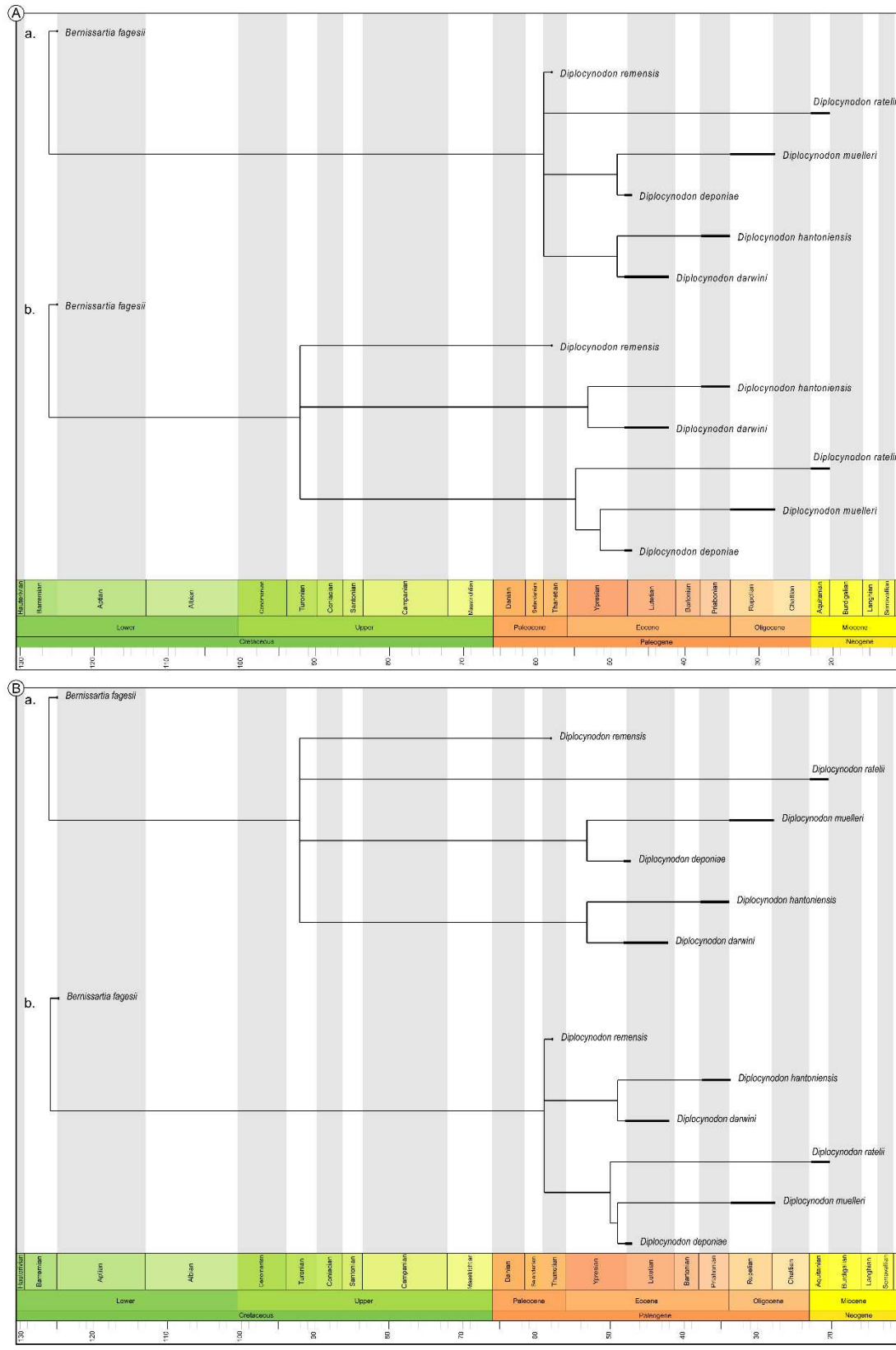


Figure 10: Consensus trees obtained using the modified dataset of Walter et al. (2025; Chapter 1). A, equal weighting strategy; a, strict consensus tree; b, majority consensus tree. B, extended implied weighting strategy ($k = 3$); a, strict consensus tree; b, majority consensus tree.

The analyses of the modified dataset of Chabrol et al. (2024) recovered different topologies. The EW analysis of the version treating quantitative characters continuously (Figure 11) recovered a single MPT (tree length of 11,830.794). *Diplocynodon remensis* is the earliest branching species, with *Diplocynodon muelleri*, *Diplocynodon ratelii*, *Diplocynodon hantoniensis*, *Diplocynodon deponiae* and *Diplocynodon darwini* successively recovered in more derived positions. The analysis of the same version of the dataset under EIW (k=3) provided a single MPT as well (tree length of 469.14159), but of a different topology: two sister groups are formed, respectively by *Diplocynodon muelleri* + *Diplocynodon hantoniensis*, and *Diplocynodon darwini* + *Diplocynodon ratelii* + *Diplocynodon deponiae*.

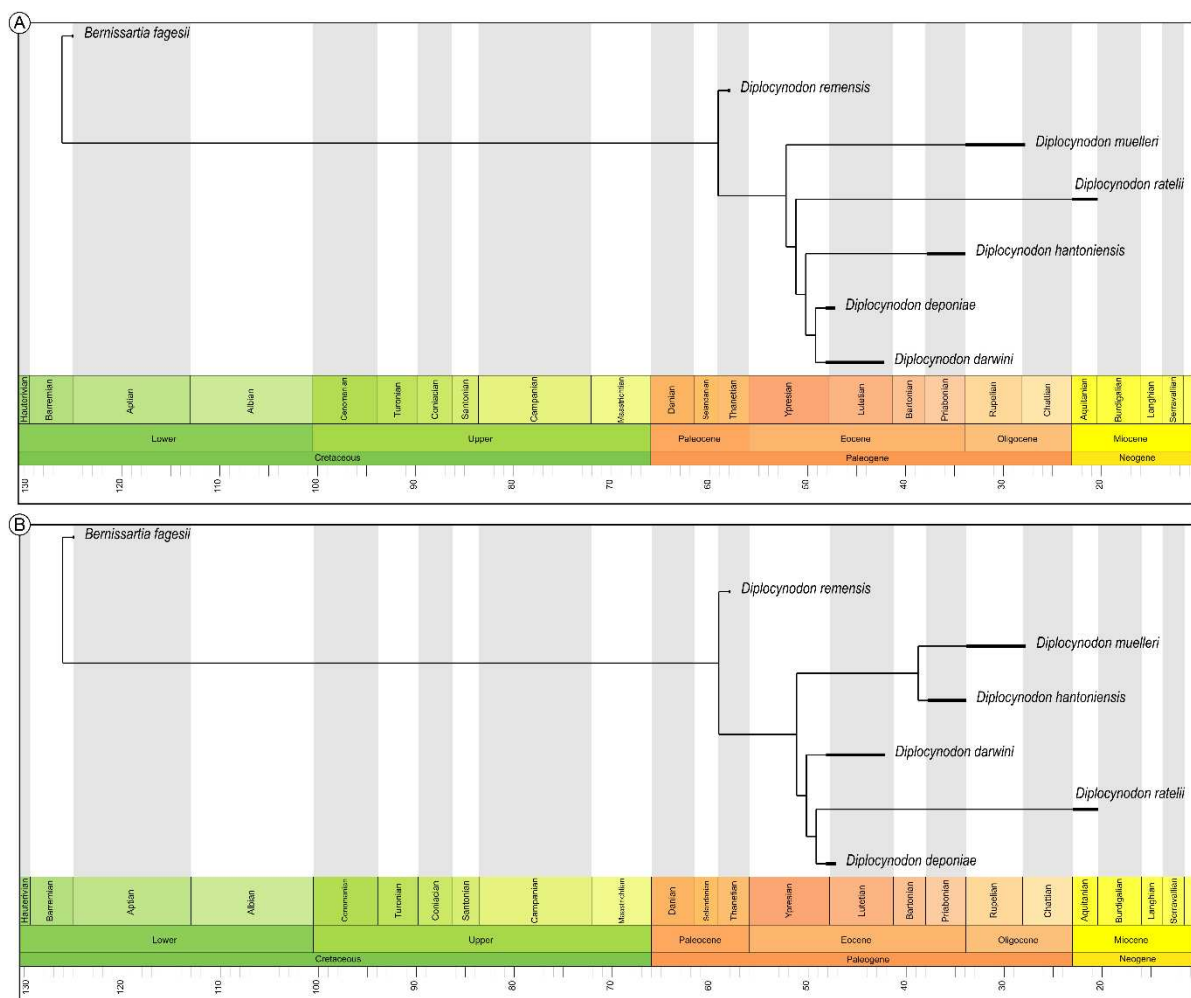


Figure 11: Consensus trees obtained using the modified dataset of Chabrol et al. (2024), continuous and discrete characters. A, equal weighting strategy, B, extended implied weighting strategy (k = 3).

Alternatively, the EW analysis of the version treating quantitative characters discretely (Figure 12) recovered 7 MPTS (tree length of 123). The strict consensus of the sample of MPTs results in a complete polytomy (Figure 12Aa), but the majority consensus tree shows that most trees present a topology where *Diplocynodon deponiae* + *Diplocynodon darwini* is the earliest branching group, sister to a polytomy involving *Diplocynodon remensis*, *Diplocynodon ratelii*, and *Diplocynodon mulleri* + *Diplocynodon hantoniensis* (Figure 12Ab). The EIW analysis of this same version of the dataset recovered a single MPT (tree length of 4.99448; Figure 12B), of the same topology as the EIW analysis of the continuous version of the dataset (Figure 11B).

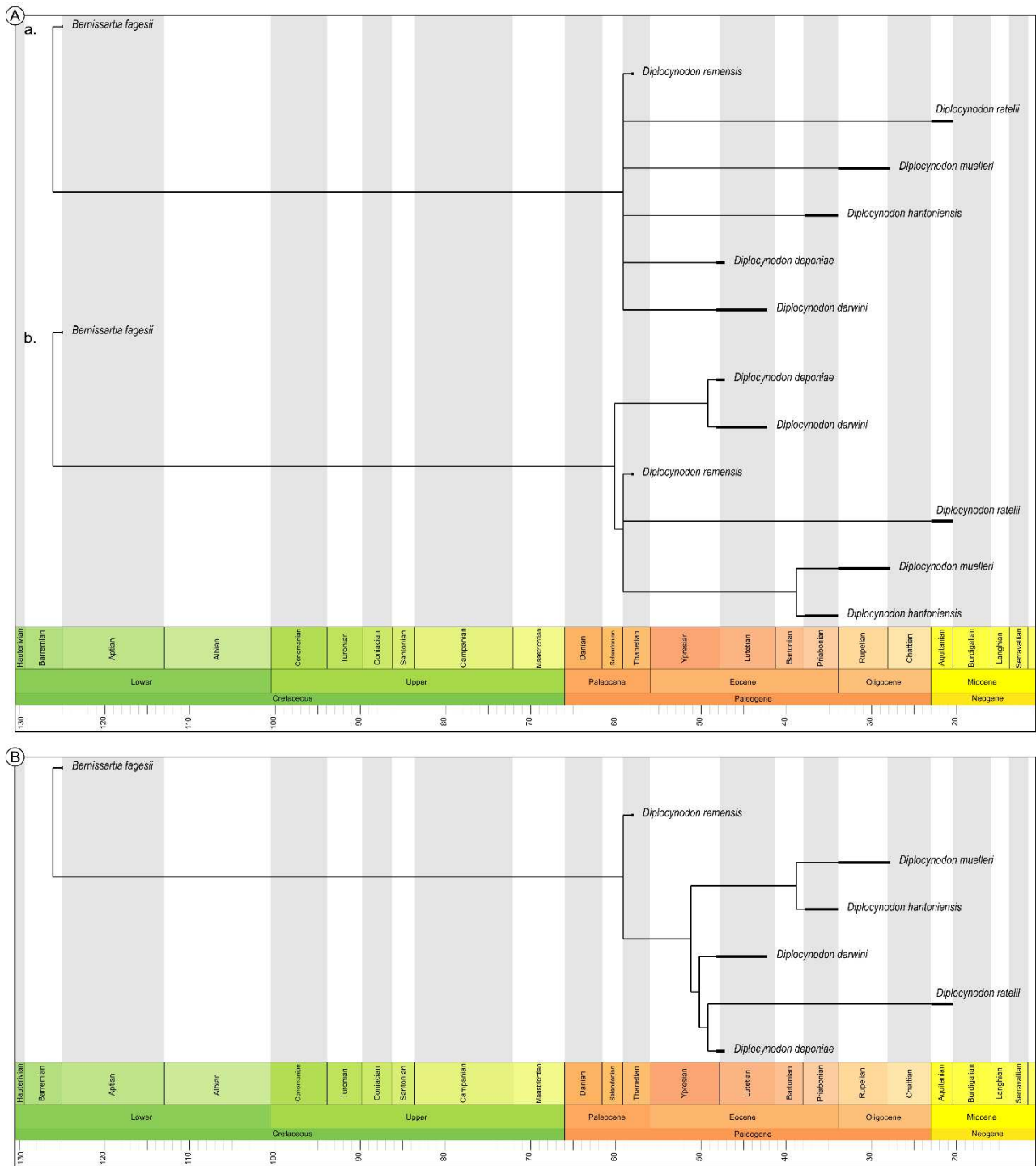


Figure 12: Consensus trees obtained using the modified dataset of Chabrol et al. (2024), discrete and rediscritised characters. A, equal weighting strategy; a, strict consensus tree; b, majority consensus tree. B, extended implied weighting strategy ($k = 3$).

5. Discussion

5.1 *Diplocynodon darwini* as two distinct populations

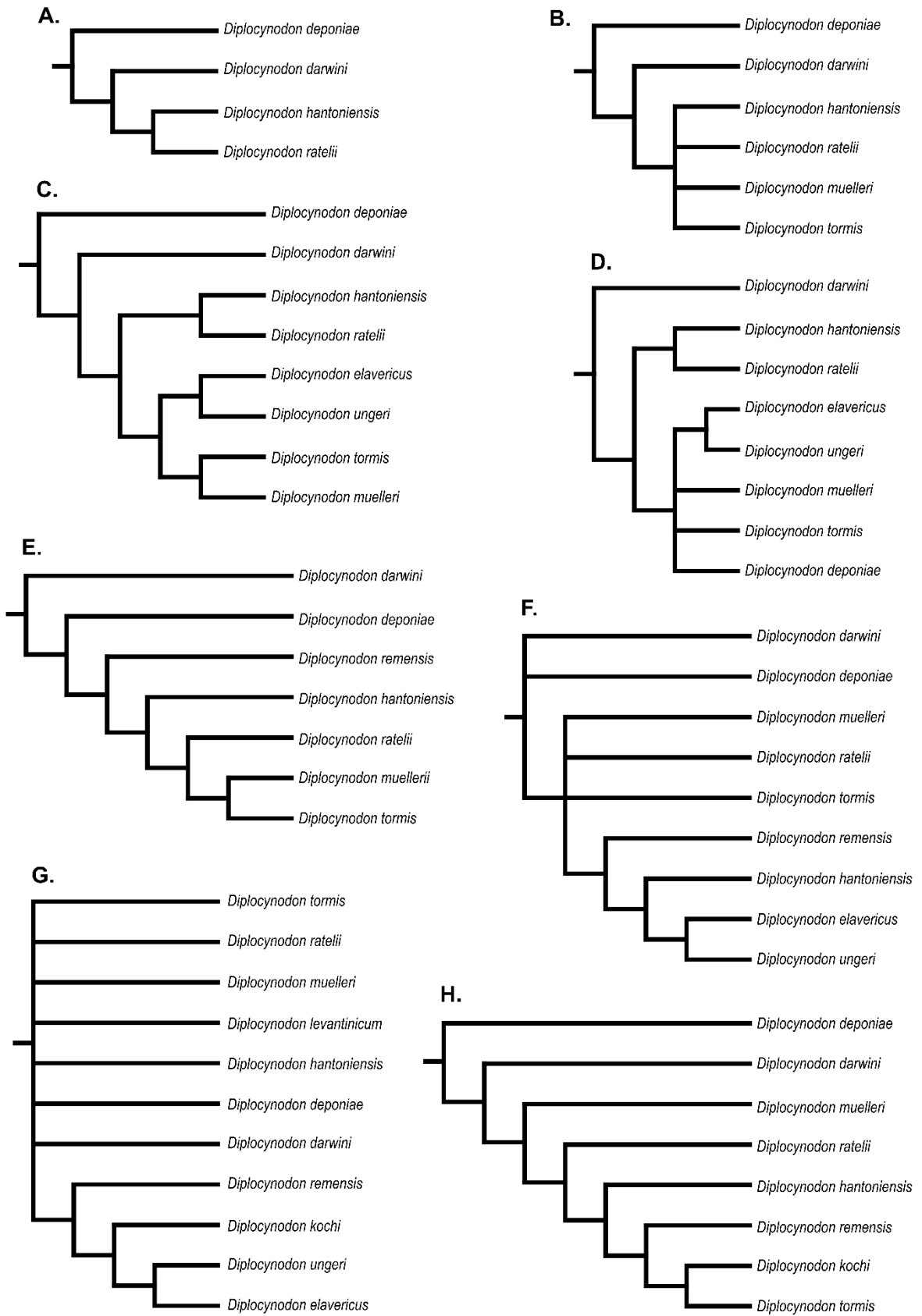
Observed differences between the populations from Messel (Darmstadt, Germany) and Geiseltal (Halle, Germany) pertain to the individuals general body-size, skull shape, and variability in some character states. While the sample from Geiseltal is largely represented by small-sized individuals of a generally gracile appearance and pointed skull (ca. ~ 20 cm in skull length), the population from Messel locality consists of larger individuals with more sturdy skulls (ca. ~ 25–30 cm in skull length).

This apparent difference can be tentatively explained by ontogenetic niche partitioning. As observed for several extant species such as *Crocodylus niloticus* (Behangana et al., 2020) or *Crocodylus moreletii* (Platt et al., 2006), crocodylian populations tend to partition their habitats by ontogeny for a combination of reasons including reduction of intraspecific competition, differing dietary habits, or predator avoidance (Tucker, 1997). Commonly, juveniles are inhabiting shallow woody vegetations and river margins microhabitats to both feed and avoid predators, including conspecific adult individuals. Sub-adults, on the other hand, occur in a wider range of microhabitats, from shallow areas to open water ways. Adults, finally, are most often found in riverbeds and occasionally on the margins for nesting (e.g. pools and or burrows). By comparison, the fossil samples of Geiseltal and Messel sites match this pattern: the swampy paleoenvironment of Geiseltal sheltered a majority of juveniles to sub-adult individuals, while the open paleolake of Messel comprised a majority of adults. This hypothesis is partly supported by Hastings & Hellmund (2017) whose results preclude the predation of medium to large-sized vertebrates by *Diplocynodon* in Geiseltal, but instead suggest a diet comparable to extant sub-adult crocodylians (fish, molluscs, or small mammals and reptiles). The taphonomical and subsequent fossilisation processes that took place in the Konservat-Lagerstätten sites of Messel and Geiseltal captured the local ontogenetic classes of the respective populations.

5.2 Ingroup relationships of *Diplocynodon*

Results from the different parsimony analyses performed in our study did not agree upon a consensual topology of *Diplocynodon* species interrelationships. This uncertainty is well documented in the literature, as nearly all previous studies recovered distinct phylogenies (Figure 13), usually expanding upon the common parent dataset of Brochu (1999). Rio & Mannion (2021) however introduced a newly built character-taxon matrix and employed different phylogenetic approaches to investigate eusuchian evolutionary relationships, but their results did not grant any consistency regarding the interrelationships of *Diplocynodon*, instead recovering the genus as a paraphyletic group in their preferred topology contra previous studies (but see Groh et al., 2020).

Figure 13 (below): Contrasting topologies (strict consensus trees) of *Diplocynodon* ingroup based on previously published studies: A. from Brochu, 1999; B. from Piras & Buscalioni, 2006; C. from Martin & Gross, 2011; D. from Delfino & Smith, 2012; E. from Martin et al., 2014; F. from Rio et al., 2020; G. from Massonne et al., 2022; H. from Venczel & Codrea, 2022.



Nevertheless, two patterns can be noted from previous phylogenies and results obtained herein, broadly congruent with the stratigraphical data (Figure 10-13; Brochu, 1999; Piras & Buscalioni, 2006; Martin & Gross, 2011; Delfino & Smith, 2012; Martin et al., 2014; Rio et al., 2020; Venczel & Codrea, 2022; Massonne & Böhme, 2022).

First, the Eocene taxa from Messel *D. darwini* and *D. deponiae* are branching relatively early within *Diplocynodon*. This is the case in the oldest phylogenies including only a few species (Figure 13A-C) as well as for studies following the reappraisal of *D. deponiae* by Delfino & Smith (2012; Figure 13D and subsequent trees). The relative completeness may play a decisive role here for *D. darwini*, as it is the best sampled and most completely scored taxon in the group (see Table 1), therefore setting the primitive condition for nearly all morphological characters. On the other hand, *D. deponiae* is the least complete taxon in our datasets (~ 50%; see Table 1) and bears a noticeably different morphotype from all other *Diplocynodon* species, which always implies a deeply nested (but poorly supported) or basal (dictated by exclusion) phylogenetic placement, as recovered in our results (Figure 10-12). These alternative positions were previously recovered by most phylogenies (Figure 13; Groh et al., 2020; Rio & Mannion, 2021).

Species	mW	mC
<i>Diplocynodon darwini</i>	83.0	81.2
<i>Diplocynodon deponiae</i>	49.8	47.9
<i>Diplocynodon hantoniensis</i>	79.5	79.4
<i>Diplocynodon muelleri</i>	58.0	44.2
<i>Diplocynodon ratelii</i>	79.9	79.4
<i>Diplocynodon remensis</i>	70.3	61.5

Table 1. Scoring completeness per species in the datasets used for phylogenetic analyses presented in the chapter. mW: modified Walter et al. (2025) dataset. mC: modified Chabrol et al. (2024) dataset. Values are in %.

Second, a central issue in the investigation of interrelationships of *Diplocynodon* relies on whether *D. remensis*, *D. darwini* or *D. deponiae* is the earliest-branching taxon. *D. remensis* has commonly been recovered in a relatively crownward position since its erection (Figure 13E-H; Groh et al., 2020; Rio & Mannion, 2021), inconsistent with its old age (late Thanetian; Martin et al., 2014). The stratigraphically early appearance of the taxon combined to shared character states with *Borealosuchus* (Martin et al., 2014; Rio et al., 2020; Walter et al., 2025, Chapter 1) would justify its placement at the root of the group but is not yet consensually recovered in phylogenetic analyses. The taxon was only recently recovered as the most basal *Diplocynodon* species in equal-weighting analyses (see discussion in Rio & Mannion, 2021), and is also retrieved in the majority of our consensus trees, more specifically from analyses under EIW (Figure 10-12).

5.3 The diversification and geographical distribution of *Diplocynodon* in the European Paleogene greenhouse context

Diplocynodon exhibits a discontinuous paleogeographical distribution across the Paleogene and Neogene periods of Europe. The literal interpretation of the stratigraphic data from fossil evidence suggests that the first appearance date of *Diplocynodon* is the late Paleocene of northeastern France (Martin et al., 2014; this thesis, Chapter 2). The Paleocene epoch represents a critical period in crocodylian evolution, characterised by the recovery and diversification of various lineages following the Cretaceous-Paleogene extinction event (Jouve & Jalil, 2020).

The subsequent Eocene epoch witnessed a distinct diversification of *Diplocynodon*, with four species spread across Europe. The earliest species of this epoch, namely *Diplocynodon darwini* and *Diplocynodon deponiae*, are reported from the fossil sites of Messel and Geiseltal in Germany. Only a few million years later appears *Diplocynodon hantoniensis* from southern United-Kingdom, and so far the northernmost specific occurrence of a *Diplocynodon* species (see Chapter 2). The warm, subtropical climates that prevailed during the Eocene provided ideal conditions for the proliferation of crocodyliforms, notably *Diplocynodon* appears to have thrived in various freshwater environments,

including rivers, lakes, and swamps. This diversification coincided with a period of elevated global temperatures, commonly referred to as the Early Eocene Climatic Optimum (Wing et al., 2010; Huber et al., 2017), which may have facilitated the dispersal and sustainability of thermophilic reptiles across higher latitudes. The presence of *Diplocynodon* in middle Eocene localities, such as the Ikovo locality in Ukraine, alongside crocodylians and turtles with similarities to those from Western Europe, may suggest the existence of a single European biogeographical zone during this time, distinct from that of Asia (Kuzmin & Zvonok, 2021).

The Oligocene epoch marked a period of significant climatic and environmental change, with a gradual cooling trend leading to more temperate conditions in Europe, which had an impact on the distribution of *Diplocynodon* while reading the fossil record literally. The genus persisted in Europe throughout the Oligocene, but its range appears to have contracted southwards compared to the Eocene, possibly due to the changing climate, geography, and emergence of new competitors. During the following Miocene epoch, *Diplocynodon* experienced further changes in its distribution, with a gradual decline in its eastern range.

Refining the paleobiogeographical distribution of *Diplocynodon* at the species level is, in the current state of the fossil record, hampered by taxonomical uncertainties. As discussed in Chapter 2, *Diplocynodon* sp. is widespread across Europe throughout the Cenozoic, but definite species occurrences are rare and usually local. Directing taxonomical research efforts towards revising known material attributed to *Diplocynodon* sp. is thus necessary, as it may 1) confirm or refute genus occurrences, and 2) possibly provide new occurrences of known species, consequently extending the temporal and geographical ranges of these taxa.

GENERAL CONCLUSION AND FUTURE PERSPECTIVES

The novel topology presented in the first chapter of this thesis better resolves the early biogeographic history of *Diplocynodon* and biogeographic distribution of *Deinosuchus*, infers possible salt tolerance for stem-crocodylians and at the root of Crocodylia, and implies a body-size reduction at the root of Alligatoroidea. A basal split of crown-group crocodylians is hypothesised in light of the resulting simpler biogeographic pattern, triggered by extreme mid-Cretaceous sea level rise.

Regarding the ingroup relationships of *Diplocynodon*, morphological diagnoses of currently known species often included shared and/or irreproducible characters, hampering specific delimitation. The first taxonomic revision of the group since its inclusion in modern phylogenetics is presented herein and invalidates the species *Diplocynodon elavericus* and *Diplocynodon tormis*. An identification key is provided along with the taxonomic revision to assist researchers in future identifications of the valid species. Moreover, the quantitative review of the fossil record of *Diplocynodon* reveals the waste-basket status of the taxon, whose reasons and implications are discussed, including recommendations for better taxonomic practices.

The reappraisal of the species *Diplocynodon darwini* updates the current knowledge of the species morphology by recognising two distinct populations from Messel and Geiseltal respectively. Morphological variation of some characters in the taxon is described, including ontogenetic evolution, and insights into morphological variability across *Diplocynodon* species are provided. The ingroup evolutionary relationships are additionally tested in two eusuchian character-taxon datasets and compared to previously published phylogenies. The results, congruent with previously published topologies, indicate the absence of consensus.

The exceptionally long survivorship of *Diplocynodon* in Europe however raises new questions with respect to results and conclusions of the thesis. Three central future perspectives can be drawn:

- 1) The extinction of the sister-group *Borealosuchus* in the middle Eocene of North America seems rather sudden compared to *Diplocynodon*, while both groups lived under similar paleolatitudes.

A possible hypothesis would be the lower physiological tolerance of *Borealosuchus* (implied by a comparably larger body-size than most species of *Diplocynodon*) to the global increase of mean temperatures in the context of pre-Paleocene/Eocene Thermal Maximum (PETM). A handful of studies have explored the potential influence of latitudinal distribution and mean temperatures on ectotherms physiology (Lindeman, 2008; Pincheira-Donoso et al., 2008), among which the first study regarding crocodylians demonstrated a positive correlation between latitude and body-mass in females based on extant taxa (Lakin et al., 2020). Such question however requires an initial complete systematics and taxonomic revision of *Borealosuchus*, in order to test the current species validity, and refine stratigraphic and biogeographical ranges.

- 2) The interrelationships of *Diplocynodon* species currently suffers from insufficiently informed scoring in datasets. Research efforts on the group should aim at improving the overall completeness of taxon scoring in existing datasets, especially for species nearing 50% of missing entries. In this regard, CT data has the potential to allow investigation of unknown characters, otherwise inaccessible to the naked eye (e.g. because of the extensive osteoderm coverage in *Diplocynodon deponiae*). Species including few articulated cranial materials would also benefit from the methods as to optimise the amount of morphological information retrieved from limited sample.
- 3) From a larger point of view, macroevolutionary interpretations for Crocodylia based on combined DNA (either directly implemented in datasets or in the form of a scaffold) and morphological data are congruent among them (see contribution to the work of Darlim et al. (2022) provided in Appendix 4.1). These methods may represent the most efficient way to take molecular informed topologies into account while investigating evolutionary relationships of crown-groups.

CANDIDATE BIBLIOGRAPHY

The following works were published or accepted for publication during the candidate's doctoral period (see Appendix 5 for the complete articles):

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APPENDICES

APPENDIX 1: Supplementary information and data for Chapter 1

The appendix (present document) is the main additional material file associated with the manuscript and phylogenetic analyses.

All the data regarding Chapter 1 is accessible under the following Figshare repository link:

<https://doi.org/10.6084/m9.figshare.27901317.v1>

The folder 'Supplementary Data 1' contains the character-taxon dataset used for the phylogenetic analyses as well as the TNT files.

The folder 'Supplementary Data 2' contains all the primary data, code and files used to determine the body size estimates (folders 1. and 2.), along with the raw data and results (folder 3.).

1. Changes applied to the dataset of Massonne et al. (2019)

For our phylogenetic analysis, we modified the dataset of Massonne et al. (2019), which in turn is based on Brochu (1999, 2004), Brochu & Storrs (2012), Wang, Sullivan & Liu (2016), Cossette & Brochu (2018), and Li, Wu & Rufolo (2019). In order to update and increase the taxon-character sample of Massonne et al. (2019), we combined it with the datasets of Gismondi et al. (2015), Bona et al. (2018), Cossette (2021), Shan et al. (2021), Stocker et al. (2021), and Walter et al. (2022), including the addition of 20 characters, 14 character states, and 17 taxa. We furthermore added the taxa *Diplocynodon remensis* and *Borealosuchus griffithi* and removed four characters due to irreproducibility, intraspecific variability or redundancy with the added character states. The complete list of characters is available in part [4] of the present document. The expanded dataset now includes a total of 219 characters and

128 taxa. See Supplementary Data 1 folder for nexus and tnt files and part [2] of the present document and Methods of the main manuscript for details of the analysis.

1.1 List of taxa added to the dataset of Massonne et al. (2019)

The following 19 taxa were added to the parent dataset (see [3] for sources):

- *Albertochampsia langstoni* Erickson, 1972
- *Borealosuchus griffithi* Wu, 2001
- *Bottosaurus fustidens* Cossette, 2021
- *Caiman wannlangstoni* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh & Antoine, 2015
- *Chinatichampsus wilsonorum* Stocker, Brochu & Kirk, 2021
- *Deinosuchus schwimmeri* Cossette & Brochu, 2020
- *Diplocynodon remensis* Martin, Smith, de Lapparent de Broin, Escuillié & Delfino, 2014b
- *Dongnanosuchus hsui* Shan, Wu, Sato, Cheng & Rufolo, 2021 (replacing the incomplete taxon “Maoming alligatoroid”; Skutschas et al. 2014, Massonne et al. 2019)
- *Eocaiman itaboraiensis* Pinheiro, Fortier, Pol, Campos & Bergqvist, 2013
- *Eocaiman palaeocenicus* Bona, 2007
- *Gnatusuchus pebasensis* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh & Antoine, 2015
- *Kuttanacaiman iquitosensis* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh & Antoine, 2015

- *Caiman brevirostris* Souza Filho, 1987
- *Mourasuchus amazonensis* Price, 1964
- *Mourasuchus arendsi* Bocquentin Villanueva, 1984
- *Necrosuchus ionensis* Simpson, 1937
- *Protocaiman peligrensis* Bona, Ezcurra, Barrios & Blanco, 2018
- *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892
- *Purussaurus mirandai* Aguilera, Riff & Bocquentin-Villanueva, 2006

1.2 List of omitted taxa

A total of 4 taxa were removed from the dataset:

- *Asiatosuchus nanlingensis* Young, 1964

This taxon was omitted due to its incompleteness (Shan et al., 2021).

- *Culebrasuchus mesoamericanus* Hastings et al., 2013

This taxon was omitted due to its poor preservation and further studies are required before it can be reintroduced into the phylogeny (see Stocker et al., 2021).

- *Melanosuchus fisheri* Medina, 1976.

The taxon was considered to be a *nomen dubium* (Bona et al., 2017).

- *Orthogenysuchus olseni*, Mook 1924

This taxon was omitted due to its poor preservation and need for osteological revision (see Stocker et al., 2021 and Walter et al., 2022).

1.3 List of updates and modifications of scores

39. Number of contiguous dorsal osteoderm rows:

Diplocynodon hantoniensis: 1 > ?

We are unaware of a complete dorsal shield preserved for this species. The character is therefore rescored as (?).

46. Alveoli size of dentary teeth: 3rd and 4th same size and confluent (0), 4th larger than 3rd and separate (1), 3rd and 4th nearly same size and separate (2).

Diplocynodon deponiae: ? > 0

Diplocynodon deponiae, as all other *Diplocynodon* species, has confluent 3rd and 4th dentary alveoli (Delfino & Smith, 2012, Fig.4). The character is therefore rescored as (0).

47. Anterior dentary teeth strongly procumbent (0) or project anterodorsally (1).

Eocaiman cavernensis: 1 > 0

The anterior dentary teeth are procumbent in the only known specimen (AMNH FARB 3158). This is also apparent in Godoy et al. (2021 figs. 1, 8) and the condition is not different from other taxa scored for this state in the dataset. To make the scorings consistent, we therefore rescore *E. cavernensis* as (0).

49. Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli.

Dongnanosuchus hsui: 0 > 1

The lower jaw of *D. hsui* is preserved in occlusion. In Shan et al. (2021 fig. 6 1), the curvature nevertheless looks deeper than in *J. nankangensis* (state 0 - Li et al., 2019 fig. 6 c), and more similar to the stronger curvature of *O. naduongensis* (state 1 - Massonne et al., 2019 fig. 8a). The character is therefore rescored as (1).

50. Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) between 11 and 14 and a series behind it, (2) 11 or 12, (3) no differentiation, (4) behind 14, (5) 10.

Bottosaurus harlani: 1 > 2

Massonne et al. (2019) changed the scoring of this species from 2 to 1 but this was apparently a misinterpretation. Based on Cossette & Brochu (2018 fig. 5) and personal observation, the condition is clearly state (2).

58. Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1).

Globidentosuchus brachyrostris: ? > 1

No splenial process is visible between the angular and coronoid (Scheyer & Delfino, 2016 fig. 9). The character is therefore rescored as (1).

59. Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1).

Globidentosuchus brachyrostris: 1 > 0

The angular-surangular suture reaches the external mandibular fenestra posteriorly (Scheyer & Delfino, 2016 fig. 9). The character is therefore rescored as (0).

60. Surangular, relative length of the anterior processes: equal (0); subequal (1).

Borealosuchus formidabilis: ? > 1

Diplocynodon deponiae: 1 > ?

Diplocynodon tormis: 1 > ?

Borealosuchus formidabilis is here scored (1) following Rio and Mannion (2021; in Appendix 2, Fig. 107). In *Diplocynodon deponiae* and *Diplocynodon tormis*, the relative extent of the surangular processes are incomplete (pers. obs.; Buscalioni et al., 1992; Delfino & Smith, 2012).

62. External mandibular fenestra absent (0) or present as narrow slit, no discrete fenestral concavity on angular dorsal margin (1) or present with discrete concavity on angular dorsal margin (2) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (3).

Orientalosuchus naduongensis: 2 > 1

Orientalosuchus naduongensis has a very small external mandibular fenestra, noticeably reduced compared to closely related taxa. To account for this obvious difference, the character is rescored as (1).

Globidentosuchus brachyrostris: 1 > 3

The foramen intermandibularis caudalis is apparent in lateral view in Scheyer & Delfino (2016 fig. 9). The character is therefore rescored as (3).

65. Surangular-angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1).

Bottosaurus harlani: ? > 1

We here follow the scoring of Cossette & Brochu (2018).

66. Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1).

Bottosaurus fustidens: 0 > ?

The limited preservation of the relevant specimen (TMM 40148-7; Cossette, 2021 fig. 5) does not allow assessment of the full extent of the surangular-articular suture. The glenoid fossa does not seem complete enough to detect a possible truncation. We here conservatively rescore the character as (?).

78. Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2).

Dongnanosuchus hsuii: 0 > 1

There does not seem to be a difference in the posterior tooth morphology between *D. hsui* and *Orientalosuchus naduongensis* (scored (1)). In *D. hsui* (Shan et al., 2021 fig. 6.6), the posterior teeth are clearly longer than wide (laterally compressed). The character is therefore rescored as (1).

84. External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest.

Dongnanosuchus hsuii: 1 > 0

The condition in *D. hsui* is not comparable to the thin crest around the naris as present in e.g. *Tsoabichi greenriverensis* (Brochu, 2010 fig. 3c) and appears as a thinner bulge instead, similar to *O. naduongensis* (without a notch posterolateral to the naris). The character is therefore rescored as (0).

Eocaiman cavernensis: 0 > ?

The external naris is not preserved in the only specimen unambiguously referred to this species (pers. obs.; Godoy et al., 2021 fig. 1). The character is therefore rescored as (?).

88. Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or projects between first premaxillary teeth (2).

Brachychampsia montana: ? > 0

The incisive foramen is located away from the toothrow (pers. obs.; Norell et al., 1994, fig. 1) as in other taxa scored for the corresponding state. The character is therefore rescored as (0).

Brachychampsa sealeyi: ? > 0

The incisive foramen is located away from the toothrow (Williamson, 1996, fig. 2) as in other taxa scored for the corresponding state. The character is therefore rescored as (0).

Albertochampsa langstoni: ? > 1

The incisive foramen abuts the toothrow (Erickson, 1972, fig. 2) as in other taxa scored for the corresponding state. The character is therefore rescored as (1).

We follow Stocker et al. (2021, ch. 89) who rescored this character due to what may have been a transcription error in one of their parent datasets.

90. Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1).

The definition of character 90 specifies early ontogenetic stage since a pit may develop into a notch during ontogeny in some taxa. Massonne et al. (2019) noticed that several taxa with a premaxillary-maxillary notch in the adult stage was scored for this character, even though the early ontogenetic stage is not actually known (in the absence of subadult specimens). In order to fix this, Massonne et al. (2019) added a new character (ch. 194 of the present study) that only considers the adult condition. To avoid double weighting of the same morphology, Massonne et al. (2019) rescored all taxa with no known subadult specimens as unknown for character 90. For few taxa, however, Massonne et al. (2019) incorrectly assumed that the juvenile condition was known, which we here correct by updating the following taxa:

Acynodon iberoccitanus: 1 > ?

Allodaposuchus precedens: 1 > ?

92. Largest maxillary alveolus is 3 (0), 5 (1), 4 (2), 4 and 5 are same size (3), 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).

Bottosaurus fustidens: 2 > ?

In the maxillae referred to this species (TMM 40148-7; Cossette, 2021; fig. 4 and TMM 41336-16; Cossette, 2021; fig. 7B), the size of the 5th alveolus is not fully discernible, thereby making an adequate comparison to that of the 4th impossible. The character is therefore rescored as (?).

97. Antorbital fenestra present (0) or absent (1).

Globidentosuchus brachyrostris: ? > 1

An antorbital fenestra is absent in this taxon (Hastings et al., 2016, fig. 4).

112. Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1).

Eocaiman cavernensis: ? > 0

The anterior palatine process is pointed in AMNH FARB 3158 (pers. obs.; Godoy et al., 2021, fig. 4) and instead of medially, it is laterally notched. The morphology differs from

the notched condition of e.g. *Paleosuchus palpebrosus*. The character is therefore rescored as (0).

115. Palatine process generally broad anteriorly (0) or in form of a thin wedge (1).

Chinatichampsus wilsonorum: 1 > 0

Based on Stocker et al. (2021, fig. 5) the anterior palatine process is round and broad instead of forming a thin wedge. We assume this was a typographical error in Stocker et al (2021). The character is therefore rescored as (0).

119. Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1).

Diplocynodon darwini: 0 > 1

Diplocynodon deponiae: 0 > 1

Diplocynodon hantoniensis: 0 > 1

Diplocynodon muelleri: 0 > 1

Diplocynodon ratelii: 0 > 1

In Massonne et al. (2019) the definition of ch. 119 was misinterpreted and this error is corrected here.

124. Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2).

We follow Stocker et al. (2021, ch. 125) who rescored this character due to what may have been a transcription error in one of their parent datasets.

128. Prefrontals separated by the frontals and nasals, anterior process of frontal extending far anterior to the anterior margin of the orbit (0) prefrontals separated by the frontal and nasals, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (1) or prefrontals meet medially, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (2).

Albertochampsa langstoni: ? > 1

The anterior process of the frontal is in line with the orbit (Erickson; 1972 fig. 1).

130. Anterior tip of frontal (0) forms simple acute point or (1) forms broad, complex sutural contact with the nasals.

Deinosuchus schwimmeri: 2 > 1

This character was previously scored with state (2) by Shan et al. (2021), but the character includes two states only. The character is therefore rescored as (1).

139. Quadratojugal spine presence: prominent (0); greatly reduced or absent (1).

Diplocynodon tormis: 1 > ?

Diplocynodon tormis does not preserve a complete lower temporal fenestra, lacking most elements posterior to the jugal in the most complete specimen (IPS-9001, pers. obs.). Other referred specimens by Buscalioni et al. (1992) consist of skull elements not pertaining to or not preserving the area of interest (see also Serrano-Martinez et al., 2019 for a description of another specimen, STUS-344). The authors also mentioned disarticulated material attributed to *Diplocynodon tormis* but without further description, figures or inventory numbers. Since the score appears to be irreproducible, we rescore this character as unknown (?).

140. Quadratojugal spine position: low, near posterior angle of fenestra (0); high, between posterior and superior angles of fenestra (1).

Diplocynodon tormis: 1 > ?

See justification under ch. 139.

148. Caudal margin of otic aperture not defined and gradually merging into the exoccipital (0) or smooth and continuous with the paraoccipital process (1) or caudal margin of otic aperture inset (2).

Diplocynodon tormis: 2 > ?

See justification under ch. 139.

150. Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae.

Globidentosuchus brachyrostris: 1 > ?

In Hastings et al. (2016, fig. 4), the frontoparietal suture cannot be clearly followed. The scores of Massonne et al. (2019) and Walter et al. (2022) are contradicting. We here therefore prefer caution over the scoring of this character and rescore it as unknown (?).

163. Prootic on external wall of braincase is extensively exposed (0); largely obscured by the quadrate and laterosphenoids externally (1).

Eoalligator chunyii: 1 > ?

Specimens of *Eoalligator chunyii* do not preserve the prootic (Wang, 2016; Wu et al. 2018). The extent of its exposure relative to the quadrate and laterosphenoid therefore cannot be assessed.

196. If largest dentary alveolus is between 11th and 14th and a series behind it, is it the (0) 11th, (1) 12th, or (2) 13th or 14th.

Bottosaurus harlani: 1 > (-)

After rescoring character 50 for this taxon (see above), character 196 is no longer applicable. The character is therefore scored as (-).

202. Ventral premaxilla-maxilla suture short and ends posteriorly before the 3rd maxillary alveoli (0) or elongated and extends or exceeds the 3rd maxillary alveoli (1). [added from Stocker et al. (2021)]

Brachychampsia montana: 0 > 1

In *B. montana* the premaxilla-maxilla suture is strongly bowed posteriorly due to the large incisive foramen. The suture reaches the level of the fourth maxillary tooth (pers. obs.; Gilmore, 1911 pl. 27; Norell et al. 1994 fig. 1). The character is therefore scored as (1).

204. Lateral edge of the skull table at the level of the postorbital-squamosal suture situated laterally or at the same level as (0), or medially to (1) the quadrate condyle in dorsal view at maturity. [added from Stocker et al. (2021)]

Boverisuchus vorax: 1 > 0

In *B. vorax*, the lateral edge of the skull table at the level of the postorbital-squamosal suture reaches the level of the medial quadrate condyle (Langston, 1975 fig.1; Brochu, 2012 fig. 3). The character is therefore scored as (0).

207. Interorbital bridge narrower to equivalent (0), or broader (1) than the width of the orbit.
[added from Stocker et al. (2021)]

Boverisuchus vorax: 0 > 1

In *B. vorax*, the interorbital bridge is wide, broader than the width of the orbit (pers. obs.; Langston, 1975 fig.1; Brochu, 2012 fig. 3). The character is therefore scored as (1).

215. Dentary teeth series behind alveoli 12-13 are pointed to slightly blunt (0); globular, different in size among them (1); globular, at least four subequal in size (2), molariform multicusped (3) or absent (4). [added from Stocker et al. (2021)]

Bottosaurus harlani: 1 > 0

In *B. harlani*, posterior teeth behind the 12th are slightly blunt rather than being globular (Cossette & Brochu, 2018 fig. 5) and resemble the corresponding teeth of e.g. *O. naduongensis* more than the condition of e.g. *Ceratosuchus burdohsi* (state 1). In order to remain consistent with the scores and morphology of other taxa, we rescore *B. harlani* as (0).

1.4 Deleted characters

Character 1 of Massonne et al. (2019)

Ventral tubercle of proatlas: more than one-half (0), or no more than one-half (1) the width of the dorsal crest. [OMITTED]

The definition of this character is imprecise regarding the angle of view necessary to score the morphology of the tubercles. A few fossil taxa were scored for this character in the parent dataset, but their scoring was irreproducible. Moreover, Sookias (2020; supplementary) evaluated the character as non-robust in his review of crocodylian morphological characters, based on a different dataset using the same version of the character (Narváez et al., 2015). The author specifies that the variation indicated by the scorings could not be observed for extant taxa. Given the uncertainty of the morphological variation and irreproducibility of the scoring distribution, we omit this character from the present analysis.

Character 194 of Massonne et al. (2019)

Nasal bone does (0) or does not (1) reach to the height of the orbita. [OMITTED]

This character was introduced in Massonne et al. (2019) and by updating ch.128 of the present dataset with an additional state (after Salas-Gismondi et al. 2015), this morphology is already included and makes ch. 194 redundant.

Character 197 of Massonne et al. (2019)

Sutural contact of the exoccipitals dorsal to the foramen magnum (0) long, at least half the height of the foramen magnum, (1) short, shorter than half the height of the foramen magnum, or (2) no sutural contact between the exoccipitals. [OMITTED]

This character was introduced in Massonne et al. (2019). In occipital view, the supraoccipital is generally triangular but its ventral extension differs among taxa. In e.g. *Acynodon iberoccitanus* Buscalioni, Ortega & Vasse 1997, the supraoccipital nearly prevents

contact between the exoccipitals (Martin, 2007 fig. 2), whereas in *Leidyosuchus canadensis* Lambe, 1907, the ventral supraoccipital process is short, allowing a long contact between the exoccipitals (Wu et al. 2001, fig. 3). However, we find that in most taxa, the condition is intermediate or the variation is continuous. In addition, fossil skulls are commonly crushed. We therefore omit this character from the present analysis.

Character 199 of Massonne et al. (2019)

Intersupratemporal bar (0) as or near as broad as the supratemporal fenestra, (1) at least twice as broad as the supratemporal fenestra, (2) around half the broadness of the supratemporal fenestra or (3) constricted, less than half the broadness of the supratemporal fenestra. [OMITTED]

This character was introduced in Massonne et al. (2019). While the extreme conditions are straightforward (broad bar in caimanines with small or nearly closed supratemporal fenestrae versus a constricted bar in gavialines with large fenestrae), variation is continuous in most other taxa. Furthermore, the character is partly correlating with ch. 209.

2. Additional data, results and discussion of phylogenetic analyses

2.1 Phylogenetic analysis of the modified Massonne et al. (2019) dataset

The character-taxon dataset (nexus and tnt files) is in Supplementary Data 1. The complete list of characters is provided in section [4] of the present document. Strict consensus tree is provided in Figure S1.



Figure S1.

Pruned strict consensus of 506 most parsimonious trees (tree length = 1185) from the parsimony analysis of the modified Massonne et al. (2019) dataset employing a molecular backbone constraint following Darlim et al. (2022) and Oaks (2011). *Borealosuchus griffithi* has two alternative positions, either as sister to *Diplocynodon* spp. or an early diverging placement within *Borealosuchus* spp. (orange triangle; see Supplementary Data 1, "Walter et al_[TNT]" for the tnt file). Alternative positions of pruned taxa (*Eocaiman* spp. and *Necrosuchus ioensis*) are furthermore indicated.

List of synapomorphies recovered for Alligatoroidea

4. Atlas intercentrum shape: wedge-shaped (0); or plate-shaped (1).

0 > 1

38. Dorsal midline osteoderms shape: rectangular (0); or nearly square (1).

0 > 1

50. Largest dentary alveolus caudal to fourth: 13 or 14 (0); 13 and 14 and series behind it (1); 11 or 12 (2); no differentiation (3); behind 14 (4); 10 (5); 11 and series behind it (6); or 12 and series behind it (7).

2 > 1

58. Splenial process: separates angular and coronoid (0); or no process between angular and coronoid (1).

0 > 1

121. Choana projecting at maturity: posteroventrally (0); or anteroventrally (1).

0 > 1

131. Ectopterygoid extension at postorbital bar: extends along medial face of postorbital bar (0); or stops abruptly ventral to postorbital bar (1).

0 > 1

139. Quadratojugal spine appearance: prominent at maturity (0); or greatly reduced or absent at maturity (1).

0 > 1

List of synapomorphies recovered for Crocodylia

17. Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1).

1 > 0

26. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

0 > 1

80. Naris projects anterodorsally (0) or dorsally (1) or posterodorsally (2). [modified by Cossette & Brochu (2020)]:

0 > 1

88. Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or projects between first premaxillary teeth (2).

0 > 1

92. Largest maxillary alveolus is 3 (0), 5 (1), 4 (2), 4 and 5 are same size (3), 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).

3 > 1

149. Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2).

0 > 1

List of synapomorphies for Alligatoidea recovered in Cossette & Brochu (2020)

60 (1): Anterior processes of the surangular are equal to subequal.

69 (1): Foramen aerum of articular set in from the margin of retroarticular process.

91 (0): All dentary teeth occlude lingual to maxillary teeth.

130 (1): Anterior tip of frontal forms broad, complex sutural contact with the nasals.

140 (1): The quadratojugal spine is high, between posterior and superior angles of infratemporal fenestra.

176 (1): Quadrate foramen aëreum on dorsal surface.

2.2 Phylogenetic analyses using a modified version of the Rio & Mannion (2021) dataset

In order to test the phylogenetic position of *Deinosuchus* and *Diplocynodon* spp., we performed a parsimony analysis on an alternative dataset using a modified version of Rio and Mannion (2021) [Supplementary Data 2, “Walter-RM” files]. Modifications are detailed below.

We added the following taxa:

Deinosuchus riograndensis Colbert & Bird, 1954

Borealosuchus griffithi Wu, 2001

We modified the scores of the following taxa:

32. Rostral ornamentation, morphology of the transverse orbital ridge (i.e. spectacle): low, lacking a posterior fossa (0); tall, with deep posterior fossa (1).

Diplocynodon remensis: 1 > 0

The ridge is low in *Diplocynodon remensis*, preserved in both the holotype MHNH F BR 4020 and specimen CE0001.

87. Supratemporal fenestra, posterior wall: quadrate forms entire ventral margin of orbitotemporal canal (no parietal-squamosal contact) (0); quadrate partially forms ventral margin of orbitotemporal canal (parietal and squamosal narrowly separated) (1); quadrate excluded from ventral margin of orbitotemporal canal (parietal and squamosal in contact) (2).

Diplocynodon hantoniensis: 1 > (?)

In the juvenile specimen NHMUK OR 25170a, the parietal and squamosal are in contact in the posterior wall of the supratemporal fenestra (2) in contrast to the (1) scoring of Rio & Mannion (2021). Moreover, the left and right squamosal-quadrate sutures in NHMUK OR30393 (Rio et al., 2020; fig. 30) appear different on each side, and might represent independent cracks. In this case, the parietal-quadrate sutures indicated on the figure may actually correspond to the squamosal-parietal contact.

Diplocynodon darwini: 1 > (?)

Direct observation of a large sample of specimens, including those cited in Rio & Mannion (2021), reveals that the material referable to this species is dorsoventrally compressed and we were unable to reproduce the previous scoring of this character. We here conservatively score this taxon as unknown (?).

142. Premaxilla, posterior extent on palate, relative to number of maxillary alveoli, in ventral view: 0 (0); 1 (1); 2 (2); 3 (3); 4 (4); 5 or more (5).

Diplocynodon darwini: ? > (0)

Based on specimen GMH XXXVI 524 1966, the premaxilla does not even extend up to the 1st maxillary alveolus.

241. Surangular, relative length of the anterior processes: unequal, ventral process <75% anteroposterior length of dorsal process (measured from surangular foramen) (0); sub-equal, ventral process \geq 75% length of dorsal process (1).

Diplocynodon hantoniensis: 1 > 0

This scoring was likely erroneously entered in the previous version of the dataset, as state 1 is clearly recognisable in fig. 9D from Rio et al. (2020).

Diplocynodon muelleri: 1 > (?)

Piras & Buscalioni (2006) described this morphology as follows “In its anterior dorsal suture with the dentary, the surangular probably bears two subequal anterior processes. This feature is also seen in the holotype and in a specimen from the Tàrrega Museum”. Direct observation of the holotype and paratype however did not allow assessment of this feature, as the surangular is fragmentary in NMB-Spa 4., and occlusion of the jaws obscures the morphology in NMB-Spa. 73. The alternative specimen of the Tàrrega Museum is not precisely referred, figured nor described, making the previous scoring irreproducible. We therefore adopt a more cautious scoring, here (?).

Diplocynodon ratelii: 1 > 0

The processes are unequal in the specimen MNHN SG 599, we therefore rescore the character as (0).

Diplocynodon remensis: 1 > 0

Based on Martin et al. (2014, fig.5; specimen CE0001), the processes are unequal. We therefore rescore the character as (0).

248. Articular, position of foramen aëreum: at medial margin of retroarticular process (0);
inset from medial margin of retroarticular process (1).

Borealosuchus formidabilis: 0 > 1

Erickson (1976) describes the alligatoroid condition observed on the single specimen preserving this feature (SMM P74.24.6).

Results

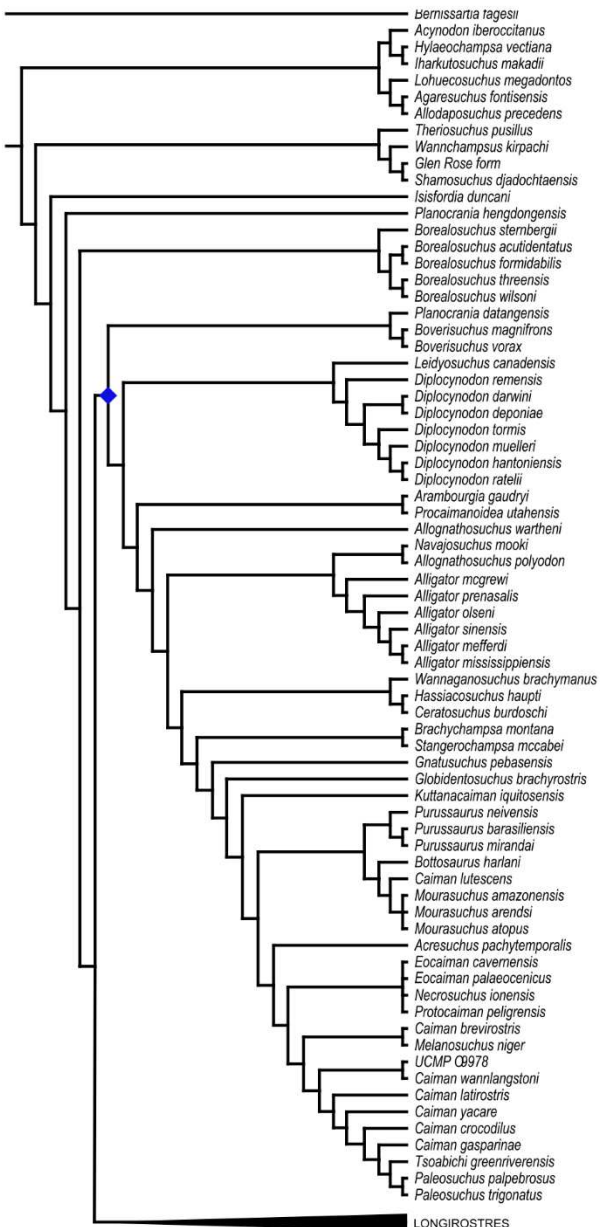
Parsimony analyses of the modified Rio & Mannion (2021) dataset were ran in TNT 1.6. We performed a first round of Traditional Search using 1000 replicates of Wagner trees, followed by a second round of Tree Bisection Reconnection (TBR) using trees saved from the first round, with 10 saves per replication.

Equal weighting parsimony analyses in TNT are as follows:

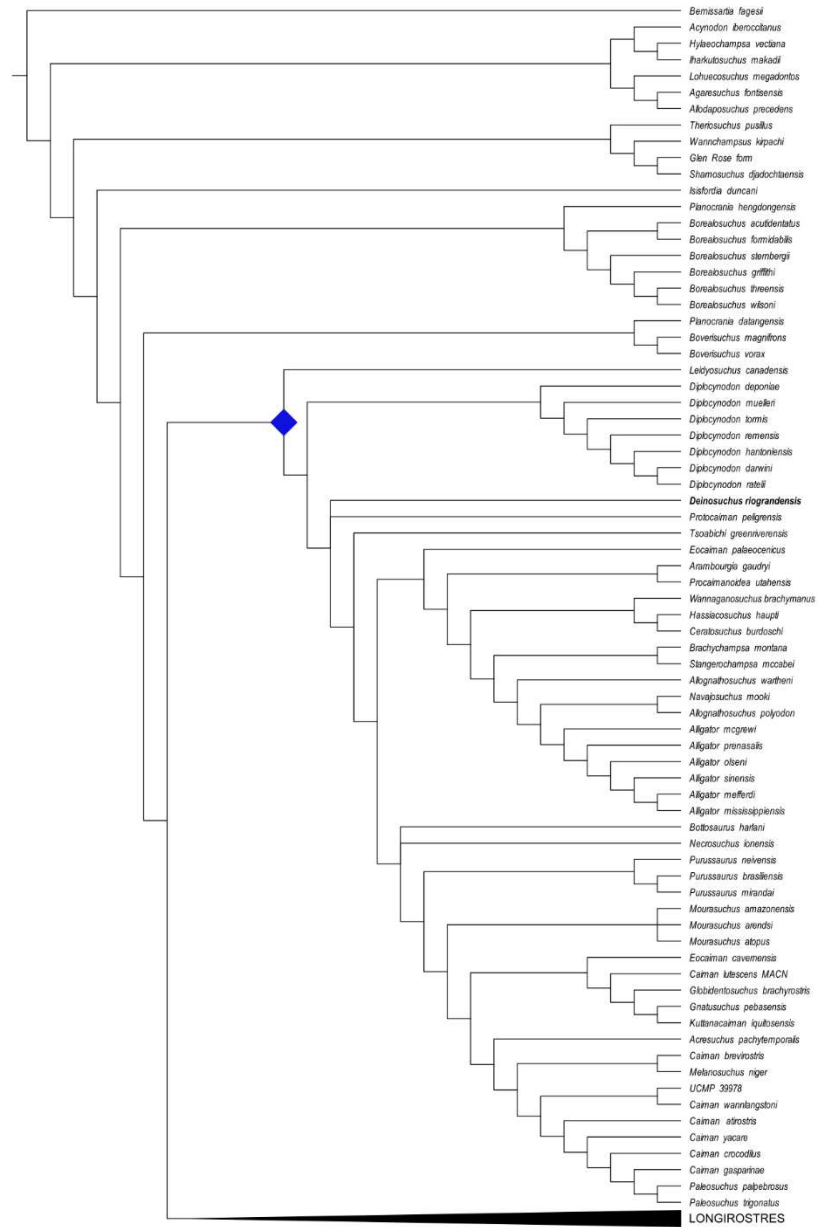
Continuous + discrete dataset (equivalent to analysis 1.1 in Rio & Mannion, 2021)

- 8 MPTs were recovered from the analysis, with a tree length of 225,845.239 (Fig. S2).
- *Diplocynodon* and *Deinosuchus* are placed at the base of Alligatoroidea, but have a poor stratigraphic fit.
- *Diplocynodon* is monophyletic under this topology.
- *Leidyosuchus* is the earliest-branching alligatoroid.
- *Borealosuchus* is monophyletic under this topology. *Planocrania hengdongensis* is sister to the latter clade.
- Planocraniids are not recovered in Alligatoroidea under this topology, in contrast to Rio & Mannion (2021).
- 8 synapomorphies are recovered for Alligatoroidea
 - 1: 1.382-1.608 > 1.614–1.710 - Skull proportions, ratio of mediolateral rostrum width at the level of the anterior orbital margin, to mediolateral width across anterior margin of the cranial table.
 - 104: 0 > 1 - Quadratojugal, position of spina quadratojugal: high, between posterior and dorsal angles of infratemporal fenestra.
 - 117: 0 > 1 - Quadrate, foramen aërum position on posterior quadrate ramus: on dorsal surface.

- 181: 2 > 0 - Ectopterygoid, morphology of posterior process on the medial jugal surface: acute, extends beyond level of posterior margin of postorbital bar.
- 195: 0 > 2 - Choanae, ornamentation of margins: elevated forming a wall which extends to the anterolateral (but not anterior) margins of the choanae.
- 217: 1 > 0 - Dentary, alveoli 3 and 4: confluent.
- 221: 1 > 0 - Mandibular symphysis, posterior extent, adjacent to number of full dentary alveoli: < 6.248: 0 > 1 - Articular, position of foramen aërum: inset from medial margin of retroarticular process.



6 MPTs; tree length 225, 142.3



8 MPTs; tree length 225, 845.239

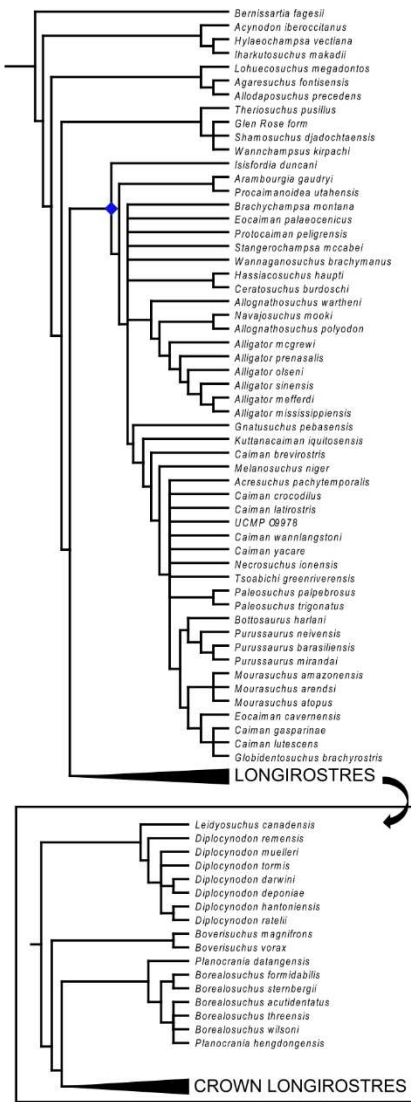
Figure S2.

Strict consensus tree of the Analysis 1.1 of Rio & Mannion (2021) continuous + discrete character dataset (left) and the modified dataset of Rio & Mannion (2021) used in the present study (right). Blue diamond denotes the node Alligatoroidea.

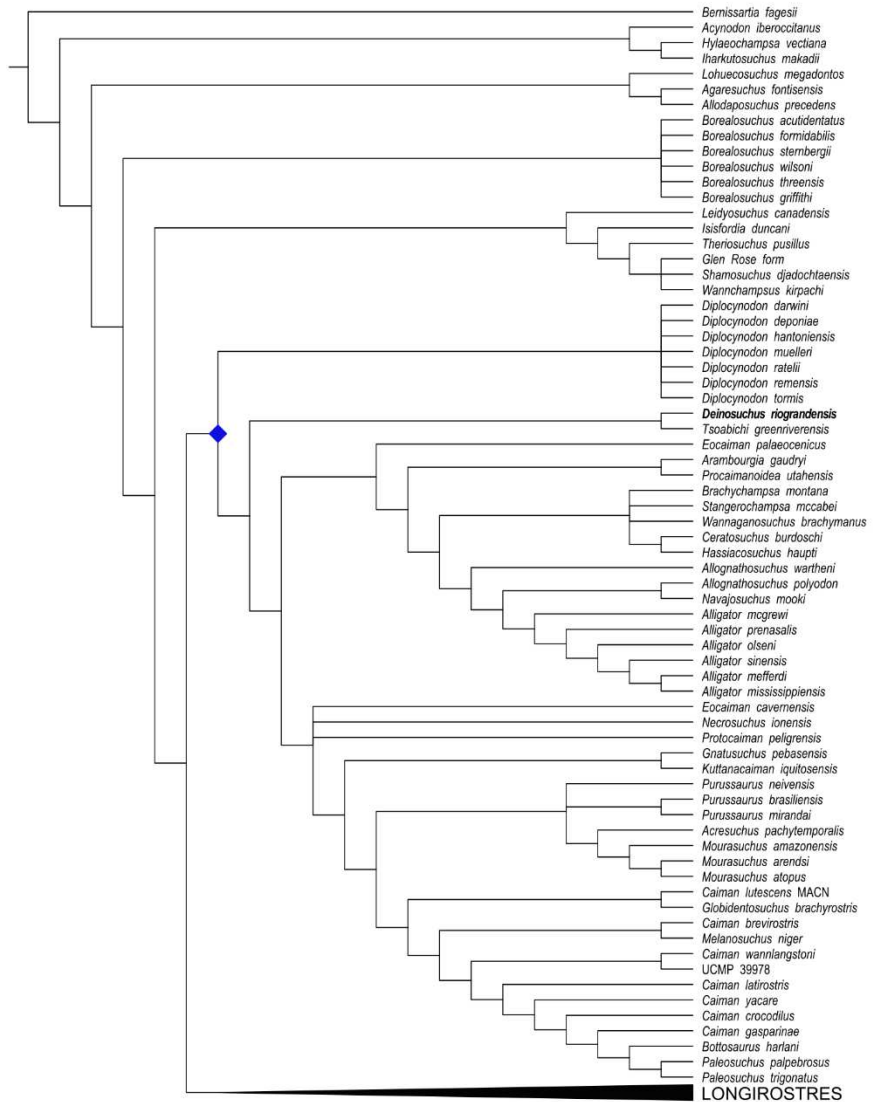
Re-discretised + discrete dataset (equivalent to analysis 2.1 in Rio & Mannion, 2021):

- number of MPTs > 99999, tree length of 2270 steps (Fig. S3).
- Similarly to the continuous + discrete version of the dataset, *Diplocynodon* and *Deinosuchus* are placed at the base of Alligatoroidea, contra Rio & Mannion (2021) result which recovered *Diplocynodon*, *Leidyosuchus* and *Borealosuchus* as early-branching Longirostres.
- *Diplocynodon* is monophyletic under this topology.
- *Deinosuchus* is recovered as a basal alligatoroid, placed one step crownward to *Diplocynodon*.
- *Leidyosuchus* is recovered as a ste-crocodylian under this topology. In contrast to Rio & Mannion (2021), *Isisfordia* is not recovered in Alligatoroidea, but forms a sister clade to crown-Crocodylia together with *Leidyosuchus* and other traditional early-branching eusuchians.
- 10 synapomorphies are recovered for Alligatoroidea:
 - 94: 0 > 1 - Orbit, dorsal profile of jugal forming posteroventral margin: posteroventrally sloping, gradually descending into the lower temporal bar.
 - 103: 0 > 1 - Quadratojugal, development of spina quadratojugal (at maturity): greatly reduced or absent.
 - 104: 0 > 1 - Quadratojugal, position of spina quadratojugal: high, between posterior and dorsal angles of infratemporal fenestra.
 - 152: 0 > 1 - Occlusion pattern, 4th dentary tooth occludes in a pit between premaxilla and maxilla; no notch early in ontogeny.

- 180: 0 > 1 - Ectopterygoid, dorsal extent along medial surface of postorbital bar: small, level with or ventral to level of ventral orbital margin.
- 222: 0 > 2 - Splenial, participation in symphysis: no participation.
- 267: 0 > 1 - Atlantal rib, dorsal margin shape: with prominent process.
- 283: 0 > 1 - Cervical rib 8, length in proportion to cervical rib 9: short, equal to or less than half the length of cervical rib 9.
- 294: 0 > 1 - Caudal vertebrae, articular surfaces of chevrons posterior to the first: completely fused.
- 330: 0 > 1 - Limb armour: densely covered in well-formed osteoderms.



>400,000 MPTs; tree length 2,279



>99,999 MPTs; tree length 2,270

Figure S3.

Strict consensus trees of the redescribed + discrete dataset modified from Rio & Mannion (2021). Left: Analysis 2.1 of Rio & Mannion (2021) parent dataset; Right: this study, modified dataset of Rio & Mannion (2021). Blue diamond denotes the node Alligatoroidea.

Discussion

- *Deinosuchus* is consistently recovered inside Alligatoroidea in the modified Rio & Mannion (2021) dataset, crownward to *Diplocynodon*. This, however, involves a poor stratigraphic fit since representatives of *Deinosuchus* are Campanian and the earliest *Diplocynodon* species is late Paleocene.
- As in previous phylogenies, the stratigraphic fit within *Diplocynodon* is poorly resolved. The oldest species, *Diplocynodon remensis* from the late Paleocene is recovered in a derived position and *Diplocynodon* is monophyletic. On the other hand, this stratigraphic incongruence is resolved in our preferred and alternative topology using the modified Massonne et al. (2019) dataset (Fig. S1; Figs. 1-2), which furthermore recognizes the unique shared derived traits of *Diplocynodon* and *Borealosuchus*.
- The synapomorphies of Alligatoroidea retrieved by these analyses are mostly ambiguous and are not unique to the clade.

3. Sources for taxa

Acynodon adriaticus: Delfino et al., 2008; MCSNT 57248; MCSNT 57032

Acynodon iberoccitanus: Martin, 2007; ACAP-FX1, ACAP-FX2, an ACAP-QR1, ACAP-M1343, ACAP-M260, ACAP-QR7

Agaresuchus subjuniperus: Puértolas-Pascual et al., 2014

Albertochampsia langstoni: Erickson, 1972; Norell et al., 1994;

Alligator mcgrewi: Schmidt, 1941; Brochu, 1999; AMNH FAM 7905, AMNH FAM 8700, AMNH 17090

Alligator mefferdi: Mook, 1941; Brochu, 1999; AMNH 7016

Alligator mississippiensis: O'Brien et al., 2019; Paiva et al., 2022;

Alligator olseni: White, 1942; Brochu, 1999; *Alligator prenasalis*: Brochu, 1999; AMNH 4994, YPM PU

13799, YPM PU 16273, YPM PU 14063

Alligator sinensis: Shan et al., 2013; Iijima et al., 2016; O'Brien et al., 2019; Paiva et al., 2022

Alligator thomsoni: Mook, 1923; Brochu, 1999

Allodaposuchus precedens: Delfino et al., 2008; Martin et al., 2016; PSMUBB V 438; MAFI Ob 3131

Allognathosuchus polyodon: Brochu, 2004b; AMNH 6049

Allognathosuchus wartheni: Brochu, 2004b; YPM PU 16989

Arambourgia gaudryi: Kälin, 1939; MNHN QU17155 (holotype)

Arenysuchus gascabadiolorum: Puértolas-Pascual, 2011

Asiatosuchus germanicus: Berg, 1966; Vasse, 1992; HLMD-Me 5345; GMH-XIV 420; GMH-XIV 4757a; GMH-XIV 4757

Asiatosuchus depressifrons: Delfino & Smith, 2009; Delfino et al., 2017; MNHN G 159, IRScNB IG 9912, IRScNB R 251, IRScNB R 253, IRScNB R 254

Australosuchus clarkae: Willis & Molnar, 1991;

Bernissartia fagesii: Buscalioni & Sanz, 1990; Sookias, 2020; Martin et al., 2020; IRScNB 1538

Borealosuchus acutidentatus: Sternberg, 1932; Lucas & Sullivan, 1986; Brochu, 1997;

Borealosuchus formidabilis: Erickson, 1976; Brochu, 1997; YPM 16242, YPM 16241, YPM 6512; photos from digital collection of SMM

Borealosuchus griffithi: Wu et al., 2001; Lindblad et al., 2022

Borealosuchus sternbergii: Gilmore, 1910; Brochu, 1997; photos from digital collection of USNM

Borealosuchus threensis: Brochu, 2012

Borealosuchus wilsoni: Mook, 1959; Brochu, 1997; Hester, 2018; AMNH 6050, AMNH 7637; photos from digital collection of USNM

Bottosaurus harlani: Cossette & Brochu, 2018;

Bottosaurus fustidens: Cossette, 2021;

Boverisuchus magnifrons: Rossmann, 1998; Brochu, 2012; all material in GMH, HLMD

Boverisuchus vorax: Langston, 1975; Rossmann, 1998; Brochu, 2012; YPM 249 (holotype),

Brachychampsia montana: Norell et al., 1994; Carpenter & Lindsey, 1980; Brochu, 1999; Sullivan & Lucas, 2003; AMNH 5032 (holotype)

Brachychampsia sealeyi: Williamson, 1996

Brachyuranochampsia eversolei: Zangerl, 1944; Mook, 1962; Brochu, 2000; AMNH FARB 6048

Brochuchus pigotti: Conrad et al., 2013

Caiman brevirostris: Fortier et al., 2014; Scheyer & Delfino, 2016

Caiman crocodilus: O'Brien et al., 2019; Paiva et al., 2022

Caiman latirostris: O'Brien et al., 2019; Paiva et al., 2022

Caiman wannlangstoni: Salas-Gismondi et al., 2015; Scheyer & Delfino, 2016

Caiman yacare: O'Brien et al., 2019; Paiva et al., 2022

Centenariosuchus gilmorei: Hastings et al., 2016; Stocker et al., 2021

Ceratosuchus burdoshi: Bartels, 1983; Brochu, 1999

Chinatichampsus wilsonorum: Stocker et al., 2021

Crocodylus acer: Mook, 1921; AMNH 7121

Crocodylus affinis: Mook, 1921; AMNH 1213, AMNH 1719, AMNH

6166, AMNH 16609, AMNH 16622, AMNH 6176, YPM 1352, YPM 265, YPM 266, YPM

246

Crocodylus megarhinus: Mook, 1927; Müller, 1927; Andrews, 2016; AMNH 5061, AMNH

5062

Crocodylus niloticus: O'Brien et al., 2019; Paiva et al., 2022

Crocodylus porosus: O'Brien et al., 2019; Paiva et al., 2022

Crocodylus rhombifer: O'Brien et al., 2019; Paiva et al., 2022

Deinosuchus riograndensis: Cossette & Brochu, 2020; AMNH 3073 (holotype)

Deinosuchus swimmeri: Cossette & Brochu, 2020

Diplocynodon darwini: Ludwig, 1877; SMF-Me 896, SMF-Me 898, SMF-Me 900, SMF-Me 1137, SMF-Me 1289, SMF-Me 2748, SMF-Me 3780; HLMD-Me 233, HLMD-Me 236, HLMD-Me 5317, HLMD-Me 5349, HLMD-Me 5485, HLMD-Me 7492, HLMD-Me 7500, HLMD-Me 10262, HLMD-Me 10496, HLMD-Me 14600a; GMH-XXXVI 524; GMH 6077; SMNK-PAL 6517

Diplocynodon deponiae: Delfino & Smith, 2012; SMF-Me 899; SMF-Me 2609; HLMD-Me 147; HLMD-Me 8080; HLMD-Me 7496

Diplocynodon hantoniensis: Rio et al., 2020; Rio & Mannion, 2021; specimens in Rio et al. (2020)

Diplocynodon muelleri: Piras & Buscalioni, 2006; NMB-Spa 4 (holotype); NMB-Spa 73

Diplocynodon ratelii: MNHN-SG 599; MNHN 13728a; MNHN 13728b

Diplocynodon remensis: Martin et al., 2014b; MNHN-F-BR 4020 (holotype); MNHN-F-BR 13105; MNHN-F-BR 13106; MNHN-F-BR 13100; MNHN-F-BR 3501; CT-scan of CE 0001

Diplocynodon tormis: Buscalioni et al., 1992; IPS 36361 (holotype, IPS-9001 in Buscalioni et al., 1992; housed in ICP)

Dollosuchooides densmorei: Brochu, 2007

Dongnanosuchus hsui: Shan et al., 2021

Eoalligator chunyii: Wu et al., 2018; IVPP V.2716

Eocaiman cavernensis: Simpson, 1933; Godoy et al., 2021; AMNH 3158 (holotype)

Eocaiman itaboraiensis: Pinheiro, 2013

Eocaiman palaeocenicus: Bona, 2007

Eogavialis africanum: Andrews, 1901; Müller, 1927; YPM 6263;

Eosuchus lerichei: Delfino et al., 2005

Eosuchus minor: Brochu, 2006

Eothoracosaurus mississippiensis: Brochu, 2004a

Euthecodon arambourgi: Ginsburg, 1978

Gavialis gangeticus: O'Brien et al., 2019; Paiva et al., 2022;

Gavialis lewisi: Lull, 1944; YPM VP 3226

Gavialosuchus eggenbrugensis: Toula & Kail, 1885; Nicholl et al., 2020

Globidentosuchus brachyrostris: Scheyer et al., 2013; Scheyer & Delfino, 2016

Gnatusuchus pebasensis: Salas-Gismondi et al., 2015; Cidade et al., 2019; Rio & Mannion, 2021; photos from Rodolfo Salas-Gismondi

Gryposuchus colombianus: Salas-Gismondi et al., 2016

Hassiacosuchus haupti: HLMD-Me 4415; HLMD-Me-137; HLMD-Me 9119; HLMD-Me 6117; GMH-Ce-IV 6042

Hylaeochampsa vectiana: Clark, 1992; NHMUK R177

Iharkutosuchus makadii: Ösi, 2008; Ösi & Weishampel, 2009; material in MTM

Jiangxisuchus nankangensis: Li et al., 2019

Kambara implexidens: Salisbury, 1996

Kentisuchus spenceri: Brochu, 2007

Krabisuchus siamogallicus: Martin & Laupraset, 2010; Kr-C-006; Kr-C-007; Kr-C-010; Kr-C-012; Kr-C-015

Kuttanacaiman iquitosensis: Salas-Gismondi et al., 2015

La Venta Caiman: Langston, 1965

Leidyosuchus canadensis: Wu et al., 2001; Brochu, 1997; RTMP 86.221.01, RTMP 96.12.74

Lohuecosuchus mechinorum: Narvaez et al., 2015

Lohuecosuchus megadontos: Narvaez et al., 2015

Maomingosuchus petrolica: Shan et al., 2017

Mecistops cataphractus: O'Brien et al., 2019; Paiva et al., 2022

Melanosuchus niger: Vieira et al., 2016; O'Brien et al., 2019; Paiva et al., 2022

Mourasuchus amazonensis: Paiva et al., 2022

Mourasuchus arendsi: Paiva et al., 2022

Mourasuchus atopus: Paiva et al., 2022

Navajosuchus mooki: Lucas & Estep, 2000; Brochu, 2004b; AMNH 6780, AMNH 5186

Necrosuchus ionensis: Brochu, 2011; Cidade et al., 2019a

Orientalosuchus naduongensis: Massonne et al., 2019; GPIT/RE/09761; GPIT/RE/09730; GPIT/RE/09729; GPIT/RE/09784; GPIT/RE/09727

Osteolaemus osborni: O'Brien et al., 2019; Paiva et al., 2022

Osteolaemus tetraspis: O'Brien et al., 2019; Paiva et al., 2022

Pachycheilosuchus trinquei: Rogers, 2003

Paleosuchus palpebrosus: O'Brien et al., 2019; Paiva et al., 2022

Paleosuchus trigonatus: O'Brien et al., 2019; Paiva et al., 2022

Paratomistoma courti: Brochu, 2000

Pietraroiasuchus ormezzonai: Buscalioni et al., 2011

Piscogavialis jugaliperforatus: Kraus, 1998; Salas-Gismondi, 2016; SMNK 1282 PAL

Planocrania datangensis: Brochu, 2012; IVPP V5016

Planocrania hengdongensis: Brochu, 2012; IVPP V6074

Procaimanoidea kayi: Mook, 1941a; Wasserug & Hecht, 1967; Brochu, 1999

Procaimanoidea utahensis: Gilmore, 1946

Prodiplocynodon langi: Mook, 1941b; AMNH FARB 108

Protoalligator huiningensis: Wang et al., 2016; Massonne et al., 2019

Protocaiman peligrensis: Bona et al., 2018; Shan et al., 2021

Purussaurus brasiliensis: Aguilera, 2006; Paiva et al., 2022

Purussaurus mirandai: Aguilera, 2006; Scheyer et al., 2019; Paiva et al., 2022

Purussaurus neivensis: Paiva et al., 2022

Quinkana spp.: Molnar, 1981; Rossmann, 1998

Rimasuchus lloydi: Storrs, 2003

Shamosuchus djadochtaensis: Pol, 2009; Turner, 2015; AMNH FARB 6412

Stangerochampsia mccabei: Wu, 1996; digital collection of RTMP

Thecachampsia antiqua: Myrick, 2001; Weems, 2018

Thoracosaurus macrorhynchus: Koken, 1888; Voiculescu-Holvad, 2022; (Ca.)

Thoracosaurus neocesariensis: Voiculescu-Holvad, 2022

Tomistoma caireense: Müller, 1927

Tomistoma lusitanica: Antunes, 1961

Tomistoma schlegelii: O'Brien et al., 2019; Paiva et al., 2022

Toyotamaphimeia machikanensis: Kobayashi, 2006

Trilophosuchus rackhami: Willis, 1993; Ristevski et al., 2021

Tsoabichi greenriverensis: Brochu, 2010; Walter et al., 2022; SMNK-PAL 2333a; SMNK-PAL 2333b; SMNK-PAL 2334; AMNH FR 3666

Voay robustus: Brochu, 2007; Bickelmann & Klein, 2009; AMNH FR 3101; AMNH FR 3102; AMNH FR 3103; AMNH FR 310; AMNH FR 3105

Wannaganosuchus brachymanus: Brochu, 1999; Erickson, 1982

Institutional abbreviations:

ACAP: Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois, Cruzy, France;

AMNH: American Museum of Natural History, New York, USA;

GMH: Geiseltal Museum of Martin-Luther-University Halle-Wittenberg, Halle (Saale), Germany;

GPIT: Geologisch-Paläontologisches Institut Tübingen, Tübingen, Germany;

HLMD: Hessisches Landesmuseum Darmstadt, Darmstadt, Germany;

IPS: Institut de Paleontologia Miquel Crusafont of Sabadell, Sabadell, Spain (= **ICP**; Institut Català de Paleontologia Miquel Crusafont);

IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China;

Kr-C: Sirindhorn Museum, Kalasin Province, Thailand;

MAFI: Magyar Állami Földtani Intézet, Hungarian Geological Institute, Budapest, Hungary;

MCSNT: Museo Civico di Storia naturale di Trieste, Trieste, Italy;

MNHM: Museum National d'Histoire Naturelle, Paris, France;

MTM: Magyar Természettudományi Múzeum, (Natural History Museum of Hungary), Budapest, Hungary;

NHMB: Naturhistorisches Museum Basel, Basel, Switzerland;

PSMUBB: Paleontology-Stratigraphy Museum, University Babes, -Bolyai, Cluj-Napoca, Romania;

RTMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada;

SMM: Science Museum of Minnesota, Saint Paul, Minnesota, USA;

SMNK: Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany;

SMF: Senckenberg Museum Frankfurt, Frankfurt, Germany;

TMM: Texas Memorial Museum, Austin, Texas, USA;

USNM: United States National Museum, Smithsonian Institution, Washington DC, USA;

YPM: Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Table S1. List of extant and extinct gigantic crocodyliforms ($\geq 7\text{m}$ in total length)

Age	Species	Source for body-size estimate and association with aquatic mega-ecosystems
Present	<i>Crocodylus porosus</i>	Britton et al., 2012
Pleistocene	Kali Gedeh <i>Crocodylus</i>	Delfino and De Vos, 2014; Sémah et al., 2010, 2016
Plio-Pleistocene	<i>Crocodylus thorbjarnarsoni</i> ; <i>Euthecodon brumpti</i>	Brochu & Storrs, 2012; Brochu, 2020; Nutz et al., 2020
Mio-Pliocene	<i>Rhamphosuchus crassidens</i>	Head, 2001; More et al., 2016; Behrensmeyer et al., 2005; Martin, 2019
Mio-Pliocene	<i>Gryposuchus croizati</i>	Riff and Aguilera, 2008; Kern et al., 2020
Miocene	<i>Purussaurus brasiliensis</i>	Aureliano et al., 2015; Kern et al., 2020
Miocene	<i>Piscogavialis jugaliperforatus</i>	Kraus, 1998; Di Celma et al., 2016; Collareta et al., 2021
late Miocene	<i>Mourasuchus mirandai</i>	Aguilera et al. 2006; Kern et al., 2020
late Oligocene	<i>Astorgosuchus bugtiensis</i>	Martin et al., 2019
early Eocene	<i>Phosphatosaurus gavialoides</i>	Buffetaut, 1979
Campanian	<i>Deinosuchus riograndensis</i>	Erickson & Brochu, 1999; Schwimmer, 2002
Cenomanian	<i>Stomatosuchus inermis</i>	Stromer, 1925; Smith et al., 2001; Khalifa et al. 2008
Aptian–Albian	<i>Sarcosuchus imperator</i>	Sereno et al., 2001; Dridi, 2018
Early Cretaceous	<i>Chalawan thailandicus</i>	Buffetaut & Ingavat, 1980; Martin et al., 2014a

4. List of morphological characters

This list includes the characters in our analysis of the modified Massonne et al. (2019) matrix. The following eleven multistate characters form morphoclines and were therefore ordered in the phylogenetic analysis: 39, 48, 62, 81, 124, 149, 151, 154, 159, 193 and 203.

Character states were added to the following characters:

- 46, 48, 70, 79, 128, 137, and 156 (from Salas-Gismondi et al., 2015)

- 53, 80, 136, and 155 (from Cossette & Brochu, 2020)

- 151 and 159 (from Walter et al., 2022)

- 103 was adapted from the dataset of Rio & Mannion (2021)

The added states are highlighted in bold below and the characters were rescored.

(1) Fused proAtlas boomerang-shaped (0), strap-shaped (1), or massive and block-shaped (2).

(2) ProAtlas with prominent anterior process (0) or lacks anterior process (1).

(3) ProAtlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1).

(4) Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0), or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1).

(5) Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1).

(6) Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end.

(7) Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other.

(8) Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1).

- (9) Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1).
- (10) Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1).
- (11) Axis neural spine crested (0) or not crested (1).
- (12) Posterior half of axis neural spine wide (0) or narrow (1).
- (13) Axis neural arch lacks (0) or possesses (1) a lateral process (diapophysis).
- (14) Axial hypapophysis located toward the center of centrum (0) or toward the anterior end of centrum (1).
- (15) Axial hypapophysis without (0) or with (1) deep fork.
- (16) Hypapophyseal keels present on eleventh vertebra behind atlas (0), twelfth vertebra behind atlas (1), or tenth vertebra behind atlas (2).
- (17) Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1).
- (18) Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1).
- (19) Cervical and anterior dorsal centra lack (0) or bear (1) deep pits on the ventral surface of the centrum.
- (20) Presacral centra amphicoelous (0) or procoelous (1).
- (21) Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0), or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1).

(22) Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1).

(23) Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1).

(24) Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1).

(25) Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1).

(26) Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

(27) M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1).

(28) Olecranon process of ulna narrow and sub-angular (0) or wide and rounded (1).

(29) Distal extremity of ulna expanded transversely with respect to long axis of bone; maximum width equivalent to that of proximal extremity (0) or proximal extremity considerably wider than distal extremity (1).

(30) Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2).

(31) Anterior end of interclavicle flat (0) or rod-like (1).

(32) Iliac anterior process prominent (0) or virtually absent (1).

(33) Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (wasp-waisted; 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4).

(34) Supraacetabular crest narrow (0) or broad (1).

(35) Limb bones relatively robust, and hind limb much longer than forelimb at maturity (0) or limb bones very long and slender (1).

(36) *M. caudofemoralis* with single head (0) or with double head (1).

(37) Dorsal osteoderms not keeled (0) or keeled (1).

(38) Dorsal midline osteoderms rectangular (0) or nearly square (1).

(39) Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity.

(ORDERED)

(40) Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3).

(41) Ventral armor absent (0) or single ventral osteoderms (1) or paired ventral ossifications that suture together (2).

(42) Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1).

(43) Ventral scales have (0) or lack (1) follicle gland pores.

(44) Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2).

(45) Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales (2).

(46) Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0), fourth alveolus larger than third, and alveoli are separated (1), **or 3 and 4 are nearly the same size and separated (2)**. [modified by Salas-Gismondi et al. (2015)].

(47) Anterior dentary teeth strongly procumbent (0) or project anterodorsally (1).

(48) Dentary symphysis extends to fourth or fifth alveolus (0), or sixth through eighth alveolus (1), **or eight to twelfth alveolus (2), or twelfth to sixteenth (3), beyond the sixteenth (4)**. [modified by Salas-Gismondi et al. (2015)]. (ORDERED)

(49) Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli.

(50) Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) between 11 and 14 and a series behind it, (2) 11 or 12, (3) no differentiation, (4) behind 14, (5) 10.

(51) Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1).

(52) Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2).

(53) Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide 'V' within symphysis (3) or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis

and forms narrow 'V' (4) or **splenia reaches mandibular symphysis but does not touch other splenia** (5). [modified by Cossette & Brochu (2020)].

(54) Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2).

(55) Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1).

(56) Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

(57) Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1).

(58) Process of splenia separates angular and coronoid (0) or no splenia process between angular and coronoid (1).

(59) Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1).

(60) Anterior processes of surangular unequal (0) or sub-equal to equal (1).

(61) Surangular with spur bordering the dentary toothrow lingually for at least one alveolus length (0) or lacking such spur (1).

(62) External mandibular fenestra absent (0) or present as narrow slit, no discrete fenestral concavity on angular dorsal margin (1) or present with discrete concavity on angular dorsal margin (2) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (3). (ORDERED)

(63) Surangular-dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1).

(64) Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1).

(65) Surangular-angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1).

(66) Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1).

(67) Articular-surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3).

(68) Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1).

(69) Foramen aerum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1).

(70) Retroarticular process projects posteriorly (0) projects posterodorsally, **not higher than the posterior edge of the articular fossa (1), or projects posterodorsally higher than the posterior edge of the articular fossa (2)**. [modified by Salas-Gismondi et al. (2015)]

(71) Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1).

(72) Surangular-articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

(73) Sulcus between articular and surangular (0) or articular flush against surangular (1).

- (74) Dorsal projection of hyoid cornu flat (0) or rod-like (1).
- (75) Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1).
- (76) Lingual osmoregulatory pores small (0) or large (1).
- (77) Tongue with (0) or without (1) keratinized surface.
- (78) Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2).
- (79) Maxillary and dentary teeth with smooth carinae (0) serrated (1), **or with neither carinae nor serrations (2)**. [modified by Salas-Gismondi et al. (2015)]
- (80) Naris projects anterodorsally (0) or dorsally (1) **or posterodorsally (2)**. [modified by Cossette & Brochu (2020)]
- (81) External naris bisected by nasals (0) or nasals contact external naris, but do not bisect it (1) or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3). (ORDERED)
- (82) Naris circular or keyhole-shaped (0) or wider than long (1) or anteroposteriorly long and prominently teardrop-shaped (2).
- (83) External naris of reproductively mature males (0) remains similar to that of females or (1) develops bony excrescence (ghara).
- (84) External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest.
- (85) Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1).
- (86) Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny.

(87) Incisive foramen small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects premaxillary-maxillary suture (2).

(88) Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or projects between first premaxillary teeth (2).

(89) Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1).

(90) Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1).

(91) All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between seventh and eighth maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with maxillary toothrow (2).

(92) Largest maxillary alveolus is 3 (0), 5 (1), 4 (2), 4 and 5 are same size (3), 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).

(93) Maxillary tooth row curved medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli.

(94) Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1).

(95) Canthi rostralii absent or very modest (0) or very prominent (1) at maturity.

(96) Preorbital ridges absent or very modest (0) or very prominent (1) at maturity.

(97) Antorbital fenestra present (0) or absent (1).

(98) Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary-maxillary suture (1).

(99) Vomer entirely obscured by maxillae and palatines (0) or exposed on palate between palatines (1).

(100) Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1).

(101) Medial jugal foramen small (0) or very large (1).

(102) Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1).

(103) Ectopterygoid, contact with maxillary toothrow, forming the medial wall of at least one maxillary alveolus: absent, ectopterygoid-maxilla suture anteromedially orientated and separated from toothrow margin (0); absent, ectopterygoid-maxilla suture parallel and adjacent to medial toothrow margin (1); present (2) (modified by Rio & Mannion, 2021).

(104) Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of the lower temporal bar (1).

(105) Penultimate maxillary alveolus less than (0) or more than (1) twice the diameter of the last maxillary alveolus.

(106) Prefrontal dorsal surface smooth adjacent to orbital rim (0) or bearing discrete knob-like processes (1).

(107) Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1).

(108) Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1).

(109) Prefrontal pillar solid (0) or with large pneumatic recess (1).

(110) Medial process of prefrontal pillar wide (0) or constricted (1) at base.

(111) Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making lateral margin concave (1).

(112) Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1).

(113) Anterior ectopterygoid process tapers to a point (0) or forked (1).

(114) Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra.

(115) Palatine process generally broad anteriorly (0) or in form of thin wedge (1).

(116) Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1).

(117) Palatine-ptyergoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra.

(118) Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1).

(119) Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1).

(120) Anterior border of the choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1).

(121) Choana projects posteroventrally (0) or anteroventrally (1) at maturity.

(122) Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form neck surrounding aperture (2) or everted from flat surface to form neck surrounding aperture (3).

- (123) Posterior rim of internal choana not deeply notched (0) or deeply notched (1).
- (124) Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2). (ORDERED)
- (125) Ectopterygoid-pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1).
- (126) Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity.
- (127) Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2).
- (128) Prefrontals separated by **the** frontals and nasals, **anterior process of frontal extending far anterior to the anterior margin of the orbit (0)**, **prefrontals separated by the frontal and nasals, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (1)** or prefrontals meet medially, **anterior process of frontal around the same level or posterior to the anterior margin of the orbit (2)**. [modified by Salas-Gismondi et al. (2015)]
- (129) Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2).
- (130) Anterior tip of frontal (0) forms simple acute point or (1) forms broad, complex sutural contact with the nasals.
- (131) Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).
- (132) Postorbital bar massive (0) or slender (1).

(133) Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0) or bears process that is short and generally not prominent (1).

(134) Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1).

(135) Postorbital bar continuous with anterolateral edge of skull table (0) or inset (1).

(136) Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or orbital margin telescoped (2) **or anterior margins of orbit telescoped (3)**. [modified by Cossette & Brochu (2020)]

(137) **Anterior margin of orbit not upturned**, ventral margin gently circular (0) **or anterior margin upturned, ventral margin gently circular (1)**, **or anterior margin upturned**, ventral margin with a prominent notch (1). [modified by Salas-Gismondi et al. (2015)]

(138) Palpebral forms from single ossification (0) or from multiple ossifications (1).

(139) Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1).

(140) Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1).

(141) Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (2).

(142) Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3).

(143) Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1).

(144) Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1).

(145) Postorbital-squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

(146) Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1).

(147) Quadrate and squamosal not in contact on the external surface of the skull, posteriorly to the external auditory meatus (0) or quadratosquamosal suture extends dorsally along caudal margin of the external auditory meatus (1) or extends only to the caudoventral corner of the external auditory meatus (2).

(148) Caudal margin of otic aperture not defined and gradually merging into the exoccipital (0) or smooth and continuous with the paraoccipital process (1) or caudal margin of otic aperture inset (2).

(149) Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2). (ORDERED)

(150) Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae.

(151) Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0), or **parietal overhangs the rim at maturity (1)**, or **postorbital, squamosal and parietal overhang the rim at maturity (2)**, or fenestra is closed at maturity (3). [modified by Walter et al. (2022)] (ORDERED)

(152) Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1).

(153) Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1).

(154) Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2). (ORDERED)

(155) Skull table surface slopes ventrally from sagittal axis (0) or planar (1) **or skull table surface slopes ventrally towards sagittal axis at maturity, lateral elements planar (2)** at maturity. [modified by Cossette & Brochu (2020)]

(156) Squamosal **on skull table** is horizontal or nearly so (0), or upturned to form a **posterolateral** discrete horn (1), **or producing a high transversely oriented eminence at the posterior margin (2) late in ontogeny**. [modified by Salas-Gismondi et al. (2015)]

(157) Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1).

(158) Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process.

(159) Supraoccipital exposure on dorsal skull table **absent (0), small (1)**, large (2), or large such that parietal is excluded from posterior edge of table (3). [modified by Walter et al. (2021)] (ORDERED)

(160) Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum.

(161) Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1).

(162) Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen.

(163) Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1).

(164) Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process or palatine (1).

(165) Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

(166) Parietal with recess communicating with pneumatic system (0) or solid, without recess (1).

(167) Significant ventral quadrate process on lateral braincase wall (0) or quadrate-pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1).

(168) Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity.

(169) External surface of basioccipital ventral to occipital condyle oriented posteroventrally (0) or posteriorly (1) at maturity.

(170) Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2).

(171) Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital.

(172) Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1).

(173) Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital process; process lateral to cranioquadrate opening long (1).

(174) Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal.

(175) Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process ventrally to basioccipital tubera (2).

(176) Quadrate foramen aerum on mediodorsal angle (0) or on dorsal surface (1) of quadrate.

(177) Quadrate foramen aereum is small (0), comparatively large (1), or absent (2) at maturity.

(178) Quadrate lacks (0) or bears (1) prominent, mediolaterally thin crest on dorsal surface of ramus.

(179) Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0) or prominent knob (1).

(180) Quadrate with small, ventrally-reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aerum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3).

(181) Iris (0) greenish/yellowish or (1) brown.

(182) Two or more (0) or one (1) row of postoccipital osteoderms.

(183) Fewer than eight (0) or eight to 14 (1) or more than 14 (2) paired midline scale rows.

(184) Ectopterygoid maxillary ramus forms less than (0) or more than (1) two-thirds of lateral margin of suborbital fenestra.

(185) Ectopterygoid maxillary ramus terminates at lateral margin of suborbital fenestra (0) or lateral to it, with maxilla separating the ectopterygoid from fenestra for short distance.

(186) Palatine-maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1).

(187) Frontal lacks (0) or bears (1) prominent midsagittal crest between orbits.

(188) All cervical neural spines anteroposteriorly broad (0) or posterior neural spines thin and rod-like (1).

(189) Largest premaxillary tooth is the second (0), the third (1) or the fourth (2) or the third and fourth similarly largest (3) or all similarly same in size (4) or the fourth and fifth similarly largest (5) or the first four similarly equal in size (6)

(190) Dorsal surface of the surangular is smooth (0), or bears a large sulcus next to the anterior half of the glenoid fossa (1).

(191) 'U'-shaped depression of the frontal at the point of maximum constriction between the orbits: absent (0); present (1).

(192) Skull in lateral view relatively flat (0) or formed like a wedge **and trapezoid in shape** (1).

(193) Anterior process of jugal extends anterior (0), lies at the same level as (1), or well posterior to the anterior process of frontal (2). (ORDERED)

(194) Notch between the premaxilla and maxilla present (0) or absent (1) in adult individuals.

(195) Anterior maxillary teeth without (0) or with (1) ridges on their lateral surface

(196) If largest dentary alveolus is between 11th and 14th and a series behind it, is it the (0) 11th, (1) 12th, or (2) 13th or 14th.

(197) Surangular-angular suture lingually originates (0) near the ventral border of the external mandibular fenestra, (1) near the dorsal border of the external mandibular fenestra and straight, (2) near the dorsal border of the external mandibular fenestra and bowed.

(198) If supraoccipital exposure on skull table is large or very large, is it (0) trapezoid, (1) triangular, or (2) block-shaped.

(199) Edge of the maxillary tooth alveoli lower or at the same level than the space between toothrow (0) or edge of maxillary tooth alveoli higher than the space (1). [added from Stocker et al. (2021)]

(200) Ventral border of exoccipital convex and ventrally projected, hiding the posterior opening of the cranioquadrate passage from the occipital view (0), or straight, sharpen or smoothly convex and does not hide the posterior opening of the cranioquadrate passage from the occipital view (1). [added from Stocker et al. (2021)]

(201) Occipital surface sloped, visible in dorsal view (0), or vertical or not visible in dorsal view (1) at maturity. [added from Stocker et al. (2021)]

(202) Ventral premaxilla-maxilla suture short and ends posteriorly before the 3rd maxillary alveoli (0) or elongated and extends or exceeds the 3rd maxillary alveoli (1). [added from Stocker et al. (2021)]

(203) Less than 18 teeth (0), 18 to 22 teeth (1), or more than 22 teeth (2) on maxilla. [added from Stocker et al. (2021)] (ORDERED)

(204) Lateral edge of the skull table at the level of the postorbital-squamosal suture situated laterally or at the same level as (0), or medially to (1) the quadrate condyle in dorsal view at maturity. [added from Stocker et al. (2021)]

(205) Frontal ends at the same level or posterior (0) or extends well anterior (1) to the anterior extension of the prefrontal. [added from Stocker et al. (2021)]

(206) Maxilla posterior process without tooth, short or absent (0), or long, longer than the distance between the three last teeth (1) in ventral view. [added from Stocker et al. (2021)]

(207) Interorbital bridge narrower to equivalent (0), or broader (1) than the width of the orbit. [added from Stocker et al. (2021)]

(208) Supratemporal fenestra longer than wide or rounded, posterior bar of supratemporal fenestra thick (0), or wider than long, posterior bar of supratemporal fenestra thick (1), or wider than long, posterior bar thin (2) at maturity. [added from Stocker et al. (2021)]

(209) Presence (0), or absence (1) of a medial crest on the basioccipital. [added from Stocker et al. (2021)]

(210) Absence (0), or presence (1) of a posterior dentary process between splenial and angular on the ventral side. [added from Stocker et al. (2021)]

(211) Dorsal margin of the articular on the retroarticular process largely visible in lateral view (0), or slightly or not visible in lateral view (1). [added from Stocker et al. (2021)]

(212) Posterior margin of the orbit anterior to the posterior margin of the suborbital fenestra (0), or posterior or at the same level than the posterior margin of the suborbital fenestra (1) measured at the level of the postorbital-frontal suture in the orbital margin. [added from Stocker et al. (2021)]

(213) Basioccipital-exoccipital process ventral to occipital condyle (basioccipital plate) with parallel or ventrally convergent sides (0) or ventrally divergent sides (1) in posterior view. [added from Stocker et al. (2021)]

(214) Absence (0) or presence (1) of a smooth medial depression ventral to the basioccipital and posterior to the medial Eustachian foramen. [added from Stocker et al. (2021)]

(215) Dentary teeth series behind to alveoli 12-13 are pointed to slightly blunt (0); globular, different in size among them (1); globular, at least four subequal in size (2), molariform multicusped (3) or absent (4). [added from Stocker et al. (2021)]

(216) First four alveoli in the dentary are the same size or smaller than other dentary alveoli (0) or are the largest within the dentary (1). [added from Stocker et al. (2021)]

(217) Orbits longer than wide (0) or wider than long to rounded (1) late in ontogeny. [added from Stocker et al. (2021)]

(218) The series composed by the last three premaxillary teeth diverge posteriorly to paraxial (0) or tend to converge posteriorly, straight among them (1). [added from Stocker et al. (2021)]

(219) Dentary, level of the first and fourth alveoli: lower than the level of the eleventh and twelfth alveoli (0); equal to higher than the level of the eleventh and twelfth alveoli (1). [added from Stocker et al. (2021)].

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6. Table: Data and Results from the phylogenetic body-size analysis

Table of estimations provided by the phylogenetic body-size analysis for each taxon, from the minimum (min) to maximum (max). Head width (HW) measurements are also provided, together with the specimen number (Specimen no).

Taxon	HW (cm)	min	2,5 %q	25% q	median	mean	75% q	97,5 %q	max	Specimen no
<i>Acynodon adriaticus</i>	10.6	90.8 477 2 378 6	107. 169 596 3	107. 169 596 3	143. 143. 5075 338	143.9 143.9 9653 4	159.4 159.4 5997 34	196.6 196.6 3807 57	239.28 45519	MCSN T 57248
<i>Acynodon iberoccitanus</i>	11.0	91.0 453 5 622 3	108. 322 028 8	108. 322 028 8	149. 149. 1158 77	148.9 148.9 3423 68	164.8 164.8 5526 01	202.4 202.4 3412 42	265.67 48491	ACAP FX1
<i>Agaresuchus subjuniperus</i>	25.4	175. 354 4 420 8	211. 863 594	211. 863 594	289. 289. 7710 601	289.7 289.7 4033 62	320.3 320.3 5454 47	391.9 391.9 8378 53	521.80 83361	MPZ 2012 288
<i>Albertochampsia langstoni</i>	14.3	120. 048 818 7	141. 464 311 7	141. 464 311 7	175. 175. 8596 88	175.9 175.9 0508 26	188.1 188.1 9071 83	220.0 220.0 4000 82	250.38 79851	SMM P67 15 3
<i>Alligator mcgrewi</i>	5.08	49.5 927 330 7	58.0 730 482 4	58.0 730 482 4	74.4 74.4 2226 953	74.56 74.56 1461 48	81.07 81.07 2544 94	94.59 94.59 8943 59	113.77 22018	AMNH 7303
<i>Alligator mefferdi</i>	20	169. 007 784 8	193. 979 861 2	193. 979 861 2	225. 225. 7380 026	226.1 226.1 3044 62	238.0 238.0 0194 66	266.5 266.5 4245 53	298.27 88951	AMNH 7016
<i>Alligator olseni</i>	13.7	123. 302 8 318 3	140. 074 892 5	140. 074 892 5	165. 165. 9408 81	165.5 165.5 8184 3	175.6 175.6 4047 39	194.4 194.4 6130 46	208.51 21404	MCZ 1887
<i>Alligator prenasalis</i>	16.7	142. 351 768	160. 982 792 8	160. 982 792 8	194. 194. 6075 628	194.3 194.3 6794 52	206.8 206.8 0508 53	235.2 235.2 8589 45	287.00 34178	SDSM 243
<i>Alligator thomsoni</i>	24.6	199. 627 4 628 5	223. 117 676 6	223. 117 676 6	264. 264. 4636 939	264.1 264.1 5108 18	279.8 279.8 0114 38	315.8 315.8 1164 92	370.87 61906	TMM 31219 233

<i>Allodaposuchus precedens</i>	34.7 6	224. 099 741 1	278. 027 015 6	278. 027 015 6	373. 8681 886	374.8 1814 44	416.2 2547 68	503.2 2087 62	695.80 54252	MMS VBN 12 10A
<i>Allognathosuchus polyodon</i>	13.6	111. 037 752 7	131. 220 836 3	131. 220 836 3	167. 1821 733	167.4 3079 24	182.3 4853 26	212.2 3098 86	257.76 11823	AMNH 6049
<i>Allognathosuchus wartheni</i>	6.12	57.1 984 407 2	68.6 650 641 8	68.6 650 641 8	88.0 6634 823	88.24 8871 49	95.63 0105 6	112.7 0493 97	137.68 17341	YPM- PU 16989
<i>Arambourgia gaudryi</i>	6.43	58.1 966 525 4	70.6 852 613 1	70.6 852 613 1	91.8 0491 892	91.85 3281 84	100.3 0701 56	119.6 7654 34	144.93 8035	MNHN QU 17155
<i>Arenysuchus gascabadiolorum</i>	10.8 6	86.2 164 376 2	106. 459 900 5	106. 459 900 5	146. 6237 186	146.6 1145 06	163.8 3468 43	199.3 9997 56	254.18 60834	ELI 1
<i>Asiatosuchus depressifrons</i>	37.3	242. 770 529 1	306. 597 608 1	306. 597 608 1	403. 6861 004	403.8 6916 81	442.5 7514 21	531.6 7782 65	647.36 01774	IRSNB R251
<i>Asiatosuchus germanicus</i>	32.4	184. 759 902 2	268. 359 731 2	268. 359 731 2	357. 7715 04	358.7 9379 74	395.8 0970 86	478.5 5149 73	643.60 47432	HLMD- Me 5345
<i>Australosuchus clarkae</i>	15.3 3	116. 872 144 8	150. 075 714 8	150. 075 714 8	200. 9853 527	201.2 5592 75	222.6 5030 27	274.2 7984 2	378.14 53133	QM F16788
<i>Bernissartia fagesii</i>	6.25	63.7 408 193 6	75.1 337 968 4	75.1 337 968 4	94.5 8569 69	94.54 4429 28	102.6 6800 41	118.4 3338 22	143.63 25711	IRSNB R46
<i>Borealosuchus acutidentatus</i>	21.4 5	132. 542 951 7	181. 841 530 3	181. 841 530 3	252. 8230 188	252.4 1778 78	281.3 7380 37	342.5 5158 5	460.29 52813	NMC 8544
<i>Borealosuchus formidabilis</i>	34.8 3	189. 187 457 6	265. 066 244 3	265. 066 244 3	371. 2249 998	372.8 9221 54	415.9 8134 11	513.8 8690 93	683.31 10702	SMM P75 22 29

<i>Borealosuchus griffithi</i>	19.5 2	118. 391 206 3	172. 150 850 2	172. 150 850 2	234. 6925 284	234.1 6408 53	261.5 2042 29	322.0 6460 13	413.21 77796	UALVP 40955
<i>Borealosuchus sternbergii</i>	18.8 7	120. 092 274 1	170. 596 502 9	170. 596 502 9	228. 4365 06	228.8 1303 46	254.4 1199 66	311.4 7552 19	413.81 28298	USNM 6533
<i>Borealosuchus wilsoni</i>	20.5 6	132. 106 510 3	173. 726 653 5	173. 726 653 5	245. 2979 885	244.0 7844 09	273.3 3249 21	338.8 9432 65	468.19 10897	AMNH 7637
<i>Bottosaurus harlani</i>	43.7 9	277. 429 185 1	342. 391 031	342. 391 031	411. 7649 118	412.3 4980 77	438.2 1750 35	503.4 4335 72	602.09 86596	NJSM 11265
<i>Boverisuchus magnifrons</i>	12.4 7	89.5 203 113 5	120. 817 890 1	120. 817 890 1	163. 8699 935	163.8 3664 76	181.9 0563 48	220.8 6439 44	267.97 59758	GMH XXXVI 274
<i>Boverisuchus vorax</i>	24.0 4	158. 013 247 8	204. 964 543	204. 964 543	277. 9325 846	277.6 4109 51	307.9 9521 76	375.7 2169 06	467.99 1545	FMNH PR399
<i>Brachychampsa montana</i>	21.9 3	161. 264 001 1	196. 782 289 4	196. 782 289 4	247. 7339 681	247.4 6837 94	266.5 8377 08	315.1 8169 79	366.02 22456	UCMP 133901
<i>Brachyuranochampsa eversolei</i>	21.9	162. 360 465 1	194. 708 919 6	194. 708 919 6	263. 3842 286	263.5 5281 96	291.2 7690 05	355.2 2875 46	463.16 36287	CM 9372
<i>Brochuchus pigotti</i>	15.9 8	136. 442 365 3	157. 253 231 1	157. 253 231 1	187. 9534 821	187.9 1095 22	199.3 3410 97	227.9 1548 73	257.52 66671	Conrad et al. 2013
<i>Caiman breviostris</i>	14.6	112. 037 222 3	137. 087 813 7	137. 087 813 7	168. 2570 54	168.9 6316 22	182.0 6052 91	208.6 3371 94	268.95 93228	UFAC 5388
<i>Caiman wannlangstoni</i>	18.2 4	139. 725 990 9	162. 795 926	162. 795 926	202. 7008 972	202.0 3115 85	218.2 4797 74	249.7 5918 29	301.87 51328	MUSM 2377

<i>Ceratosuchus burdoshi</i>	3.65	35.4 767 958	44.6 899 427 1	44.6 899 427 1	58.4 3663 788	58.50 2721 39	64.32 7353 27	78.20 2824 19	91.247 80195	FMNH P15576
<i>Chinatichampsus wilsonorum</i>	15.4 3	119. 040 773 9	141. 141. 629 539	141. 141. 629 539	184. 184. 7898 783	184.9 6513 51	202.3 1341 44	241.7 7867 93	279.53 82831	TMM 45911- 1
<i>Crocodylus affinis</i>	33.7 2	234. 115 600 9	279. 771 769 5	279. 771 769 5	371. 371. 5172 945	373.1 7532 76	410.7 7303 21	492.2 3500 05	639.17 00053	YPM 1345
<i>Crocodylus megarhinus</i>	34	208. 893 269 4	278. 394 349 3	278. 394 349 3	379. 379. 1505 798	377.9 9042 61	421.6 7836 3	514.3 9913 83	668.45 87974	AMN 5061
<i>Deinosuchus riograndensis</i>	60.4	381. 573 373 1	434. 553 791 7	434. 553 791 7	580. 580. 5383 708	580.9 3827 04	643.8 2951 37	766.7 6448 28	1050.9 14204	TMM 43620- 1
<i>Deinosuchus schwimmeri</i>	48	315. 015 706 1	366. 918 680 4	366. 918 680 4	483. 483. 6960 092	483.2 8042 38	533.6 6298 5	637.4 6025 95	764.72 0199	MMNS VP-256
<i>Diplocynodon darwini</i>	13.4 9	93.3 045 452 1	123. 123. 394 793	123. 123. 394 793	174. 174. 3857 06	174.0 5376 87	195.0 7056 22	247.9 4001 87	312.37 84732	SMF- Me 900
<i>Diplocynodon deponiae</i>	7.23	54.8 626 188 7	75.5 204 239 1	75.5 204 239 1	106. 106. 0454 133	105.6 9652 54	119.2 7858 04	148.3 3180 08	199.94 50568	SMF- Me 2609
<i>Diplocynodon hantoniensis</i>	25.6 1	160. 709 446 5	206. 457 362 1	206. 457 362 1	292. 292. 0928 25	291.9 4846 8	330.2 9806 96	416.1 4318 67	588.61 25879	NHMU K OR 30392
<i>Diplocynodon muelleri</i>	7.23	45.3 573 230 7	73.6 823 388 3	73.6 823 388 3	105. 105. 8340 274	105.5 8913 06	119.3 5087 36	152.7 2341 87	185.32 36114	Spa-4
<i>Diplocynodon ratelli</i>	15.4 5	98.4 391 120 1	134. 134. 925 111	134. 134. 925 111	193. 193. 4808 446	194.0 9718 81	221.0 5268 11	277.8 0443 92	415.65 92521	MNHN SG 539

<i>Diplocynodon remensis</i>	20.2 1	135. 079 9	176. 344 957 4	176. 344 957 4	240. 0152 739	241.5 0208 93	267.9 6997 25	334.1 5079 21	409.25 38182	MNHN F BR 13105
<i>Diplocynodon tormis</i>	9.4	68.5 815 228 4	90.5 650 043 5	90.5 650 043 5	130. 6519 647	130.2 4026 09	146.5 5158 02	182.7 4676 68	254.63 46682	IPS- 9001
<i>Dollosuchoides densmorei</i>	20.4	171. 609 019 4	193. 149 973 5	193. 149 973 5	255. 4888 59	255.9 2013 62	280.4 6419 25	332.8 5329 48	399.64 15818	IRSNB 1748
<i>Dongnanosuchus hsui</i>	14.9 5	114. 991 116 2	140. 091 310 2	140. 091 310 2	184. 3681 743	184.7 3818 11	203.3 7697 5	247.1 5869 5	343.69 90965	DM000 001- F00000 1
<i>Eosuchus lerichei</i>	17.6 8	165. 306 703 4	193. 705 682 6	193. 705 682 6	241. 4112 591	242.3 9228 41	262.7 3590 08	307.5 8606 01	344.69 63279	IRSNB R48
<i>Eosuchus minor</i>	16.0 5	142. 938 373 9	176. 633 771 9	176. 633 771 9	223. 0896 28	223.5 4788 19	242.1 7829 22	281.9 0395 92	336.04 59463	USNM 299730
<i>Eothoracosaurus mississippiensis</i>	39.7 8	337. 500 387 2	381. 175 123 9	381. 175 123 9	470. 5618 2	469.7 8061 22	502.9 6162 47	577.8 0016 01	665.30 50214	MSU 3293
<i>Euthecodon arambourgi</i>	11.2 3	104. 574 227 8	119. 283 991 9	133. 032 881 7	141. 4357 221	141.7 0827 86	150.6 1904 2	169.3 1624 48	195.68 62119	KNM- LT 23177
<i>Globidentosuchus brachyrostris</i>	15.3 4	118. 645 514 5	135. 544 128 8	135. 544 128 8	183. 5747 74	183.5 8821 97	203.5 7946 99	250.7 9032 83	321.89 62323	AMU- CURS- 222
<i>Gnatusuchus pebasensis</i>	21.6	140. 403 018 4	178. 670 514 4	178. 670 514 4	241. 8640 086	241.2 3307 67	268.3 3072 64	320.8 3312 23	426.36 4726	MUSM- 990
<i>Gryposuchus colombianus</i>	41.8 2	398. 291 302 6	484. 740 727 4	484. 740 727 4	581. 0271 54	579.7 5820 02	614.9 4470 45	698.8 8691 76	802.23 19311	IGM 184696

<i>Hassiacosuchus haupti</i>	8.95	76.0 891 377 7	90.9 060 353 7	90.9 060 353 7	119. 7806 711	119.5 3526 97	130.9 8854 71	154.9 5100 12	194.34 27482	HLMD- Me 1435
<i>Iharkutosuchus makadii</i>	5.06	46.1 597 617 1	59.3 393 897 2	59.3 393 897 2	79.7 9490 758	79.63 9839 39	87.97 4205 08	106.6 4883 79	137.36 9355	MTM 2006 52 1
<i>Jiangxisuchus nankangensis</i>	13.4	115. 618 711 6	134. 709 941 8	134. 709 941 8	168. 6841 605	169.1 3636 29	182.2 5187 65	215.3 6825 27	255.69 21268	IVPP V 19125
<i>Kambara implexidens</i>	15.9 4	126. 318 770 3	158. 896 176 3	158. 896 176 3	207. 5346 757	207.0 0620 34	226.0 8493 04	271.0 5930 62	366.70 47485	QMF29 662
<i>Kuttanacaiman iquitosensis</i>	15.8 2	105. 835 928 3	131. 868 300 2	131. 868 300 2	183. 6991 317	184.1 3576 93	203.6 4946 71	251.3 6259 11	329.29 42661	MUSM- 1490
<i>La venta Caiman</i>	24.8 8	178. 915 911 8	209. 592 627 8	209. 592 627 8	259. 9481 613	259.5 0526 32	280.6 6506 55	318.3 6365 39	424.56 97916	UCMP- 39978
<i>Leidyosuchus canadensis</i>	21.6 9	133. 192 541 7	193. 708 390 8	193. 708 390 8	256. 8001 526	257.0 0378 66	282.6 7106 98	337.7 6227 54	422.77 10134	CMN 8543
<i>Lohuecosuchus mechinorum</i>	17.2 5	131. 053 543	155. 996 909	155. 996 909	213. 8272 604	213.0 7291 11	235.7 2720 73	288.5 7009 48	397.97 20872	MDE CM 616
<i>Lohuecosuchus megadontos</i>	25.1 8	164. 769 733 7	214. 550 123 9	214. 550 123 9	289. 3362 065	288.8 0035 11	320.0 0894 7	392.4 6819 78	481.51 37276	HUE 02920
<i>Maomingosuchus petrolicus</i>	15.6 6	143. 669 153 6	168. 580 122	168. 580 122	217. 8027 725	216.8 6892 47	235.9 7671 13	275.1 9538 16	341.11 73392	DM F0001
<i>Mourasuchus amazonensis</i>	59	348. 915 983 9	401. 231 488 2	401. 231 488 2	521. 6027 037	521.1 3546 31	571.5 3356 66	673.6 0268 3	863.43 41829	DGM- 526-R

<i>Mourasuchus arendsi</i>	45.2	290. 328 116 6	325. 699 025 7	325. 699 025 7	418. 5522 565	420.6 0893 25	459.3 6068 62	541.0 9605 86	666.54 21558	CIAAP- 1297
<i>Mourasuchus atopus</i>	27	185. 657 520 1	221. 055 734 4	221. 055 734 4	276. 9687 083	277.5 9635 18	300.7 6588 68	353.1 9799 6	424.06 42711	UCMP- 38012
<i>Navajosuchus mooki</i>	15.4	128. 037 614 3	148. 779 017 7	148. 779 017 7	184. 9310 042	185.0 4161 95	199.5 7521 88	232.5 5514 35	283.85 36491	AMNH 6780
<i>Orientalosuchus naduongensis</i>	16.1	114. 785 769	147. 070 153 4	147. 070 153 4	195. 4126 596	195.5 9578 77	215.0 4109 93	261.1 4626 73	342.46 68924	GPIT RE 09761
<i>Pachycheilosuchus trinquei</i>	6.07	61.4 901 919 3	70.7 577 695 9	70.7 577 695 9	91.6 8600 181	91.83 6949 05	99.93 4628 18	119.0 0968 18	149.07 10197	SMU 75281- 75286
<i>Pietraroiasuchus ormezzanoi</i>	6.81	70.4 410 247 9	78.3 574 916 9	78.3 574 916 9	100. 7186 859	100.9 2051 64	109.4 1693 97	129.9 0949 15	156.72 29707	PC-1
<i>Piscogavialis jugaliperforatus</i>	33.4 2	337. 883 950 3	397. 216 128 7	397. 216 128 7	484. 1955 904	483.9 4946 9	517.5 0617 77	593.0 4917 7	666.86 11248	SMNK PAL 1282
<i>Planocrania datangensis</i>	8.08	71.2 374 715 8	85.1 179 914	85.1 179 914	115. 5830 137	115.6 0670 95	127.4 3824 45	155.8 8183 25	196.65 28817	IVPP V5016
<i>Planocrania hengdongensis</i>	5.53	50.6 453 912 7	62.9 543 579 4	62.9 543 579 4	85.2 8651 4	85.45 5766 7	94.87 6531 43	116.9 5933 21	141.96 81022	IVPP V6079
<i>Procaimanoidea kayi</i>	6.56	60.6 816 926 1	72.7 408 086 1	72.7 408 086 1	93.5 7741 946	93.46 4932 89	101.9 9406 97	121.5 8404 24	140.72 27263	CM 9600
<i>Procaimanoidea utahensis</i>	5.31	47.9 423 526 8	59.6 202 656 5	59.6 202 656 5	78.4 9624 117	78.54 6855 42	86.25 0883 53	103.1 4584 26	117.07 48054	USNM 15996

<i>Prodiplocynodon langi</i>	37.88	258.7114	314.5361	314.5361	402.9178713	404.1172595	444.1098768	524.7979246	604.940862	IMG5557
<i>Purussaurus brasiliensis</i>	98	535.0774282	595.9300069	595.9300069	783.054438	781.309559	860.5425503	1028.097609	1382.171601	UFAC-1403
<i>Purussaurus mirandai</i>	78.6	438.1776	492.5412	492.5412	655.1702498	654.9233747	718.9251677	855.4977208	1212.291645	CIAAP-1369
<i>Purussaurus neivensis</i>	50.1	314.7471739	359.9038533	359.9038533	457.5453604	457.9250579	498.549859193	587.9088568	701.5597102	UCMP-39704
<i>Rimasuchus lloydi</i>	47.75	322.1398064	365.8506581	365.8506581	452.8752849	451.1408064	482.8384575	552.1658237	604.4546023	KNMER1682
<i>Shamosuchus djadochaensis</i>	9.25	72.07593819	97.45099525	97.45099525	128.6660482	128.5374094	141.1343057	170.1546114	213.3213292	IGM100/1195
<i>Stangerochampsa mccabei</i>	14.48	105.1803896	140.0767673	140.0767673	178.3246415	177.8523575	192.8415833	222.6003602	254.0844563	RTMP.86.61.1
<i>Thecachampsa antiqua</i>	44.01	289.0362	351.3299279	351.3299279	483.7119724	483.833817	540.7332124	670.862899	817.6562841	USNM25243
<i>Thoracosaurus macrorhynchus</i>	24.5	199.5762154	259.2780543	259.2780543	318.5589574	317.4914295	339.9009597	388.7723278	446.9291682	RGM12458
<i>Toyotamaphimeia machikanensis</i>	50.76	477.419848967	477.9980922	477.9980922	571.425292	570.8307961	606.7399152	683.9600305	793.7691944	MOUFO0001
<i>Trilophosuchus rackhami</i>	6.2	70.254.3807941	70.20573684	70.20573684	97.40454948	97.08344723	108.048995	133.9503891	239.7420934	QMF16856

<i>Tsoabichi greenriverensis</i>	7.44	66.6	80.1	80.1							
		056	062	062	99.8	100.0	108.2	126.1			TMM.4
		401	072	072	2537	4089	3870	8782	141.98		2509-1
		8	1	1	707	78	02	76	47748		
<i>Voay robustus</i>	22.3	166.	199.	199.							
		053	463	463	239.	239.1	254.0	288.9			MCZ
		641	430	430	1649	4445	0722	1959	327.28		1006
		6	2	2	24	52	9	48	53277		
<i>Wannaganosuchus brachymanus</i>	13.2	112.	129.	129.							
		820	578	578	165.	164.7	178.0	204.6			SMM
		461	602	602	3276	8512	9739	8506	280.90		P76.28.
		8	8	8	892	46	08	93	88853		247

7. Dataset: Walter et al., primary dataset (.tnt)

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Bernissartia_fagesii

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Acynodon_adriaticus

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Acynodon_iberoccitanus

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Agaresuchus_subjuniperus

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Albertochampsia_langstoni

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Alligator_mcgrewi

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Alligator_mefferdi

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Alligator_mississippiensis

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Alligator_olseni

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Alligator_prenasalis

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Alligator_sinensis

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Alligator_thomsoni

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Allodaposuchus_precedens

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Allognathosuchus_polyodon

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Allognathosuchus_wartheni

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Arambourgia_gaudryi

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Arenysuchus_gascabadiolorum

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Asiatosuchus_depressifrons

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Asiatosuchus_germanicus

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Australosuchus_clarkae

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Borealosuchus_acutidentatus

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Borealosuchus_formidabilis

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Borealosuchus_griffithi

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Borealosuchus_sternbergii

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Borealosuchus_threensis

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Borealosuchus_wilsoni

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Bottosaurus_fustidens

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Bottosaurus_harlani

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Boverisuchus_magnifrons

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Boverisuchus_vorax

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Brachychampsa_montana

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Brachychampsa_sealeyi

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Brachyuranochampsa_eversolei

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Brochuchus_pigotti

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Caiman_brevirostris

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Caiman_crocodilus

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Caiman_latirostris

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Caiman_wannlangstoni

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Caiman_yacare

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Centenariosuchus_gilmorei

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Ceratosuchus_burdoshi

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Chinatichampsus_wilsonorum

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Crocodylus_acer

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Crocodylus_affinis

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Crocodylus_megarhinus

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Crocodylus_niloticus

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101220010010101011101011110011000003011000012000000?0?0110010000001100000?
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Crocodylus_porosus

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00100110000001002100011001102000110100[01]000110100000100000111110000101110
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Crocodylus_rhombifer

01000001?10101000101110011111201100011120110111002101010001012000111020111
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Deinosuchus_riograndensis

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Deinosuchus_schwimmeri

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Diplocynodon_darwini

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Diplocynodon_deponiae

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Diplocynodon_hantoniensis

00????1?1?01000010001000011111??0400?10??20??011021010????001200000112101?
????00120?0?001??1300?0100?1000001?0?000000101100010100010111100?110100?012
010101101010??0?1??010011?010001??000012100?0??0?11001?000001100?00?1

Diplocynodon_muelleri

?????????????????????1?01??1??????4?0?10??21????01002??2?????0?120??100??100?
????00120?1000?011300001000100000????00000111110000010001?1?1100?110??0?02?
01010110101?????????0100110010001????000?000210??01??0100000?????????0??

Diplocynodon_ratelii

?????0??????000??010?00?1111001400?10??21????01002101?????00120000011?101?
????00110?00001011300001000101000?00?000000111100010100010111100?1?01001011
00010110101000001?10100110010001??000012000?00??011001000000110000001

Diplocynodon_remensis

????0100????????????0001000001111??400?10??20??01002000?????00020?00011?001?
????00020?000000?1300001000[01]00000????00000011?11?0?010000?111100??0?0000
01010100101010??0?10?0100000010001????0?00?3100000?2?0??00?00000?110?0000?

Diplocynodon_tormis

?????????????????????1?????????????????10?????????01?021?1?????0??2?00?????1???
????0?120??000?0?130000100?1000001????00000011?100?0?100010111100??0100001?
01010110101?0??1?001?0110010001??0000???0010?????11??1?0000??00?????

Dollosuchoides_densmorei

01?????111010?0001?0?001111??1?00?????????1 120???0?????000200?0??0201??
???00120?00?001?210000100??02000????01?0 101001000001 1000?01 1110?????????1??
20010?1010101?????????10?01000?003???00001300?100??01 100100020?1100000?1

Dongnanosuchus_hsui

???1 101???0?????0?????0?????1????
???10110?000011?110001100??01000??0001 101101 1101010000?11 1110?1 12?1?1022
20000010112??0??????100110000001???0000?20001000?001 1001000000??00000?1

Eoalligator_chunyii

010??????000?????????????????????????1?????????0?11?[12]?????????????10?01?0
1????10?????????????????????0?????????????????1?????1?????????0??1?1?????0?????
12??0?0010112??????????1??1?00?003?????????11?????0?0??1?????0??1?????0???

Eocaiman_cavernensis

???10000??2?????01120?????????????
???00?????????????0?0?0?1?????000????0?10?000?1?????????????1?11?0?????????????
???0???0?0??0??0?00? ???????00?00

Eocaiman_itaboraiensis

???1?1????2?????0?????0?????0??
???0?????0?????0?????0?????0?????0??
???0?????0?????0?????0?????0?????0???

Eocaiman_palaeocenicus

???1 1120??2?????0??20?????11?????
???0?????0?????0?????0?????0?????0??
???0?????0?????0?????0?????0?????0???

Eogavialis_africanum

???????1?????11????010?????????????0?????????0?????1 122??03??????10?200000??2101?
???00120?000?01?25?000100?00200000000000 1010010000010000000121?000100?111
1001000010000?000?0101010100000??00?013?0?0?????10010000?0?00?0?????

Eosuchus_lerichei

?????0??????01????01?????????1?????????0?????????1 122???3??????0?????0?????
???00120?0000?1?250000100?0000000??0000 101001000001000000?0110?000?0??11?
2001000010?1?????????10?01?101003???000012?00000??1010000000??010000?1

Eosuchus_minor

?????0?????0??111????01?00?0?01??0000?000?0?0??1 122??0300?0000?20?000002100?
???00120?0000?1?25?000100?000000?000000 1010010000?100000000110??0100?11?
100100001?1100??1???101010101003???00001200000??1010000000?1010000?1

Eothoracosaurus_mississippiensi

?????0?????????????01??000?????????00?00??0???? 122???3??????0?0??00?021?0?
???00120?000??1?25000010??000000??0000 101001000??000?000100??01???111
00010?001?10?????????100010000000??000016000200??1001101?010?1010001?1

Euthecodon_arambourgii

???0?????????????????????1??
???00020?0000?1?250001100?1020001101000000??0?????000011 1110??11011?012
210100101110?????1??11?0?1000?003???0000? ??????01 11010000?????????????

Gavialis_gangeticus

20000000?001111011010000000111000000?000000001 1323003000000002000000021000
100001301000001025?00010000000000000000 101001000001 100000012200001000111
110100001010000000001210101000000 1001013000200?0?100120111211001 1001?1

Gavialis_lewisi

????????????????????010????????????????????????????????22???3??????0?200000??2?0??
????00?30?0??????2??0??1?0?0?0000??0?0000?0?00100?0?1???00000122?000100?111
??0?000010100?????00121010100000??00101?????????????0??011101??011??1??

Gavialosuchus_eggenburgensis

????????????????????1??
????00120?0000?1?240000100??0?000??000?0101001000?012000?0?1110?0??????1?2
21010?10101?????????11??10000003??0000?000?0??0?0110010?010??00??????

Globidentosuchus_brachyrostris

????????????????????01????????????????????????????????1[01]01??0?11?10?130110311101
1????0012??000??0??200001??1?00?0??????0??0?11?????1?2??1?1100??????0?0
??2?21??101?3??????????1??1?????0????????0?00?010??00?1?0?00000??0?2000?

Gnatusuchus_pebasensis

??2020?12000?01111201000011001?
??02110?010010?0000001????0000?0????1????11?1001101?1?1??1100??0?0?1?12
20211?10103?????1??0100110210001?????????????????011001000000110040101

Gryposuchus_colombianus

??0?0??001?????01????000??????????????????0??11323?030100?000200000002100?
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11010000201000100?00121010100000??001010?0?00??100?10?0?1?00?100??1

Hassiacosuchus_haupti

01?1?0?1?????1????01?000?1111?????0??11?11??111110?0?????01?20??0??11101?
??00010?00????0?0?00001??????0001?0?????0?????11101?111100?1?0200?022
20010210100?????????01??10010001??00001?0011101??011?000000001??100?1

Hylaeochampsia_vectiana

??0??
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Iharkutosuchus_makadii

??10124??????????110??00??10?1?
??0001?000001?0610001?0??2110??00000010011000012111001?100?1?0?00?0?
?13??100?2?????1??1000000??110??1010?4?00?10??00110000?0??0?0300?1

Jiangxisuchus_nankangensis

????????????????????010????????????????????????????????1100?[01]01?????0[01]021??????
????????10110?000111?110000100??0000??00010001011201110000?11110001?0011
101111000010111?????????100110000001??0000?1?0?000?1?011001000000??01000?
1

Kambara_implexidens

?????0?????????????01?????11????1100?10??1??11102101?????00120000110?011?
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20010010101011101?11110010000001??000012000100?0?01100100000?11000?0??

Kentisuchus_spenceri

?????0??1?????0?????0??2000?110??11?
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20010?10101?????????111?0?100?0?03??0000?000200??0?100100000?1100??0??

Krabisuchus_siamogallicus

????????????????????1??0?????????1?0??11??1??11011??1?????01?2101?0?0?001?
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?0?0??2001??1?112?????????????????0??1??0?0?0?00??1?100?1?0?00000??0000
0?1

Kuttanacaiman_iquitosensis

??1110211200?0101120?102011001?
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21211210103?????1?0?0100?10210001?????????????????01100100000011002000?

La_venta_Caiman

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????00110?000010?020010100?001000????1000000111111111?0????1?0????0?????
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Leidyosuchus_canadensis

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Lohuecosuchus_mechinorum

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???00011?000000??20001?00?00200????000100100100???1100?00?1110??0??0?00
0?100?10?01????1????1?00?010000??0010?2?0020????00?00010100?00???1??

Lohuecosuchus_megadontos

??11005101???0??010??011??101??
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0110001010?????????110010?010000??0000?[13]000200???00000000100?100?001?1

Maomingosuchus_petrolica

???000010101000?0001?000?11??01?00?10??11??1112010300000000200100012010?
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20000010101????010??110010000003??0000?2000111?1?001001000000[01]000000?1

Mecistops_cataphractus

0?001001?000010000011100111112012000111101101111041010100010020001110201?1
0010012000000100210000100010100011010000101101000101000001111000010111012
2001001010101110101111001000000300?11101?000100?0?0110010000001100000?1

Melanosuchus_niger

01111001?1?00100000101011111100110001112212101100211210101111201102011001?
?11001100000020102001011000000001100100000011110111110111111001102011022
21211210103000101100100110210001002000012000110??2011001000000110000001

Mourasuchus_amazonensis

???0????????????????????
?????120?10???1???0?1???0?????1????????????????????????221??11?12?1102?0?0?
2121??1?1?3?????????????????1?????????????????????????????0??210?00????????0?

Mourasuchus_arendsi

?????????????????1?00??110011?????01?????????????11?2???2?????????????????1?0??
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??????1?103?????????????????0?????????????????????????????0??210?00????????001

Mourasuchus_atopus

0??100?1?00?010?00?1?10?011????1300?11??1??1102?112?????01120?100011000?
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2121??121030?????1???100110?10001??00?0???0?1????0110210?000????0?1001

Navajosuchus_mooki

?????0?1?????0???0?00???1111??1??0?101111??11101010?????01?21??00??110??
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2?0102101010?????1??010??10010001??0000120001102??01100?000000?1001000?

Necrosuchus_ionensis

?????0?????????????0???01?111??1300?11??1??11000??2??????2??0?????0??
??00??
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Orientalosuchus_naduongensis

???1????????000???01?0?0???????[14]0??[01]1???1???110111?1[02]??0101?111110?
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000?1

Osteolaemus_osborni

?1?00001?0010101000111001111120111001111110111002101010000012000011010111
0011011000010100210001100010200011011001001001020001000001111010010101012
213100101110111010111011000000310000001??00?0???011001?0000?1100??0?1

Osteolaemus_tetraspis

?1?00001?0010101000111001111120111001111110111002101010001012000011010111
0011010000010100210001100010200011011001011101020001000101111010010101012
213100101110111010111011000000311000001?000?00?0?0110010000001100000?1

Pachycheilosuchus_trinquei

?????????????????0?1?00010?10?000??10??0??1?03?????????1?0??0??0??0??
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????0?0?0?2?????????0?0????????2000?????0?????????????0?????????????1?0??1

Paleosuchus_palpebrosus

00111111?010010101010001111112113000111321120110021222111?1120110201100?0
111101100001010102000010000000001100010001111110111000111111011102011022
21?1?21010200010110010011021000111100001?000210?0101100100000?110000001

Paleosuchus_trigonatus

00111111?0100101000100011111121130001113211201100212221111112011020110010
111101100001010102000010000000001100010001111110111000111111011102011022
21?1?21010200010110010011021000110100001?000?10?01011001000000110000001

Paratomistoma_courti

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??00????????????2??0?0????????0001?0????????????????0000?1??11?????1??1??
200100001010?1000?101?0?100?00?????????1?01????0??1??1?000?1?00?????

Pietraroiasuchus_ormezzanoi

?????????????????????1?000??0?????????0?10021????11?3?????????????10????????00??
??00?21?00?0?0?050??1?0??????0??0??000000??2000?1?00?0??????0???
010?0?00?1????????????01??????1??????0?4000210??0?0000000?0?????01??

Piscogavialis_jugaliperforatus

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??00120?001001?250000100?001000????0000101001000000?0000000111?1?00010111
20010000201?0?1?0?0?12??1?10?000????010?0?00200?0?1001201102????01?001?1

Planocrania_datangensis

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???20010?000??1?030000100??0?000??0000?001??????0?0?1?110??0000?01
00010010??1????????????10??0?0??0000?2?00?00??0?1?0?0??00??????0?1

Planocrania_hengdongensis

????????????????????1????????????????????????1110???1????????[12]????0?01?0
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Procaimanoidea_kayi

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Procaimanoidea_utahensis

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20010?101010??????0100110010001??0000?200?2102??0??000000?011?000001

Prodiplocynodon_langi

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???00110?0000??030000100??1[12]0001??000010011?1000001??0?111100??0?0??0
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Protoalligator_huiningensis

??1100????????????112????????????
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Protocaiman_peligrensis

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??10????02?01022
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Purussaurus_brasiliensis

??11002??2?????1113??????110??
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Purussaurus_mirandai

????????????????????????1?11001?????11?0?1?????????1100?0?2??1?11?1301100?11?01?
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Purussaurus_neivensis

01?100?1?000010?0??1????011??????0?11??1??1100??1?1010?111301100011001?
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2001?210103000101??010??10210001??00?0?0??0?10??20?100100000?010001001

Quinkana_spp

??1?0???1????????????????1??
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11101221010010102?11101?11??01?000??1??????????0?00??0?0?0????????????
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Rimasuchus_lloydi

??1????????????????????1??
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Shamosuchus_djadochtaensis

????????????????????1?01?????0?1?????0?11?????????????????0?????1?0?????0?10????
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000?0?00?????????????????0?10?00?00????????011?000010??0?0?00000000?0010?0??

Stangerochampsia_mccabei

???110????010010?0001000001111001?00?[01]1??11???11010100?????0112110000?110
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Thecachampsia_antiqua

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200100101000??00??11100100?2003??000013?0?0????01?00110000??000??0??

Thoracosaurus_macrorhynchus

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01010?0010100??0?0100010000000??0000?2?0?0????1001100??10??010?????

Thoracosaurus_neocesariensis

?????0??????111?1?010?????0011??0??0?00??0??1122???3??????10?000?02?0??
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Tomistoma_cairense

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Tomistoma_lusitanica

?????0????????????01????????????????10??1??1??2???4?????00?20000??0201??
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Tomistoma_schlegelii

21000001?001010001011000111110110001013011011122?104000001002000000020100
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Toyotamaphimeia_machikanensis

0100100??1111110010110001111101100?00??1?????22??04?????10020?0000??0100
0?00120?000011?04000010??00000??0000?010010000?10000001110??00?1??1??
21010?1010??????????110010?00003??000012100000?0?0?1001000[02]001100000??

Trilophosuchus_rackhami

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21010000102011101?111?0?1000?001?????0?0?????0?????01?0?0000??00??0??

Tsoabichi_greenriverensis

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212?1?101?2????????????????100????????0?300001???10?0??10?00??????0001

Voay_robustus

?????0?????????0??011?????111??1110?????1??1110210101000001200011111011?
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Wannaganosuchus_brachymanus

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- [/1 5 -[/1 6 -[/1 7 -[/1 8 -[/1 9
- [/1 10 -[/1 11 -[/1 12 -[/1 13 -[/1 14
- [/1 15 -[/1 16 -[/1 17 -[/1 18 -[/1 19
- [/1 20 -[/1 21 -[/1 22 -[/1 23 -[/1 24
- [/1 25 -[/1 26 -[/1 27 -[/1 28 -[/1 29
- [/1 30 -[/1 31 -[/1 32 -[/1 33 -[/1 34
- [/1 35 -[/1 36 -[/1 37 +[/1 38 -[/1 39
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- [/1 45 -[/1 46 +[/1 47 -[/1 48 -[/1 49
- [/1 50 -[/1 51 -[/1 52 -[/1 53 -[/1 54
- [/1 55 -[/1 56 -[/1 57 -[/1 58 -[/1 59
- [/1 60 +[/1 61 -[/1 62 -[/1 63 -[/1 64
- [/1 65 -[/1 66 -[/1 67 -[/1 68 -[/1 69
- [/1 70 -[/1 71 -[/1 72 -[/1 73 -[/1 74
- [/1 75 -[/1 76 -[/1 77 -[/1 78 -[/1 79
- +[/1 80 -[/1 81 -[/1 82 -[/1 83 -[/1 84
- [/1 85 -[/1 86 -[/1 87 -[/1 88 -[/1 89
- [/1 90 -[/1 91 -[/1 92 -[/1 93 -[/1 94
- [/1 95 -[/1 96 -[/1 97 -[/1 98 -[/1 99
- [/1 100 -[/1 101 -[/1 102 -[/1 103 -[/1 104
- [/1 105 -[/1 106 -[/1 107 -[/1 108 -[/1 109
- [/1 110 -[/1 111 -[/1 112 -[/1 113 -[/1 114
- [/1 115 -[/1 116 -[/1 117 -[/1 118 -[/1 119
- [/1 120 -[/1 121 -[/1 122 +[/1 123 -[/1 124
- [/1 125 -[/1 126 -[/1 127 -[/1 128 -[/1 129
- [/1 130 -[/1 131 -[/1 132 -[/1 133 -[/1 134
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{0 Fused_proatlas_shape boomerang-shaped strap-shaped block-shaped;
 {1 Proatlas_process with_anterior_process without_anterior_process;
 {2 Proatlas_dorsal_keel with_dorsal_keel without_dorsal_keel;
 {3 Atlas_intercentrum_shape wedge-shaped plate-shaped;
 {4 Dorsal_margin_of_atlantal_rib_process smooth dorsal_process;
 {5 Atlantal_ribs_lamina without_lamina with_lamina;
 {6 Atlantal_ribs_articular_facets without_facets with_facets;
 {7 Axial_rib_tuberculum_tip broad_dorsal_tip acute_dorsal_tip;
 {8 Axial_rib_tuberculum_diapophysis contact_late_in_ontogeny contact_early_in_ontogeny;
 {9 Axis_neural_spine_shape horizontal_anteriorly slopes_anteriorly;
 {10 Axis_neural_spine_crested not_crested;
 {11 Posterior_half_of_axis_neural_spine_wide narrow;
 {12 Axis_neural_arch_lacks_diapophysis bears_diapophysis;
 {13 Axial_hypapophysis_location_center_of Centrum anterior_end_of_Centrum;
 {14 Axial_hypapophysis_shape without_deep_fork with_deep_fork;
 {15 Hypapophyseal_keels_presence 11th_vertebra_behind_atlas
 12th_vertebra_behind_atlas 10th_vertebra_behind_atlas;

{16 Third_cervical_vertebra_hypapophysis prominent not_prominent;

{17 Neural_spine_on_third_cervical long short;

{18 Cervical_and_anterior_dorsal_centra lack_deep_pits_ventrally bear_deep_pits_ventrally;

{19 Presacral_centra amphicoelus procoelus;

{20 Anterior_sacral_rib_capitulum broadly_visible_in_dorsal_view obscured_in_dorsal_view;

{21 Scapular_blade_shape flares_dorsally sides_sub-parallel;

{22 Deltoid_crest_of_scapula very_thin_with_sharp_margin very_wide_with_broad_margin;

{23 Scapulocoracoid_synchondrosis closes_late_in_ontogeny closes_early_in_ontogeny;

{24 Scapulocoracoid_facet_shape narrow_anterior_to_glenoid_fossa
broad_anterior_to_glenoid_fossa;

{25 Proximal_edge_of_deltopectoral_crest_of_humerus not_concave concave;

{26 M._teres_major_and_M._dorsalis_scapulae_insertion seperately single_insertion_scar;

{27 Olecranon_process_of_ulna_shape narrow_and_sub-angular wide_and_rounded;

{28 Ulna_shape proximal_extremity_equal_to_distal proximal_extremity_wider_than_distal;

{29 Interclavicle_shape without_dorsoventral_flexure with_moderate_dorsoventral_flexure
with_severe_dorsoventral_flexure;

{30 Anterior_end_of_interclavicle_flat rodlike;

{31 Iliac_anterior_process_prominent virtually_absent;

{32 Dorsal_margin_of_iliac_blade__rounded_with_smooth_border
rounded_with_modest_dorsal_indentation rounded_with_strong_dorsal_indentation
narrow_with_dorsal_indentation rounded_dorsal_tip_deep;

{33 Supraacetabular_crest narrow borad;

{34 Limb_bones_form robust slender;

{35 M._caudofemoralis_single_head souble_head;

{36 Dorsal_osteoderms_keel not_keeled keeled;

{37 Dorsal_midline_osteoderms_shape rectangular nearly_square;

{38 Number_of_contiguous_dorsal_osteoderms_per_row_four six eight ten;

{39 Nuchal_shield grades_continously_into_dorsal_shield_with_four_nuchal_osteoderms
six_nuchal_osteoderms eight_nuchal_osteoderms_in_two_parallel_rows;

{40 Ventral_armor_absent single_ventral_osteoderms paired_ventral_osteoderms;

{41 Anterior_margin_of_dorsal_midline_osteoderms_with_anterior_process
without_anterior_process;

{42 Ventral_scales_pores have_follicle_gland_pores lack_follicle_gland_pores;

{43 Ventral_collar_scales_not_enlarged single_enlarged_row two_parallel_enlarged_rows;

{44 Median_pelvic_keel_scales_along_tail two_parallel_rows single_row
merge_with_lateral_keel_scales;

{45 Alveoli_size_of_dentary_teeth_3_and_4_same_size_and_confluent
4_larger_than_3_and_seperated 3_and_4_are_nearly_the_same_size_and_separated;

{46 Anterior_dentary_teeth strongly_procumbent project_anterodorsaly;

{47 Dentary_symphysis_extension fourth_and_fifth_alveolus sixth_through_eight_alveolus
eighth_to_twelfth_alveolus twelfth_to_sixteenth beyond_the_sixteenth;

{48 Dentary_curvature_between_fourth_and_tenth_alveoli gently_deeply_linear;

{49 Largest_dentary_alveolus_caudal_to_fourth 13_or_14
between_11_and_14_and_a_series_behind_it 11_or_12 no_differentiation behind_14 10;

{50 Splenial_with_anterior_perforation_for_cranial_nerv_V existent lacking;

{51 Mandibular_ramus_of_cranial_nerv_V only_anterior single_perforation_posterior
double_perforation_posterior;

{52 Mandibular_symphysis_size splenial_participates
splenial_excluded,_anterior_tip_of_splenial_ventral_to_Meckelian_groove
splenial_excluded,_anterior_tip_of_splenial_dorsal_to_Meckelian_groove
deep_splenial_symphysis,_splenial_forms_wide_V
deep_splenial_symphysis,_splenial_forms_narrow_V
splenial_reaches_mandibular_symphysis_but_does_not_touch_other_splenial;

{53 Coronoid_position_for_foramen_intermandibularis_medius
bounding_posterior_half_of_foramen_completely_surrounding_foramen
obliterates_foramen_;

{54 Coronoid_superior_edge sloping_strongly_anteriorly almost_horizontal;

{55 Coronoid_inferior_process laping_over_inner_surface_of_meckelian_fossa
remains_on_medial_surface_of_mandible;

{56 Coronoid_perforation imperforate
perforation_posterior_to_foramen_intermandibularis_medius;

{57 Splenial_process separatesAngular_and_coronoid
no_process_betweenAngular_and_coronoid;

{58 Angular-surangular_suture_with_ext.mand.fenestra
contacting_fenestra_at_posterior_angle passing_along_ventral_margin_of_fenestra;

{59 Surangular_anterior_processes unequal sub-equal_to_equal;

{60 Surangular_spur_on_lingual_tooth_row spur_for_at_least_one_alveolus_length no_spur;

{61 External_mandibular_fenestra absent present_as_narrow_slit
present_with_discrete_concavity_onAngular_dorsal_margin present_and_very_large;

{62 Surangular-dentary_suture_intersection_with_ext.mand.fenestra
anterior_to_posterodorsal_corner at_posterodorsal_corner;

{63 Angular_anterior_tip_to_foramen_intermandibularis_caudalis
towards_anterior_end_of_foramen_not_towards_anterior_end_of_foramen;

{64 Surangular-angular_suture_lingually_meets_articular at_ventral_tip dorsal_to_tip;

{65 Surangular_at_lateral_wall_of_glenoid_fossa continuing_to_dorsal_tip truncated;

{66 Articular-surangular_suture_form simple
articular_bears_anterior_lamina_dorsal_to_lingual_foramen

articular_bears_anterior_lamina_ventral_to_lingual_foramen
articular_bears_lamina_above_and_below_foramen;

{67 Lingual_foramen_for_articular_artery perforates_surangular_entirely
perforates_surangular/angular_suture;

{68 Foramen_aerum_position at_lingual_margin_of_retroarticular_process
set_in_from_margin_of_retroarticular_process;

{69 Retroarticular_process_projection posteriorly
posterodorsally,_not_higher_than_the_posterior_edge_of_the_articular_fossa
projects_posterodorsally,_higher_than_the_posterior_edge_of_the_articular_fossa;

{70 Surangular_extension posterior_end_of_retroarticular_process
pinched_off_anterior_to_tip_of_retroarticular_process;

{71 Surangular-articular_suture_orientation_within_glenoid_fossa anteroposteriorly
bowed_strongly_laterally;

{72 Articular-surangular_connection sulcus_between_articular_and_surangular
articular_flush_against_surangular;

{73 Hyoid_cornu_dorsal_projection_form flat_rodlike;

{74 Hyoid_cornu_dorsal_projection_lateromedial narrow_with_parallel_sides flared;

{75 Lingual_osmoregulatory_pores small large;

{76 Tongue with_keratinized_surface without_keratinized_surface;

{77 Teeth_and_alveoli_of_maxilla/dentary_form circular_in_cross-section
posterior_teeth_laterally_compressed_all_teeth_compressed_;

{78 Maxillary_and_dentary_teeth_serration smooth_carinae serrated
with_neither_carinae_nor_serrations;

{79 Naris_projection anterodorsally dorsally posterodorsally;

{80 External_naris_and_nasal_interaction external_naris_birsected_by_nasals
nasal_contacts_external_naris_without_bisection nasal_excluded_externally_from_naris
nasal_and_premaxilla_not_in_contact;

{81 Naris_shape circular_or_key-hole_shaped wider_than_long
anteroposteriorly_long_and_teardrop-shaped;

{82 External_naris_of_reproductively_mature_males similar_to_that_of_females
with_bony_excrescence;

{83 External_naris_opening flush_with_dorsal_surface_of_premaxilla
circumscribed_by_thin_crest;

{84 Premaxilla_surface_lateral_to_naris smooth with_deep_notch;

{85 Number_of_teeth_in_premaxilla_early_in_ontogeny five four;

{86 Incisive_foramen_size small
large_and_more_than_half_the_greatest_width_of_premaxillae
large_and_intersects_premaxillary-maxillary_suture;

{87 Incisive_foramen_position situated_far_from_premaxillary_tooth_row
abuts_premaxillary_tooth_row projects_between_first_premaxillary_teeth;

{88 Dorsal_premaxillary_process short long_behind_3th_maxilla_tooth;

{89 Dentary_tooth_four_early_in_ontogeny in_notch_between_premaxilla_and_maxilla
in_pit_between_premaxilla_and_maxilla;

{90 Dentary_teeth_position all_teeth_lingual_to_maxillary_teeth
occlusion_pit_between_seventh_and_eighth_maxillary_teeth
dentary_teeth_in_line_with_maxillary_tooth_row;

{91 Largest_maxillary_alveolus third fifth fourth four_and_five_the_same_size six
maxillary_teeth_homodont maxillary_alveoli_gradually_increase_in_diameter;

{92 Maxillary_tooth_row_form_posterior_to_first_six_maxillary_alveoli
medially_curved_or_linear broadly_curved_laterally;

{93 Dorsal_surface_of_rostrum curves_smoothly bears_medial_dorsal_boss;

{94 Canthi_rostralii_at_maturity absent_or_very_modest very_prominent;

{95 Preorbital_ridges_at_maturity absent_or_very_modest very_prominent;

{96 Antorbital_fenestra present absent;

{97 Vomer_position_anterior entirely_obscured_by_premaxilla_and_maxilla
exposed_on_palate_at_premaxillary-maxillary_suture;

{98 Vomer_position_posterior entirely_obscured_by_maxillae_and_palatines
exposed_on_palate_between_palatines;

{99 Surface_of_maxilla_within_narial_canal imperforate with_linear_array_of_pits;

{100 Medial_jugal_foramen_size small very_large;

{101 Maxillary_foramen_for_cranial_nerve_V_size small_or_not_present very_large;

{102
Ectopterygoid_contact_with_maxillary_toothrow_forming_medial_wall_of_at_least_1_mx_alve-
olus absent_and_ectpt-
mx_suture_anteromedially_orientated_and_separated_from_toothrow_margin
absent_and_ectopt-mx_suture_parallel_and_adjacent_to_medial_toothrow_margin present;

{103 Maxilla_termination_in_palatal_view anterior_to_lower_temporal_bar
comprises_part_of_the_lower_temporal_bar;

{104 Penultimate_maxillary_alveolus_size less_than_twice_the_diameter_of_the_last_one
more_than_twice_the_diameter_of_the_last_one;

{105 Prefrontal_dorsal_surface_appearance smooth_adjacent_to_orbital
bearing_discrete_knoblike_processes;

{106 Dorsal_half_of_prefrontal_pillar narrow expanded_anteroposteriorly;

{107 Medial_process_of_prefrontal_pillar expanded_dorsoventrally
expanded_anteroposteriorly;

{108 Prefrontal_pillar_form solid with_large_pneumatic_recess;

{109 Medial_process_of_prefrontal_pillar_at_base wide constricted;

{110 Maxilla_appearance_on_suborbital_fenestra linear_medial_margin
broad_shelf_lateral_margin_concave;

{111 Anterior_face_of_palatine_process_anteriorly rounded_or_pointed notched;

{112 Anterior_ectopterygoid_process tapered_to_a_point forked;

{113 Palatine_process_extension_beyond_anterior_end_of_suborbital_fenestra
not_beyond_anterior_end_of_suborbital_fenestra;

{114 Palatine_process_form_broad_anterioly_form_of_a_thin_wedge;

{115 Lateral_edges_of_palatines_appearance_smooth_anterioly
lateral_process_projecting_into_suborbital_fenestra;

{116 Palatine-pterygoid_suture_at_posterior_angle_of_suborbital_fenestra
far_from_posterior_angle_of_suborbital_fenestra;

{117 Pterygoid_ramus_of_ectopterygoid_form
straight_posterolateral_fenestra_margin_linear
bowed_posterolateral_fenestra_margin_concave;

{118 Lateral_edges_of_palatines_form_parallel_posterior_flare_posteriorly,_producing_shelf;

{119 Anterior_border_of_choana_comprised_of_palatines
entirely_surrounded_by_pterygoids;

{120 Choana_projecting_at_maturity_posteroventrally_anteroventrally;

{121 Pterygoid_surface_around_choana_flush_with_choanal_margin
pushed_inward_anterolateral_to_choana_aperture
pushed_inward_around_choana_to_form_neck_surrounding_aperture
everted_from_flat_surface_to_form_neck_surrounding_aperture;

{122 Posterior_rim_of_internal_choana_not_deeply_notched_deeply_notched;

{123 Internal_choana_appearance_not_septated
with_septum_that_remains_recessed_within_choana
with_septum_that_projects_out_of_choana;

{124 Ectopterygoid-pterygoid_flexure_appearance_flexure_disappeares_during_ontogeny
flexure_remains_throughout_ontogeny;

{125 Ectopterygoid_extention_at_maturity_to_posterior_tip_of_lateral_pterygoid_flange
__not_to_posterior_tip_of_lateral_pterygoid_flange;

{126 Maxilla_connection_with_lacrimal
lacrimal_makes_broad_contact_with_nasal,_no_process
maxilla_with_posterior_process_within_lacrimal
maxilla_with_posterior_process_between_lacrimal_and_prefrontal;

{127 Prefrontal_form
separated_by_frontals_and_nasals,_anterior_process_of_frontal_extending_far_anterior_to_
the_anterior_margin_of_the_orbit
prefrontals_separated_by_the_frontal_and_nasals,_anterior_process_of_frontal_around_the_
_same_level_or_posterior_to_the_anterior_margin_of_the_orbit
prefrontals_meet_medially,_anterior_process_of_frontal_around_the_same_level_or_posteri
or_to_the_anterior_margin_of_the_orbit;

{128 Lacrimal_and_prefrontal_size_lacrimal_longer_than_prefrontal
prefrontal_longer_than_lacrimal_lacrimal_and_prefrontal_same_size_and_elongated;

{129 Anterior_tip_of_frontal_form_simple_acute_point
broad,_complex_sutural_contact_with_nasals;

{130 Ectopterygoid_extension_at_postorbital_bar
extends_along_medial_face_of_postorbital_bar_stops_abruptly_ventral_to_postorbital_bar;

{131 Postorbital_bar_form massive slender;

{132 Postorbital_process prominent,_dorsoventrally_broad,_two_spines short_and_generally_not_prominent;

{133 Ventral_margin_of_postorbital_bar flush_with_lateral_jugal_surface inset_from_lateral_jugal_surface;

{134 Postorbital_bar_connection_with_skull_table continuous_with_anterolateral_edge_of_skull_table inset_from_skull_table;

{135 Margin_of_orbit flush_with_skull_surface dorsal_edges_of_orbit_upturned orbital_margin_telescoped anterior_margins_of_orbit_telescoped;

{136 Ventral_margin_of_orbit_form not_upturned,_ventral_margin_gently_circular anterior_margin_upturned,_ventral_margin_gently_circular anterior_margin_upturned,_ventral_margin_with_a_prominent_notch;

{137 Palpebral_form single_ossification multiple_ossifications;

{138 Quadratojugal_spine_appearance prominent_at_maturity greatly_reduced_or_absent_at_maturity;

{139 Quadratojugal_spine_position_into_infratemporal_fenestra low,_near_posterior_angle_of_fenestra high,_between_posterior_and_superior_angles_of_fenestra;

{140 Posterior_angle_of_infratemporal_fenestra quadratojugal_forms_posterior_angle_of_fenestra jugal_forms_posterior_angle_of_fenestra quadratojugal-jugal_suture_lies_at_posterior_angle_of_fenestra;

{141 Postorbital_contacts_neither_quadrate_nor_quadratojugal_medially quadratojugal_but_not_quadrate_medially quadrate_and_quadratojugal_at_dorsal_angle_of_infratemporal_fenestra quadratojugal_with_significant_descending_process;

{142 Quadratojugal_process long_anterior_process_along_lower_temporal_bar _modest_process,_or_none_at_all,_along_lower_temporal_bar;

{143 Quadratojugal_extention extends_to_superior_angle_of_infratemporal_fenestra does_not_extend_to_superior_angle_of_infratemporal_fenestra;

{144 Postorbital-squamosal_suture_orientation_to_skull_table passes_ventrally passes_medially;

{145 Dorsal_and_ventral_rims_of_squamosal_groove parallel flaring_anteriorly;

{146 Quadrate_and_squamosal_on_external_auditory_meatus not_in_contact_posteriorly suture_extends_dorsally_along_caudal_margin_of_meatus extends_only_to_caudoventral_boarder_of_meatus;

{147 Caudal_margin_of_otic_aperture not_defined_and_merging_into_exoccipital smooth_and_continuous_with_paroccipital_process inset;

{148 Frontoparietal_suture_position deeply_within_supratemporal_fenestra making_modest_entry_into_supratemporal_fenestra_at_maturity on_skull_table_entirely;

{149 Frontoparietal_suture_between_supratemporal_fenestrae concavoconvex linear;

{150 Supratemporal_fenestra_appearance dermal_bones_do_not_overhang_rim_of_fenestra parietal_overhangs_the_rim_at_maturity

postorbital,_squamosal_and_parietal_overhang_rim_at_maturity
fenestra_closes_during_ontogeny;

{151 Anteromedial_corner_of_supratemporal_fenestra shallow_fossa_or_no_fossa smooth;

{152 Medial_parietal_wall_of_supratemporal_fenestra imperforate bearing_foramina;

{153 Parietal_and_squamosal_on_supratemporal_fenestra
widely_separated_by_quadrate_on_posterior_fenestra_wall
approaching_each_other_on_fenestra_without_making_contact
meeting_along_posterior_wall_of_fenestra;

{154 Skull_table_surface_at_maturity sloping_ventrally_from_sagittal_axis planar
slopes_ventrally_toward_sagittal_axis_at_maturity,_lateral_elements_planar;

{155 Squamosal_on_skull_table horizontal_or_nearly_so
upturned_to_form_a_discrete_posterolateral_horn
producing_a_high_transversely_oriented_eminence_at_the_posterior_margin_late_in_ontog
eny;

{156 Posterolateral_squamosal_rami rami_along_paroccipital_process_short
rami_along_paroccipital_process_significant;

{157 Squamosal_form does_not_extend_to_lateral_extent_of_paroccipital_process
extends_to_lateral_extent_of_paroccipital_process;

{158 Supraoccipital_exposure_on_dorsal_skull_table absent small large
large_such_that_parietal_is_excluded_from_posterior_edge_of_table;

{159 Anterior_foramen_of_cranial_nerve_VII ventrolateral_to_basisphenoid_rostrum
ventral_to_basisphenoid_rostrum;

{160 Braincase_wall_lateral_to_basisphenoid_rostrum sulcus_on_anterior_braincase_wall
braincase_wall_smooth,_no_sulcus;

{161 Basisphenoid_anterior_to_trigeminal_foramen not_exposed_extensively
exposed_extensively;

{162 Prootic_on_external_braincase_wall extensively_exposed
largely_obscured_by_quadrate_and_laterosphenoid_externally;

{163 Laterosphenoid_bridge comprised_entirely_of_laterosphenoid
with_ascending_process_or_palatine;

{164 Capitate_process_of_laterosphenoid oriented_laterally_toward_midline
oriented_anteroposteriorly_toward_midline;

{165 Parietal_pneumatic_system
parietal_with_recess_communicating_with_pneumatic_system
parietal_solid,_without_recess;

{166 Lateral_braincase_wall significant_ventral_quadrate_process_on_braincase_wall q-
pt_suture_linear_from_basisphenoid_exposure_to_trigeminal_fo;

{167 Lateral_carotid_foramen opens_lateral_to_basisphenoid_at_maturity
dorsal_to_to_basisphenoid_at_maturity;

{168 External_surface_of_basioccipital_ventral_to_occipital_condyle
oriented_posteroventrally_at_maturity oriented_posteriorly_at_maturity;

{169 Posterior_pterygoid_process tall_and_prominent small_and_project_posteroventrally
small_and_project_posteriorly;

{170 Basisphenoid_appearance_ventral_to_basioccipital thin_anteroposteriorly_wide;

{171 Basisphenoid_exposure not_broadly_exposed_ventral_to_basioccipital exposed_as_broad_sheet_ventral_to_basioccipital;

{172 Exoccipital_on_paroccipital_process with_very_prominent_boss with_small_or_no_boss_on_paroccipital_process;

{173 Lateral_eustachian_canal_openings dorsal_to_medial_eustachian_canal lateral_to_medial_eustachian_canal;

{174 Exoccipital_termination dorsal_to_basioccipital_tubera sending_robust_process_ventrally,_participating_in_bo_tubera sending_slender_process_ventrally_to_basioccipital_tubera;

{175 Quadrate_foramen_aerum_position on_mediadorsal_angle_of_quadrate on_dorsal_surface_of_quadrate;

{176 Quadrate_foramen_aerum_size_at_maturity small_comparatively_large absent;

{177 Quadrate_appearance_on_dorsal_surface_of_ramus lacking_prominent,_mediolaterally_thin_crest bearing_prominent,_mediolaterally_thin_crest;

{178 Attachment_scar_for_posterior_mandibular_abductor_muscle forming_modest_crest_on_ventral_surface_of_quadrate_ramus forming_prominent_knob_on_ventral_surface_of_quadrate_ramus;

{179 Quadrate_hemicondyle small,_ventrally-reflected_medial_hemicondyle small_medial_hemicondyle_dorsal_notch_for_foramen_aerum with_prominent_dorsal_projection_between_hemicondyles with_expanded_medial_hemicondyle;

{180 Iris_colour greenish/yellowish brown;

{181 Postoccipital_osteoderms two_or_more one;

{182 Paired_midline_scale_rows fewer_than_eight eight_to_14 more_than_14;

{183 Ectopterygoid_maxillary_ramus_form less_than_two-thirds_of_lateral_margin_of_suborbital_fenestra more_than_two-thirds_of_lateral_margin_of_suborbital_fenestra;

{184 Ectopterygoid_maxillary_ramus_termination at_lateral_margin_of_suborbital_fenestra lateral_to_it,_maxilla_separating_the_ectopterygoid_from_fenestra;

{185 Palatine-maxillary_suture_intersection_at_suborbital_fenestra at_its_anteromedial_margin nearly_at_its_antermost_limit;

{186 Frontal_with_midsagittal_crest_between_orbits lacks bears;

{187 Cervical_neural_spines_form anteroposteriorly_broad posterior_neural_spines_thin_and_rod-like;

{188 Largest_premaxilla_tooth second third fourth third_and_fourth_similar_largest all_similar_in_size fourth_and_fifth_similarly_largest first_for_similar_in_size;

{189 Dorsal_surface_of_surangular smooth large_sulcus_next_to_the_anterior_half_of_the_glenoid_fossa;

{190 U-shaped_depression_of_the_frontal_at_the_point_of_maximum absent present;

{191 Head_shape relatively_flat formed_like_a_wedge_and_trapezoid_in_cross-section;

{192 Anterior_jugal_process_extends_anterior_to_the_anterior_process_of_frontal_at_the_same_level_as_the_anterior_process_of_frontal_well_posterior_to_the_anterior_process_of_frontal_;

{193 Notch_between_the_premaxilla_and_maxilla_in_adults present not_present;

{194 Anterior_maxilla_and_dentary_teeth
without_or_weak_dorsoventral_ridges_on_the_lateral_surface
with_dominant_dorsoventral_ridges_on_the_lateral_surface;

{195 If_largest_dentary_alveolus_is_between_11th_and_14th_and_a_series_behind_it 11th
12th 13th_or_14th;

{196 Surangular-angular_suture_lingually_originates_
near_the_ventral_border_of_the_external_mandibular_fenestra_
near_the_dorsal_border_of_the_external_mandibular_fenestra_and_straight
near_the_dorsal_border_of_theexternal_mandibular__fenestra_and_bowed;

{197 If_supraoccipital_exposure_on_skull_table_is_large_or_very_large,_is__ trapezoid
triangular block-shaped;

{198 Edge_of_the_maxillary_alveoli
lower_or_at_the_same_level_than_the_space_between_toothrow_
edge_of_maxillary_tooth_alveoli_higher_than_the_space;

{199 Ventral_border_of_exoccipital_
ventrally_projected,_hiding_the_posterior_opening_of_the_cranioquadrate_passage_from_t
he_occipital_view_
straight,_sharpen_or_smoothly_convex_and_does_not_hide_the_posterior_opening_of_the_
cranioquadrate_passage_from_the_occipital_view_;

{200 Occipital_surface_at_maturity sloped,_visible_in_dorsal_view_
vertical_or_not_visible_in_dorsal_view;

{201 Ventral_premaxilla-maxilla_suture_
short_and_ends_posteriorly_before_the_3rd_maxillary_alveoli
elongated_and_extends_or_exceeds_the_3rd_maxillary_alveoli_;

{202 Number_of_teeth_on_maxilla less_than_18_teeth 18_to_22_teeth
more_than_22_teeth;

{203 Lateral_edge_of_the_skull_table_at_the_level_of_the_postorbital-squamosal_suture_
situated_laterally_or_at_the_same_level_as_the_quadrate_condyle_in_dorsal_view_at_mat
urity situated_medially_to_the_quadrate_condyle_in_dorsal_view_at_maturity;

{204 Frontal_ending
at_the_same_level_or_posterior_to_the_anterior_extension_of_the_prefrontal
extends_well_anterior_to_the_anterior_extension_of_the_prefrontal;

{205 Maxilla_posterior_process_without_tooth_in_ventral_view short_or_absent
long_longer_than_the_distance_between_the_three_last_teeth_;

{206 Interorbital_bridge narrower_to_equivalent_than_the_width_of_the_orbit
broader_than_the_width_of_the_orbit;

{207 Supratemporal_fenestra_at_maturity
longer_than_wide_or_rounded,_posterior_bar_of_supratemporal_fenestra_thick_
wider_than_long,_posterior_bar_of_supratemporal_fenestra_thick_
wider_than_long,_posterior_bar_thin_;

{208 Medial_crest_on_the_basioccipital present absent;

{209 Posterior_dentary_process_between_splenic_and___angular_on_the_ventral_side
absent present;

{210 Dorsal_margin_of_the_articular_on_the_retroarticular_process_
largely_visible_in_lateral_view slightly_or_not_visible_in_lateral_view_;

{211 Posterior_margin_of_the_orbit_measured_at_the_level_of_the_postorbital-
frontal_suture_in_the_orbital_margin_
_anterior_to_the_posterior_margin_of_the_suborbital_fenestra
posterior_or_at_the_same_level_than_the_posterior_margin_of_the_suborbital_fenestra;

{212 Basioccipital-
exoccipital_process_ventral_to_occipital_condyle_(basioccipital_plate)_in_posterior_view
with_parallel_or_ventrally_convergent_sides_ventrally_divergent_sides_;

{213
Smooth_medial_depression_ventral_to_the_basioccipital_and_posterior_to_the_medial_Eus-
tachian_foramen absent present;

{214 Dentary_teeth_series_behind_to_alveoli_12-13_pointed_to_slightly_blunt
globular,_different_in_size_among_them_globular,_at_least_four_subequal_in_size_
molariform_multicusped absent;

{215 First_four_alveoli_in_the_dentary same_size_or_smaller_than_other_dentary_alveoli_
the_largest_within_the_dentary_;

{216 Orbit_late_in_ontogeny longer_than_wide_wider_than_long_to_rounded_;

{217 The_series_composed_by_the_last_three_premaxillary_teeth
diverge_posteriorly_to_paraxial tend_to_converge_posteriorly,_straight_among_them_;

{218 Dentary,_level_of_the_first_and_fourth_alveoli
lower_than_the_level_of_the_eleventh_and_twelfth_alveoli_
equal_to_higher_than_the_level_of_the_eleventh_and_twelfth_alveoli;

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Ancstates

-0	-1	-2	-3	-4	-5	-6	-7	-8	-9
-10	-11	-12	-13	-14	-15	-16	-17	-18	-19
-20	-21	-22	-23	-24	-25	-26	-27	-28	-29
-30	-31	-32	-33	-34	-35	-36	-37	-38	-39
-40	-41	-42	-43	-44	-45	-46	-47	-48	-49
-50	-51	-52	-53	-54	-55	-56	-57	-58	-59
-60	-61	-62	-63	-64	-65	-66	-67	-68	-69
-70	-71	-72	-73	-74	-75	-76	-77	-78	-79
-80	-81	-82	-83	-84	-85	-86	-87	-88	-89
-90	-91	-92	-93	-94	-95	-96	-97	-98	-99
-100	-101	-102	-103	-104	-105	-106	-107	-108	-109
-110	-111	-112	-113	-114	-115	-116	-117	-118	-119

-120 -121 -122 -123 -124 -125 -126 -127 -128 -129
-130 -131 -132 -133 -134 -135 -136 -137 -138 -139
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-160 -161 -162 -163 -164 -165 -166 -167 -168 -169
-170 -171 -172 -173 -174 -175 -176 -177 -178 -179
-180 -181 -182 -183 -184 -185 -186 -187 -188 -189
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-200 -201 -202 -203 -204 -205 -206 -207 -208 -209
-210 -211 -212 -213 -214 -215 -216 -217 -218

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taxcode

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+40 +41 +42 +43 +44 +45 +46 +47
+48 +49 +50 +51 +52 +53 +54 +55
+56 +57 +58 +59 +60 +61 +62 +63
+64 +65 +66 +67 +68 +69 +70 +71
+72 +73 +74 +75 +76 +77 +78 +79
+80 +81 +82 +83 +84 +85 +86 +87
+88 +89 +90 +91 +92 +93 +94 +95
+96 +97 +98 +99 +100 +101 +102 +103
+104 +105 +106 +107 +108 +109 +110 +111
+112 +113 +114 +115 +116 +117 +118 +119
+120 +121 +122 +123 +124 +125 +126 +127

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blocks 0;

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force

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Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiassuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsa_mccabei
Thecachampsa_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Alligator_mississippiensis Alligator_sinensis Caiman_crocodylus Caiman_latirostris
Caiman_yacare Melanosuchus_niger Paleosuchus_palpebrosus Paleosuchus_trigonatus
(Bernissartia_fagesii Acynodon_adriaticus Acynodon_iberoccitanus
Agaresuchus_subjuniperus Albertochampsa_langstoni Alligator_mcgrewi Alligator_mefferdi
Alligator_olseni Alligator_prenasalis Alligator_thomsoni Allodaposuchus_precedens
Allognathosuchus_polyodon Allognathosuchus_wartheni Arambourgia_gaudryi
Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons Asiatosuchus_germanicus
Australosuchus_clarkae Borealosuchus_acutidentatus Borealosuchus_formidabilis
Borealosuchus_griffithi Borealosuchus_sternbergii Borealosuchus_threeensis
Borealosuchus_wilsoni Bottosaurus_fustidens Bottosaurus_harlani
Boverisuchus_magnifrons Boverisuchus_vorax Brachychampsa_montana
Brachychampsa_sealeyi Brachyuranochampsa_eversolei Brochuchus_pigotti
Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichiei Eosuchus_minor Eothoracosaurus_mississippiensi
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi

Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiасuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_pelignensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairensis Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Osteolaemus_osborni Osteolaemus_tetraspis (Bernissartia_fagesii Acynodon_adriaticus
Acynodon_iberoccitanus Agaresuchus_subjuniperus Albertochampsia_langstoni
Alligator_mcgrewi Alligator_mefferdi Alligator_olseni Alligator_prenasalis Alligator_thomsoni
Allodaposuchus_precedens Allognathosuchus_polyodon Allognathosuchus_wartheni
Arambourgia_gaudryi Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons
Asiatosuchus_germanicus Australosuchus_clarkae Borealosuchus_acutidentatus
Borealosuchus_formidabilis Borealosuchus_griffithi Borealosuchus_sternbergii
Borealosuchus_threensis Borealosuchus_wilsoni Bottosaurus_fustidens
Bottosaurus_harlani Boverisuchus_magnifrons Boverisuchus_vorax
Brachychampsia_montana Brachychampsia_sealeyi Brachyuranochampsia_eversolei
Brochuchus_pigotti Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichei Eosuchus_minor Eothoracosaurus_mississippiensis
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsia_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiасuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_pelignensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairensis Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Mecistops_cataphractus Osteolaemus_osborni Osteolaemus_tetraspis (Bernissartia_fagesii
Acynodon_adriaticus Acynodon_iberoccitanus Agaresuchus_subjuniperus
Albertochampsia_langstoni Alligator_mcgrewi Alligator_mefferdi Alligator_olseni
Alligator_prenasalis Alligator_thomsoni Allodaposuchus_precedens
Allognathosuchus_polyodon Allognathosuchus_wartheni Arambourgia_gaudryi
Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons Asiatosuchus_germanicus
Australosuchus_clarkae Borealosuchus_acutidentatus Borealosuchus_formidabilis

Borealosuchus_griffithi Borealosuchus_sternbergii Borealosuchus_threeensis
Borealosuchus_wilsoni Bottosaurus_fustidens Bottosaurus_harlani
Boverisuchus_magnifrons Boverisuchus_vorax Brachychampsa_montana
Brachychampsa_sealeyi Brachyuranochampsa_eversolei Brochuchus_pigotti
Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichiei Eosuchus_minor Eothoracosaurus_mississippiensi
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiiasuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsa_mccabei
Thecachampsa_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Crocodylus_niloticus Crocodylus_porosus Crocodylus_rhombifer Mecistops_cataphractus
Osteolaemus_osborni Osteolaemus_tetraspis (Bernissartia_fagesii Acynodon_adriaticus
Acynodon_iberoccitanus Agaresuchus_subjuniperus Albertochampsa_langstoni
Alligator_mcgrewi Alligator_mefferdi Alligator_olseni Alligator_prenasalis Alligator_thomsoni
Allodaposuchus_precedens Allognathosuchus_polyodon Allognathosuchus_wartheni
Arambourgia_gaudryi Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons
Asiatosuchus_germanicus Australosuchus_clarkae Borealosuchus_acutidentatus
Borealosuchus_formidabilis Borealosuchus_griffithi Borealosuchus_sternbergii
Borealosuchus_threeensis Borealosuchus_wilsoni Bottosaurus_fustidens
Bottosaurus_harlani Boverisuchus_magnifrons Boverisuchus_vorax
Brachychampsa_montana Brachychampsa_sealeyi Brachyuranochampsa_eversolei
Brochuchus_pigotti Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichiei Eosuchus_minor Eothoracosaurus_mississippiensi
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman

Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiasuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Caiman_crocodylus Caiman_latirostris Caiman_yacare Melanosuchus_niger
(Bernissartia_fagesii Acynodon_adriaticus Acynodon_iberoccitanus
Agaresuchus_subjuniperus Albertochampsia_langstoni Alligator_mcgrewi Alligator_mefferdi
Alligator_olseni Alligator_prenasalis Alligator_thomsoni Allodaposuchus_precedens
Allognathosuchus_polyodon Allognathosuchus_wartheni Arambourgia_gaudryi
Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons Asiatosuchus_germanicus
Australosuchus_clarkae Borealosuchus_acutidentatus Borealosuchus_formidabilis
Borealosuchus_griffithi Borealosuchus_sternbergii Borealosuchus_threensis
Borealosuchus_wilsoni Bottosaurus_fustidens Bottosaurus_harlani
Boverisuchus_magnifrons Boverisuchus_vorax Brachychampsia_montana
Brachychampsia_sealeyi Brachyuranochampsia_eversolei Brochuchus_pigotti
Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichei Eosuchus_minor Eothoracosaurus_mississippiensis
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsia_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiasuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Crocodylus_niloticus Crocodylus_rhombifer (Bernissartia_fagesii Acynodon_adriaticus
Acynodon_iberoccitanus Agaresuchus_subjuniperus Albertochampsia_langstoni
Alligator_mcgrewi Alligator_mefferdi Alligator_olseni Alligator_prenasalis Alligator_thomsoni
Allodaposuchus_precedens Allognathosuchus_polyodon Allognathosuchus_wartheni

Arambourgia_gaudryi Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons
Asiatosuchus_germanicus Australosuchus_clarkae Borealosuchus_acutidentatus
Borealosuchus_formidabilis Borealosuchus_griffithi Borealosuchus_sternbergii
Borealosuchus_threeensis Borealosuchus_wilsoni Bottosaurus_fustidens
Bottosaurus_harlani Boverisuchus_magnifrons Boverisuchus_vorax
Brachychampsa_montana Brachychampsa_sealeyi Brachyuranochampsa_eversolei
Brochuchus_pigotti Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinaticampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichi Eosuchus_minor Eothoracosaurus_mississippiensi
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiiasuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsa_mccabei
Thecachampsa_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Crocodylus_niloticus Crocodylus_porosus Crocodylus_rhombifer (Bernissartia_fagesii
Acynodon_adriaticus Acynodon_iberoccitanus Agaresuchus_subjuniperus
Albertochampsa_langstoni Alligator_mcgrewi Alligator_mefferdi Alligator_olseni
Alligator_prenasalis Alligator_thomsoni Allodaposuchus_precedens
Allognathosuchus_polyodon Allognathosuchus_wartheni Arambourgia_gaudryi
Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons Asiatosuchus_germanicus
Australosuchus_clarkae Borealosuchus_acutidentatus Borealosuchus_formidabilis
Borealosuchus_griffithi Borealosuchus_sternbergii Borealosuchus_threeensis
Borealosuchus_wilsoni Bottosaurus_fustidens Bottosaurus_harlani
Boverisuchus_magnifrons Boverisuchus_vorax Brachychampsa_montana
Brachychampsa_sealeyi Brachyuranochampsa_eversolei Brochuchus_pigotti
Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinaticampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichi Eosuchus_minor Eothoracosaurus_mississippiensi
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsa_vectiana Iharkutosuchus_makadii

Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiassuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Caiman_crocodylus Caiman_yacare (Bernissartia_fagesii Acynodon_adriaticus
Acynodon_iberoccitanus Agaresuchus_subjuniperus Albertochampsia_langstoni
Alligator_mcgrewi Alligator_mefferdi Alligator_olseni Alligator_prenasalis Alligator_thomsoni
Allodaposuchus_precedens Allognathosuchus_polyodon Allognathosuchus_wartheni
Arambourgia_gaudryi Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons
Asiatosuchus_germanicus Australosuchus_clarkae Borealosuchus_acutidentatus
Borealosuchus_formidabilis Borealosuchus_griffithi Borealosuchus_sternbergii
Borealosuchus_threeensis Borealosuchus_wilsoni Bottosaurus_fustidens
Bottosaurus_harlani Boverisuchus_magnifrons Boverisuchus_vorax
Brachychampsia_montana Brachychampsia_sealeyii Brachyuranochampsia_eversolei
Brochuchus_pigotti Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichi Eosuchus_minor Eothoracosaurus_mississippiensis
Euthecodon_arambourgii Gavialis_lewisi Gavialosuchus_eggenburgensis
Globidentosuchus_brachyrostris Gnatusuchus_pebasensis Gryposuchus_colombianus
Hassiacosuchus_haupti Hylaeochampsia_vectiana Iharkutosuchus_makadii
Jiangxisuchus_nankangensis Kambara_implexidens Kentisuchus_spenceri
Krabisuchus_siamogallicus Kuttanacaiman_iquitosensis La_venta_Caiman
Leidyosuchus_canadensis Lohuecosuchus_mechinorum Lohuecosuchus_megadontos
Maomingosuchus_petrolica Mourasuchus_amazonensis Mourasuchus_arendsi
Mourasuchus_atopus Navajosuchus_mooki Necrosuchus_ionensis
Orientalosuchus_naduongensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiassuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsia_mccabei
Thecachampsia_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

[Caiman_crocodylus Caiman_latirostris Caiman_yacare (Bernissartia_fagesii
Acynodon_adriaticus Acynodon_iberoccitanus Agaresuchus_subjuniperus
Albertochampsia_langstoni Alligator_mcgrewi Alligator_mefferdi Alligator_olseni

Alligator_prenasalis Alligator_thomsoni Allodaposuchus_precedens
Allognathosuchus_polyodon Allognathosuchus_wartheni Arambourgia_gaudryi
Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons Asiatosuchus_germanicus
Australosuchus_clarkae Borealosuchus_acutidentatus Borealosuchus_formidabilis
Borealosuchus_griffithi Borealosuchus_sternbergii Borealosuchus_threeensis
Borealosuchus_wilsoni Bottosaurus_fustidens Bottosaurus_harlani
Boverisuchus_magnifrons Boverisuchus_vorax Brachychampsa_montana
Brachychampsa_sealeyi Brachyuranochampsa_eversolei Brochuchus_pigotti
Caiman_brevirostris Caiman_wannlangstoni Centenariosuchus_gilmorei
Ceratosuchus_burdoshi Chinatichampsus_wilsonorum Crocodylus_acer Crocodylus_affinis
Crocodylus_megarhinus Deinosuchus_riograndensis Deinosuchus_schwimmeri
Diplocynodon_darwini Diplocynodon_deponiae Diplocynodon_hantoniensis
Diplocynodon_muelleri Diplocynodon_ratelii Diplocynodon_remensis Diplocynodon_tormis
Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
Eocaiman_cavernensis Eocaiman_itaboraiensis Eocaiman_palaeocenicus
Eogavialis_africanum Eosuchus_lerichi Eosuchus_minor Eothoracosaurus_mississippiensi
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Orientalosuchus_naduungensis Pachycheilosuchus_trinquei Paratomistoma_courti
Pietraroiassuchus_ormezzanoi Piscogavialis_jugaliperforatus Planocrania_datangensis
Planocrania_hengdongensis Procaimanoidea_kayi Procaimanoidea_utahensis
Prodiplocynodon_langi Protoalligator_huiningensis Protocaiman_peligrensis
Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsa_mccabei
Thecachampsa_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus]]

[Alligator_mississippiensis Alligator_sinensis (Bernissartia_fagesii Acynodon_adriaticus
Acynodon_iberoccitanus Agaresuchus_subjuniperus Albertochampsa_langstoni
Alligator_mcgrewi Alligator_mefferdi Alligator_olseni Alligator_prenasalis Alligator_thomsoni
Allodaposuchus_precedens Allognathosuchus_polyodon Allognathosuchus_wartheni
Arambourgia_gaudryi Arenysuchus_gascabadiolorum Asiatosuchus_depressifrons
Asiatosuchus_germanicus Australosuchus_clarkae Borealosuchus_acutidentatus
Borealosuchus_formidabilis Borealosuchus_griffithi Borealosuchus_sternbergii
Borealosuchus_threeensis Borealosuchus_wilsoni Bottosaurus_fustidens
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Dollosuchoides_densmorei Dongnanosuchus_hsui Eoalligator_chunyii
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Purussaurus_brasiliensis Purussaurus_mirandai Purussaurus_neivensis Quinkana_spp
Rimasuchus_lloydi Shamosuchus_djadochtaensis Stangerochampsa_mccabei
Thecachampsa_antiqua Thoracosaurus_macrorhynchus Thoracosaurus_neocesariensis
Tomistoma_cairense Tomistoma_lusitanica Toyotamaphimeia_machikanensis
Trilophosuchus_rackhami Tsoabichi_greenriverensis Voay_robustus
Wannaganosuchus_brachymanus)]

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8. Dataset: Walter et al., supplementary dataset (modified Rio & Mannion, 2021 – continuous and discrete characters; .tnt)

nstates cont;

nstates 32 ;

xread 'Data saved from TNT'

330 146

&[cont]

Bernissartia_fagesii 0.494 1.272 ? ? ? 0.173 ? 0.870 7.000 0.375 0.717 ?
 ? ? ? ? 16.000 ? ? ? 60.000 ? ? ? ? ?

Isisfordia_duncani 0.646 1.482 0.657 0.180 0.093 0.232 0.362 0.823 0.000 0.525 0.663
 0.346 0.421 1.016 3.650 1.918 ? ? ? ? 30.000 ? ? 0.754 1.112 ?

Acynodon_iberoccitanus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? 13.000 ? ? ? ? ? ? ? ? ? ?

Agaresuchus_fontisensis 0.534 1.366 1.375 0.420 0.287 0.308 0.576 0.595 ? 0.591
 0.921 0.191 0.430 1.379 3.259 ? 15.000 ? ? ? ? ? ? ? ? ?

Allodaposuchus_precedens 0.563 1.778 1.700 0.254 0.388 0.388 ? 0.794 11.000
 0.529 0.913 0.129 0.366 ? 2.900 ? 14.000 ? ? ? ? ? ? ? ? ?

Glen_Rose_form ? ? ? ? ? 0.147 ? 0.699 9.000 0.525 0.598 ? 0.533
 0.308 2.858 2.421 11.000-12.000 ? ? ? ? ? ? ? ? ?

Hylaeochampsia_vectiana ? 1.517 ? ? ? 0.328 ? 1.052 0.000 0.410 0.560
 ? 0.250 0.846 ? 2.333 ? ? ? ? ? ? ? ? ?

Iharkutosuchus_makadii 0.428 1.292 1.500 0.344 ? 0.257 ? 0.667 18.000 ? ?
 ? 0.295 1.219 ? 1.664 13.000 ? ? ? ? ? ? ? ? ?

Lohuecosuchus_megadontos 0.482 1.579 1.667 0.296 ? 0.428 ? 0.693 5.000 0.420
 0.824 0.171 0.516 0.684 3.364 ? 10.000-11.000 ? ? 1.122 ? ? ? ? ?
 ?

Portugalosuchus_azenhae ? 1.074 ? ? ? 0.224 ? 0.595 0.000 0.705 0.903
 ? 0.354 1.222 ? ? ? 2.333 36.000 ? ? ? ? ? ? ?

Shamosuchus_djadochtaensis ? 0.824 ? ? 0.425 0.241 0.503 0.597 0.000 0.535
 0.800 ? ? ? 3.878 2.607 ? ? ? ? ? ? ? ? ?

Wannchampsus_kirpachi ? ? ? ? ? ? ? ? 0.733 0.000 0.651 0.537 ?
 ? ? 2.769 1.375 11.000 ? ? ? ? ? ? ? ? ?

Acresuchus_pachytemporalis 0.535 2.529 1.134 0.264 0.189 0.337 0.687 0.798 15.000
 0.518 0.488 0.147 ? ? ? 1.389 11.000 1.373 38.000 1.088 ? ? ? ? ?
 ?

Aktiogavialis_caribesi ? 0.787 ? ? ? 0.283 ? 0.657 12.000 0.640 0.794 ?
 0.386 1.130 ? 1.767 19.000 ? ? ? ? ? ? ? ?

Alligator_mcgrewi 0.444-0.478 1.495-1.518 1.291-1.429 0.242 ? 0.220-0.230 0.399-
 0.489 0.679-0.788 8.000 0.425-0.496 0.738-0.829 0.203-0.217 0.530 1.667 2.147 ?
 13.000 1.912-3.169 20.000 1.163 54.000 ? ? ? ? ?

Alligator_mefferdi 0.524 1.803 1.324 0.328 ? 0.355 0.491 0.750 4.000 0.368 1.074
 ? ? 1.438 2.622 1.750 14.000 1.914 38.000 1.158 ? ? ? ? ? ?

Alligator_mississippiensis 0.579-0.586 2.000-2.021 1.421-1.475 0.466 0.288 0.322-
 0.341 0.479-0.578 0.711-0.835 11.000 0.408-0.453 0.793-0.862 0.154-0.157 0.380
 0.947-1.000 3.330 1.607-2.048 15.000 2.200-2.618 11.000 1.174-1.391 24.000 0.832
 0.592 0.687-0.783 1.070-1.159 0.492

Alligator_olseni 0.481 1.865 1.257 ? ? 0.320 ? 0.763 8.000 0.586 0.931 ? ?
 ? 3.330 1.342 15.000 2.925 19.000 1.193 37.000 ? ? ? ? ?

Alligator_prenasalis 0.554-0.555 1.656-1.781 1.230-1.515 ? ? 0.278-0.308 0.532-
 0.617 0.669-0.755 7.000 0.516-0.604 0.711-0.737 0.213 ? ? ? ? 14.000
 2.017-2.533 22.000 1.229-1.252 24.000 0.914 0.507 0.739 1.220 ?

Alligator_sinensis 0.575 1.960 1.563 0.383 0.275 0.320 0.429 0.747 10.000 0.464 0.808
 0.163 0.471 1.267 2.326 1.950 13.000 2.059 21.000 1.154 17.000 0.869 0.581 0.689-
 0.744 1.107-1.206 0.517

Hassiacosuchus_haupti 0.417-0.538 1.778 1.333 ? ? 0.311 0.706 0.756 ? 0.500
 0.643-0.706 ? ? ? ? ? 14.000 1.412-1.500 46.000 1.250 65.000 ? ?
 0.941 1.490 ?

Navajosuchus_mooki 0.480-0.506 ? 0.867 ? ? ? ? ? ? ? ? 0.625 ?
 ? ? ? ? 14.000 1.550 21.000 ? ? 0.730 0.671 0.764 ? ?

Allognathosuchus_polyodon ? ? 1.273 ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? 1.605 ? ? ? ? ? ? ?

Allognathosuchus_wartheni 0.472 ? 1.129 ? ? ? 0.718 ? ? 0.540 ?
 0.161 ? ? ? 1.625 12.000 1.088 38.000 ? ? ? ? ? ?

Arambourgia_gaudryi 0.376 1.270 1.400 ? ? 0.216 0.370 0.730 0.000 0.481 0.846
 ? ? 1.333 ? 1.833 ? ? 31.000 ? ? ? ? ? ?

Argochampsa_krebsi ? 1.143 ? 1.237 0.409 0.304 ? 0.804 6.000 0.533 0.875
 ? ? 0.933 ? 1.813 26.000 ? ? ? ? ? ? ? ?

Asiatosuchus_germanicus 0.547 1.727 1.444 ? ? 0.410 0.436 0.791 16.000 0.327
 0.806 ? ? ? ? ? 14.000 2.167 23.000 ? 23.000 0.775 0.606 0.761 1.391
 ?

Asiatosuchus_nanlingensis ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? 0.911 ? ? ? ? ? ?

Australosuchus_clarkae 0.526-0.552 1.906-2.033 0.988 ? 0.167 0.200-0.258 0.650
 0.851-0.875 7.000 0.340-0.482 0.593-0.971 0.196 0.263 ? ? ? 14.000-15.000
 ? ? ? ? ? ? ? ?

Baru_darrowi ? ? 1.154 ? 0.517 ? ? ? ? ? ? ? 0.210 0.382 ?
 ? ? 13.000 ? ? ? ? ? ? ? ? ?

Baru_huberi ? ? 1.010 ? 0.242 ? ? ? ? ? ? ? 0.202 ? ?
 ? ? ? ? ? ? ? ? ? ? ?

Baru_wickeni ? ? 0.839 ? 0.409 ? ? ? 15.000 ? ? 0.167 0.437
 ? ? ? 12.000 1.736-1.790 ? 1.553-1.690 ? ? ? ? ?

Borealosuchus_acutidentatus 0.603 1.237 1.200 ? ? 0.203 ? 0.619 0.000 0.545
 0.949 ? ? ? ? ? 20.000 ? ? ? ? ? ? ?

Borealosuchus_griffithi ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Borealosuchus_formidabilis 0.646 1.171 1.224 ? ? 0.200 ? 0.514 0.000 0.550
 1.020 0.241 0.335 0.702 2.667 1.308 20.000 1.728 36.000 ? 55.000 1.033 0.527 ?
 1.080 0.556

Borealosuchus_sternbergii 0.574-0.600 1.257-1.552 1.152-1.471 0.110 0.276-0.296
 0.261-0.308 0.341-0.529 0.637-0.759 0.000-5.000 0.443-0.651 0.700-0.968 0.209-
 0.432 0.302-0.376 0.750-0.833 2.595 1.641-1.650 19.000 2.789-3.611 21.000-24.000
 1.059 ? ? ? 0.705 ? ?

Borealosuchus_threensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Borealosuchus_wilsoni 0.604 ? 0.867 0.321 ? 0.455 0.904 0.548 ? 0.592 1.302
 ? ? ? ? ? 18.000 ? ? 1.846 60.000 ? ? 0.710 1.231 0.377

Bottosaurus_harlani ? ? ? ? ? 0.290 1.008 0.533 8.000 0.482 0.896 ?
 ? ? ? ? ? 1.284 27.000 ? ? ? ? ? ? ?

Boverisuchus_magnifrons ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? 17.000 ? ? ? ? ? ? ? ? ? ?

Boverisuchus_vorax 0.584 1.453 0.891 0.157 ? 0.471 0.633 0.754 9.000 0.520 0.565
 0.259 0.418 1.106 ? ? 17.000 ? ? ? 13.000 ? 0.679 0.870 1.408 0.458

Brachychampsia_montana 0.583 2.522 0.885-1.000 0.088 0.163 0.402 0.721 0.935
 14.000 0.512 0.773 0.331 0.476 1.257 2.956 2.240 14.000 2.024 12.000 1.177 30.000
 ? ? ? 1.160 ?

Brochuchus_pigotti 0.658 1.765 0.931 0.397 0.282 0.382 0.492 0.897 6.000 0.377
 0.783 0.184 0.351 1.250 2.133 1.348 14.000 ? 21.000 ? ? ? ? ? ? ?

Caiman_brevirostris ? ? ? ? 0.308 ? ? ? ? ? ? ? ? ? ?
 ? 1.867 ? ? ? ? ? ? ? ? ? ? ?

Caiman_crocodilus 0.512-0.623 1.257-1.528 1.000-1.698 0.309-0.457 ? 0.214-0.303
 0.554-0.671 0.584-0.760 5.000-15.000 0.273-0.432 0.775-0.862 0.159-0.219 0.339-
 0.481 1.339-1.693 2.126 1.409-1.433 14.000-17.000 1.773-1.905 21.000-33.000 1.162-
 1.661 18.000 ? 0.530 0.771-0.803 1.100-1.282 0.636

Caiman_gasparinae ? ? 1.220 0.763 0.470 0.447 ? 0.772 14.000 0.261 0.739
 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Caiman_latirostris 0.539 2.195 1.343 0.355-0.653 0.304 0.341 0.685 0.659 8.000-9.000
 0.259 0.786 0.178 0.508 2.000 2.581 1.571 13.000 1.513 30.000 1.317 ? 0.814 0.608
 0.754-0.757 ? 0.538

Caiman_lutescens_MACN ? ? ? ? ? 0.462 ? 0.598 13.000 0.304 0.417
 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

UCMP_39978 ? ? 1.064 0.202 0.280 ? ? ? ? ? ? ? 0.187 0.450
 2.077 2.294 ? 13.000 ? ? ? ? ? ? ? ? ?

Caiman_wannlangstoni 0.479 1.333 ? ? ? 0.314 ? 0.726 7.000 0.346 0.769
 ? ? ? ? ? 12.000 ? ? ? ? ? ? ? ? ?

Caiman_yacare 0.567-0.579 1.575-1.595 1.115-1.208 0.269-0.318 0.333-0.366 0.325-
 0.329 0.686 0.646-0.663 2.000-11.000 0.349-0.353 0.667-0.692 0.177 0.385-0.406

1.941-2.063 2.316 1.348 14.000 1.618 23.000-37.000 1.342 0.000 ? ? 0.733-0.791
1.058-1.311 ?

Ceratosuchus_burdoschi 0.529 1.733 0.938 ? ? 0.343 ? 0.717 ? 0.614 1.034
0.339 ? ? ? 1.436 14.000 ? ? ? ? ? ? ? ?

Crocodylus_acutus 0.639 1.678 0.718 0.704 0.422 0.533 0.347 0.833 15.000 0.440
0.818 0.186 0.394 1.333 2.535 1.464 14.000 1.741 33.000 1.511 17.000 ? ? 0.712-
0.741 1.041-1.121 ?

Crocodylus_affinis 0.575-0.606 1.612-1.726 0.833-1.098 0.310-0.314 0.390 0.189-
0.658 0.512-0.632 0.553-0.777 2.000-8.000 0.452-0.480 0.988-1.055 0.218 0.239-
0.443 0.789-1.381 3.464 1.460-1.546 13.000-14.000 1.930-2.150 41.000 1.371-1.491
33.000 ? 0.557 ? ? ?

Crocodylus_anthropophagus ? ? 0.843 ? ? ? ? ? ? ? ? 0.195
? ? ? ? 14.000 1.166 23.000 ? 23.000 ? ? ? ? ?

Asiatosuchus_depressifrons 0.561 1.518 1.227 0.363 0.375 0.301 0.554 0.675 8.000-
13.000 0.518 0.862 ? ? ? ? 1.579 14.000 1.700 31.000 ? 17.000 ? ?
0.779 1.084 ?

Crocodylus_intermedius 0.644-0.653 1.393-1.432 0.656-0.889 0.747 0.417 0.423-0.493
0.417-0.544 0.757-0.832 3.000 0.357-0.465 0.931-1.067 0.203-0.286 0.282-0.320
1.304-1.550 2.525 1.300-1.389 14.000 1.929-2.011 34.000 1.665 ? ? ? ? ?
?

Crocodylus_johnstoni 0.686 1.138 0.815 0.498 0.421 0.294 0.524 0.688 4.000 0.547
0.841 0.265 0.275 1.085 2.487 1.404 14.000 2.117 25.000 1.877 14.000 1.014 0.468
0.690-0.729 1.116-1.192 0.432

Crocodylus_megarhinus 0.662 2.193 0.700-0.807 0.419-0.429 0.416 0.307 0.505 0.887
7.000-8.000 0.360 0.850 0.161-0.348 ? ? 2.393 1.548 13.000 1.947 ? ? ?
? ? ? ? ?

Crocodylus_mindorensis 0.548 1.495 0.703 0.511 ? 0.276 0.406 0.838 12.000-16.000
0.474 1.054 0.185 0.377 0.706 2.535 1.562 13.000 2.013 33.000 1.847 ? ? ? ?
? ?

Crocodylus_moreletii 0.603 2.255 0.830 0.629 0.455 0.519 0.463 0.896 11.000 0.432
0.829 0.125 0.415 0.640 2.067 1.719 14.000 1.366 30.000 1.367 ? ? ? 0.715-
0.719 1.035-1.106 ?

Crocodylus_niloticus 0.567-0.613 1.737 0.826 0.491 0.424 0.495 0.341 0.859 5.000
0.494 0.619 0.169 0.342 1.143 2.285 1.563 13.000-14.000 1.257 33.000 1.310 20.000
0.822-0.949 0.431-0.489 0.660-0.771 1.116-1.174 0.524-0.633

Crocodylus_novaeguineae 0.602 1.446 0.833 0.544 0.361 0.357 0.362 0.839 12.000
0.489 0.870 0.171 0.355 1.000 2.105 1.211 13.000-14.000 1.467 33.000 1.111 ? ?
? 0.721 1.227 ?

Crocodylus_palustris 0.533-0.601 2.087 0.850-0.873 0.579-0.863 0.365 0.470 0.410
0.904 3.000 0.471 0.592 0.229 0.457 2.769 2.000 ? 14.000-15.000 1.205 40.000
1.097 19.000 0.942 0.551 0.722-0.730 1.059-1.174 0.460

Crocodylus_porosus 0.602-0.634 1.967-2.008 0.768-1.051 0.648-0.667 0.403-0.412
0.348-0.519 0.420-0.437 0.820-0.908 9.000-14.000 0.410-0.413 0.653-0.902 0.108-
0.114 0.403-0.449 1.783-2.000 2.159 1.217-1.265 14.000 1.469-1.649 36.000 1.095-
1.121 17.000 0.921 0.476 0.581-0.692 1.090-1.125 0.547

Crocodylus_rhombifer 0.558-0.625 1.646 0.769 0.151-0.333 ? 0.441 0.347 ? 7.000-15.000 0.373 0.698-0.875 0.191 0.466 1.382 2.805 1.742 13.000-14.000 1.928 30.000 1.158 19.000 0.825 0.470 0.726-0.784 1.221-1.314 0.573

Crocodylus_siamensis 0.581-0.614 1.723-1.853 0.837-0.953 0.549 0.287-0.291 0.475-0.547 0.324-0.375 0.733-0.758 12.000 0.432-0.500 0.806-0.906 0.189-0.190 0.409-0.434 1.389-1.571 1.962 1.433-1.500 14.000 1.467 38.000 1.302 12.000 0.885 0.495 0.736 1.120 ?

Crocodylus_thorbjarnarsoni 0.595 1.913 1.034 0.175 0.427 0.501 0.482 0.834 12.000 0.423 0.933 0.126 0.513 1.900 2.773 ? 13.000 1.433 37.000 1.248 ? ? ? ?

Crocodylus_palaeindicus 0.531-0.568 1.714-1.785 1.130 0.675 0.367 0.439-0.473 0.333-0.385 0.771-0.793 10.000-14.000 0.346-0.415 0.759-1.037 0.189-0.221 0.422 1.600 ? 1.692 13.000-14.000 1.379 ? 1.486 ? ? 0.520 ? ? ?

Dadagavialis_gunai ? 0.938 ?

Deinosuchus_riograndensis ?

Diplocynodon_darwini 0.479-0.618 1.386-1.424 1.000 0.446-0.623 ? 0.203-0.228 0.481-0.740 0.877-0.915 1.000-6.000 0.407-0.511 0.667-0.833 ? 0.364 1.000 2.378 ? 18.000 2.818 43.000 ? 53.000 ? 0.443 0.716-0.890 1.077-1.198 ?

Diplocynodon_deponiae 0.455-0.484 ? 0.917 ? ? ? ? ? ? 2.000 0.400-0.500 0.333-0.545 ? ? ? 3.231 ? 16.000 ? ? ? ? ? ? 0.750-0.789 1.200-1.531 ?

Diplocynodon_hantoniensis 0.566-0.680 1.908-1.970 0.773-1.076 0.141-0.226 0.296-0.333 0.265-0.293 0.635-0.723 0.968-1.010 9.000-10.000 0.550-0.564 0.551-0.591 0.216-0.249 0.392-0.464 0.918-0.962 3.258 1.713-1.905 17.000 1.857-2.138 44.000-45.000 1.466 37.000-47.000 ? ? ? ? ?

Diplocynodon_muelleri 0.507 1.721 ? ? ? 0.233 ? 0.965 0.000 0.518 0.558 ? ? ? ? ? 20.000 ? ? ? 48.000 ? ? ? ? ?

Diplocynodon_ratelii 0.586 1.485 1.037 0.130 ? 0.265 0.625 0.824 8.000-9.000 0.429 0.792 ? 0.349 1.067 3.543 1.533 16.000 ? ? ? 47.000 ? 0.430 ? ? ?

Diplocynodon_remensis ? ? ? ? ? 0.244 ? ? ? ? 0.667 ? ? ? ? ? 17.000 2.211 30.000 1.316 ? ? ? ? ?

Diplocynodon_tormis 0.594 1.614 0.868 0.289 0.422 0.302 0.472 0.881 7.000 0.539 0.646 ? 0.390 ? ? ? 17.000 ? ? ? ? ? ? ? ?

Dollosuchoides_densmorei 0.668 1.225 0.813 0.385 ? 0.285 0.650 0.795 0.000 0.646 1.071 0.378 0.350 1.063 3.174 ? 15.000 ? ? ? ? ? ? ? ?

Eocaiman_cavernensis ? ? ? ? ? ? ? ? ? ? ? ? ? 0.633 ? ? ? 14.000 1.833 28.000 ? ? ? ? ? ?

Eocaiman_palaeocenicus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1.556 24.000 1.202 ? ? ? ? ? ?

Eogavialis_africanum 0.693-0.725 0.857-1.118 0.909-1.128 0.620-0.823 0.518 0.247-0.308 0.359-0.604 0.604-0.882 7.000-16.000 0.440-0.661 0.974-1.129 0.091 0.357-0.358 1.026-1.417 ? 1.433-1.886 20.000 ? 21.000 ? ? ? 0.374 ? ? 0.485

Eosuchus_lerichi 0.653 ? 0.815 ? ? ? 0.576 ? 0.000 0.576 0.868 0.250
0.410 1.733 3.646 1.524 16.000-17.000 ? ? ? ? ? ? ? ? ?

Eosuchus_minor 0.657 ? ? ? ? ? ? ? ? 1.000-5.000 ? ? ? ?
? ? ? 17.000 ? 23.000 ? ? ? ? ? ? ? ?

Eothoracosaurus_mississippiensi 0.689 0.955 1.030 ? ? 0.318 0.433 0.577-0.656
5.000 0.547-0.571 0.938-1.079 ? ? ? ? 1.936 22.000 ? ? ? ? ?
0.288 ? ? ?

Euthecodon_arambourgi 0.748 1.608 0.966 0.590 ? 0.304 0.486 0.886 1.000 0.443
0.806 0.091 ? ? ? ? 15.000 ? ? ? ? ? ? ? ? ?

Gavialis_browni ? 0.853 ? ? ? 0.441 0.550 0.588 10.000 0.568 1.216 ?
0.481 ? 2.222 ? 18.000 ? ? ? ? ? ? ? ? ?

Gavialis_gangeticus 0.716-0.727 0.799-0.892 0.719-1.045 0.429 0.581-0.605 0.387-
0.496 0.503-0.550 0.555-0.677 6.000 0.543-0.622 1.113-1.195 0.105-0.118 0.465-
0.589 1.500-2.357 3.256 1.490-1.932 23.000-24.000 1.905-2.318 23.000 1.887-2.148
40.000 1.020 0.436-0.485 0.553-0.614 1.132-1.189 0.723-0.838

Gavialis_lewisi ? 0.974 ? ? ? 0.346 0.200 0.789 8.000 0.497 0.940 ?
0.427 5.496 2.523 2.510 ? ? 33.000 ? ? ? ? ? ? ?

Gavialosuchus_eggenburgensis 0.676 1.382 0.904 ? 0.577 0.274 0.579 0.682 11.000
0.579 1.032 ? ? ? ? 1.385 15.000 ? ? ? ? ? ? ? ?

Globidentosuchus_brachyrostris ? ? ? ? ? ? ? ? 0.759 14.000 0.245
0.815 ? ? ? ? ? ? ? ? ? ? ? ? ?

Gnatusuchus_pebasensis 0.450 2.115 ? ? ? 0.165 ? 0.921 5.000 0.319 0.700
? ? ? 3.520 ? 9.000 ? ? ? ? ? ? ? ? ?

Gryposuchus_colombianus ? 0.850 ? ? ? 0.313-0.375 ? 0.563-0.631 8.000
? ? ? 0.466 ? ? ? 21.000 1.389-2.125 ? 1.469 ? ? ? ? ?
?

Gryposuchus_croizati ? ? 1.258 0.548 ? ? ? ? 27.000 ? ? ? ?
? ? 2.133 19.000 ? ? ? ? ? ? ? ?

Gryposuchus_neogaeus 0.787 ? 1.143 0.665 0.527 0.289 ? 0.483 8.000 0.675
1.266 0.080 ? ? ? 1.667 ? 2.581 18.000 ? ? ? ? ? ?

Gryposuchus_pachakamue ? 0.840 0.959 0.413 0.636 0.291-0.344 ? 0.664-0.782
19.000-29.000 0.564-0.693 1.065-1.144 ? 0.434-0.502 1.448 ? ? 22.000 1.859
29.000 ? ? ? ? ? ? ?

Ikanogavialis_gameroi ? 1.140 ? ? ? 0.240 0.923 0.520 15.000 0.654 1.294
? 0.400 ? ? 1.471 30.000 ? ? ? ? ? ? ?

Jiangxisuchus_nankangensis 0.551 1.434 ? ? ? 0.217 0.531 0.603 7.000 0.617
0.852 0.324 ? ? 2.733 ? 14.000 ? ? ? ? ? ? ?

Kambara_implexidens ? 1.256-1.466 0.820 0.427 ? 0.195-0.239 0.332-0.399
0.839-0.894 2.000 0.399-0.415 0.773-0.791 0.274 ? 0.966 ? 1.484 15.000 2.592
15.000 ? ? ? ? ? ? ?

Kambara_murgonensis ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? 16.000 ? ? ? ? ? ? ? ?

Kambara_taraina ? ? ? ? ? ? ? 0.878 7.000-11.000 0.419 0.722 ?
 ? ? 2.793 ? 14.000 ? ? ? ? ? ? ? ? ?

Kentisuchus_spenceri ? 1.022-1.395 0.875 ? ? 0.271-0.322 ? 0.722-0.752
 3.000-16.000 0.509-0.583 0.889-1.080 ? 0.341 0.969 ? 1.421-1.706 13.000 1.462
 ? ? ? ? ? ? ? ?

Kuttanacaiman_iquitosensis ? 1.840 0.662 0.344 ? 0.203 ? 0.640 9.000 0.409
 ? ? ? 1.667 1.634 ? 13.000 ? ? ? ? ? ? ? ?

Leidyosuchus_canadensis 0.596-0.615 1.710 1.079 0.121 ? 0.215 0.556 0.581 ?
 0.648 0.629 0.323 0.487-0.494 0.941-1.176 3.333 1.696 18.000 ? 30.000 ? ? ?
 ? ? ? ?

Mecistops_cataphractus 0.670 1.458 0.938 0.500 0.515 0.361 0.553 0.916 8.000 0.447
 0.794 0.282 0.314 1.625 1.785 1.333 13.000 1.964 32.000 1.705 23.000 1.057 0.410
 0.717-0.740 1.144-1.203 0.510

Mekosuchus_inexpectatus ? ? 1.000 0.119 ? ? ? ? ? ? ? ? ?
 ? ? 1.486 ? 2.250 55.000 1.040 ? ? ? ? ? ?

Mekosuchus_sanderi ? ? ? ? ? 0.409 ? 0.536 ? 0.487 0.548 ? ?
 ? ? 1.900 ? ? ? ? ? ? ? ? ?

Mekosuchus_whitehunterensis ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? 2.000 35.000 ? ? ? ? ? ? ?

Melanosuchus_niger 0.495 2.090 0.953 0.641 0.281 0.320 0.550 0.820 17.000 0.180
 0.722 0.156 0.534 2.762 2.366 1.326 13.000-14.000 1.485 47.000 1.253 7.000 0.767
 0.481 0.711-0.761 1.241-1.297 0.603

Moroccosuchus_zennaroi ? ? 1.140 0.531 0.427 0.312 ? 0.594 0.000-11.000
 0.614 1.194 ? ? ? ? ? 14.000 2.043 22.000 1.295 ? ? ? ? ? ?

Mourasuchus_amazonensis 0.745 3.178 2.057 0.340 ? 0.434 1.046 0.704 0.000
 0.211 0.579 0.332 ? ? ? ? ? ? ? ? ? ? ? ? ?

Mourasuchus_arendsi ? 3.140 ? ? ? 0.420-0.482 ? 0.570-0.691 ? 0.215-
 0.276 0.810-0.857 ? ? ? 1.922 1.528-2.000 ? ? ? ? ? ? ? ?
 ? ?

Mourasuchus_atopus ? ? ? ? ? ? ? ? ? ? ? ? ? ? 5.750
 3.152 ? ? 2.500 ? 1.250 10.000 ? ? ? ? ?

Necrosuchus_ionensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? ? 0.502 0.763 1.141 0.363

Osteolaemus_tetraspis 0.523-0.558 1.531-1.673 1.277-1.364 0.397 0.325 0.250-0.282
 0.256-0.317 0.634-0.745 0.000 0.222-0.259 0.717-1.000 0.047-0.149 0.350-0.381
 1.617-2.000 1.675 1.714-1.733 12.000 1.487-1.615 39.000 1.350-1.667 2.000 0.761-
 0.770 0.504-0.569 0.739-0.786 1.133-1.228 0.406-0.444

Paleosuchus_palpebrosus 0.544 1.210 0.674 0.306 ? 0.275 0.397 0.824 0.000 0.000
 ? 0.156 0.419 2.400 2.121 1.261 14.000-15.000 2.272 31.000-39.000 1.250 20.000
 0.758-0.791 0.507-0.651 0.750-0.821 1.260-1.300 0.590-0.599

Paleosuchus_trigonatus 0.549-0.592 1.238-1.328 1.030-1.143 0.274-0.366 0.400 0.236-
 0.279 0.390-0.500 0.754-0.837 0.000-3.000 0.000 ? 0.203-0.205 0.433-0.460 1.308-
 2.105 2.121 1.267-1.400 15.000-16.000 2.478 29.000-31.000 1.438 32.000 0.715 0.636
 0.770-0.776 1.246-1.273 0.553

Paratomistoma_courti ? ? ? ? ? 0.263 ? 0.688 6.000 0.511 0.982 ?
 ? ? ? 1.264 ? ? ? ? ? ? ? ? ? ? ?

Penghusuchus_pani 0.683 1.392 ? ? 0.313 0.289 ? 0.597 15.000 0.543 1.083
 ? 0.350 1.175 2.925 1.727 16.000 ? ? ? ? 0.788 0.488 0.610 1.206 0.602

Piscogavialis_jugaliperforatus 0.766 1.086 1.371 0.775 ? 0.223 0.486 0.800 12.000
 0.479 1.030 0.038 0.300 1.119 3.476 1.538 28.000 ? 13.000-24.000 ? ? ?
 0.356 ? ? ?

Planocrania_datangensis 0.596 1.016 1.050 ? ? 0.444 ? 0.683 ? 0.628 0.741
 ? ? ? ? ? 18.000 ? ? ? ? ? ? ? ? ?

Planocrania_hengdongensis 0.519 ? ? ? ? 0.233 0.400 0.713 ? 0.457
 0.653 ? ? ? ? 2.125 ? ? ? 1.083 ? ? ? ? ? ?

Procaimanoidea_utahensis 0.485 ? 0.900 0.184 ? 0.218 ? 0.909 ? 0.663
 0.482 0.174 ? 0.890 ? ? 13.000 ? 18.000 ? ? ? ? ? ? ?

Protocaiman_peligrensis ? ? ? ? ? 0.259 ? 0.634 12.000 0.538 0.749 ?
 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Purussaurus_brasiliensis 0.630 2.381 0.696 0.262 0.367 0.540 1.121 0.524 1.000 0.576
 0.663 0.268 0.631 4.800 ? 1.684 14.000 2.167 ? 1.000 13.000 ? ? ? ?
 ?

Purussaurus_mirandai ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0.400 ?
 ? ? 14.000 ? ? ? ? ? ? ? ? ? ?

Purussaurus_neivensis 0.549 2.136 0.654 0.368 0.279 0.403 0.929 0.757 0.000 0.410
 0.563 0.153 0.427-0.500 3.600-5.000 2.239 1.702 14.000 ? 20.000 1.154 13.000 ?
 ? ? ? ?

Quinkana ? ? 1.167 0.500 0.486-0.500 ? ? ? ? ? ? ? ? ?
 ? ? ? 12.000-14.000 ? ? ? ? ? ? ? ? ?

Siquisiquesuchus_venezuelensis 0.730 1.045 ? ? ? ? ? 0.606 ? 0.650
 1.038 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Stangerochampsia_mccabei 0.463 1.750 0.883 0.100 ? 0.243 0.687 0.718 5.000
 0.682 0.708 0.298 0.477 1.953 3.367 ? 14.000 1.450 30.000 ? 37.000 ? ?
 0.750 ? ?

Thecachampsia_antiquus ? 1.315 ? 0.617-0.676 ? 0.256 ? 0.717 11.000-
 12.000 0.402 1.242 ? ? ? ? ? 14.000 ? ? ? ? ? ? ? ?
 ?

Thecachampsia_sericondon 0.694 1.209 0.940 ? ? 0.233 0.506 0.761 15.000 0.518
 1.000 0.238 0.433 0.960 3.538 ? 14.000 ? ? ? ? ? ? ? ? ?

Thoracosaurus_isorhynchus 0.734 0.970 0.735 0.282 ? 0.364 0.500 0.707 0.000-
 2.000 0.543 1.053 ? 0.293 1.455 ? 2.182 20.000 ? ? ? ? ? ? ?
 ? ?

Thoracosaurus_neocesariensis ? ? 1.091 0.844 ? 0.301-0.399 ? 0.609-0.634
 8.000-15.000 0.593-0.623 1.123-1.300 ? ? ? ? 1.313-1.604 ? ? ? ?
 ? ? ? ? ? ?

Tomistoma_cairense ? 1.205 ? ? ? 0.260 0.468 0.849 0.000 0.419 1.038 ?
 0.363 0.909 3.692 1.350 ? ? ? ? ? ? ? ? ? ?

Tomistoma_dowsoni ? 1.347 0.758 ? 0.583 0.429 ? 0.857 0.000 0.536 0.844
? ? ? ? 1.483 15.000 ? ? ? ? ? ? ? ? ?

Tomistoma_lusitanica 0.682 1.572 0.717 0.967 ? 0.250 0.511 0.761 0.000 0.511
0.900 ? ? ? ? ? 14.000 ? ? ? ? ? ? ? ? ?

Maomingosuchus_petrolica 0.697-0.723 0.872-1.111 0.750-0.805 0.196 ? 0.308-
0.333 0.667-0.714 0.667-0.808 3.000-9.000 0.476-0.567 0.833-0.882 ? ? 0.820
? ? 15.000 ? 21.000 ? 31.000 ? ? ? ? ?

Tomistoma_schlegelii 0.666-0.670 1.217-1.655 0.704-0.907 0.800-0.835 0.636-0.720
0.293-0.345 0.436-0.489 0.848-0.942 12.000-20.000 0.458-0.500 0.846-0.983 0.157-
0.212 0.312-0.456 0.632-1.207 2.472 1.464-1.756 17.000 2.308-2.500 20.000 1.568-
1.878 44.000 0.931 0.394 0.640-0.710 1.071-1.224 0.659

Toyotamaphimeia_machikanensis 0.711 1.511 1.115 0.354 0.459 0.223 0.548 0.638
2.000 0.260 0.758 ? 0.302 1.181 3.815 1.452 16.000 2.077 24.000 1.500 40.000 0.852
0.569 0.531 ? ?

Trilophosuchus_rackhami ? ? ? ? ? ? 0.282 ? 0.000 0.518 0.349 ?
0.329 ? 1.929 1.643 ? ? ? ? ? ? ? ? ? ?

Tsoabichi_greenriverensis 0.466-0.546 1.360-1.447 0.940-1.359 ? ? 0.252-0.257
0.350 0.929-1.040 ? 0.370 0.391 ? ? ? ? ? ? ? ? ? ?
? 0.745-0.851 1.312-1.542 0.593

Ultrastenos_willisi ? ? ? ? ? 0.215 ? 0.783 13.000-16.000 0.473 0.664
? ? ? 2.615 1.642 ? ? ? ? ? ? ? ? ?

Voay_robustus 0.535 1.473 1.083 0.412 0.372 0.402 0.539 0.679 23.000 0.303 1.000
0.250 0.463 1.000 3.273 1.560 13.000 1.933 25.000 1.128 32.000 ? 0.617 ? ?
0.582

Wannaganosuchus_brachymanus 0.236 1.521 0.995 ? ? 0.271 ? 0.750 11.000
0.556 0.800 ? ? ? ? ? 13.000 ? ? ? 46.000 ? ? 0.812 1.293
0.538

Theriosuchus_pusillus ? 1.008 ? ? ? 0.220 ? 0.686 ? 0.600 0.875 ?
? 0.557 3.091 ? 13.000 ? ? ? ? ? ? ? 0.800 ? ?

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Bernissartia_fagesii

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Isisfordia_duncani

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Acynodon_iberoccitanus

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Agaresuchus_fontisensis

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Allodaposuchus_precedens

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Glen_Rose_form

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Hylaeochampsia_vectiana

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Iharkutosuchus_makadii

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2001000?0?01120001??00000101??01??000000?0?104110?1??0?00?000??0011?00?00
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Lohuecosuchus_megadontos

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010100?10011010??010301010000?00?00?1000000100112000000000000020000000?01
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Portugalosuchus_azenhae

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Shamosuchus_djadochtaensis

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Wannchampsus_kirpachi

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Acresuchus_pachytemporalis

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101?110011100?101211100100?00110001001000100102000010000000?????????1?????
0??010000?????????????????0?0??1110??1?0?11021021??0001?00120200111?00001
110000?11??0??
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Aktiogavialis_caribesi

00000??00010??1?000??0??0100??????1?0???001101100010001??0?0011?1?00???
?????????02????????00010?0??10111?1101??????00??701020000000?1000001?00?010?
0??01??????12?0001?000?0011??0??????????3??????0?????????????????????
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Alligator_mcgrewi

00000??00010??0001000010?0101?1000000001?0000101201?[01]000010?211101010100
01001?110021000110110100000000011000100000020003200[01]0100000000101001111
00110000012000011201110011000000?001110??1?001111220?1??100100011100001000
1001010000?011000100011100??11000000101?1????????????200?1101?????????????
0?????1?????

Alligator_meffferdi

000010000010??1?01000010?0101?1200000001?1?00101201?1000010?21110101010001
001?110011000110120110000000001000100?000100032000010100000001010001??011
000001200001120011??11000000?001110??1?1011001021??10001000120100011?11001
011010?00000010????????????????????????????????????00????????????????????
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Alligator_mississippiensis

000010000010??100100001000101?120000000111000101201?1000010121110101000001
001?110011000[01]1011011001000001100010010001000320000101000000010100010?10
1100000120000112001101100000001001110?11?1011001021??00011000120100011?110
01111010?0010001000111001100[01]0100010111101010[01]00000101101111000111011
00010102111100

Alligator_olseni

000010000010??1001000010?0110?120100000?0?00101201?0000010?2111010100000?
?01?110011000??0110110?1000000100?00?000100032000010000000001110?011?101?
000001200?01120011??10000000????????????1111200?0??0001000120100011?01001
111010?00???0?1101??1010????????????
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Alligator_prenasalis

00000??00010??0001000010?0101?1200000101?0?[01]010120001000[01]10?2111010100
000??01?1100110001101101100000000100010[01]0000200032000010001000000110001
0?0[01]01000001200001120011001?000000????1????????111210?0??10010001201000
11?01001011010?000??1??10?????????0000?1??1? ??????0?00??0101101110010????
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Alligator_sinensis

000010000010??1001000010?0101?120000000110000101201?1000010121110101000001

0110????????????0??
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Australosuchus_clarkae

00000?00010??00000010010000?01000000001?0?000?101010000010?011?011100001?
?1???0011100?110000?100000000?00???0?0010013100011010?000001???0000???10
0000002001????????????????0?????1?????????11021020??100??001??100?00?0?0??
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??101???

Baru_darrowi

00000?000????000001?0000000?0120000100???00101????????????????1??100000??
??000000001010000000000?1020000010?0111
10[01]00?????011200?????0??10??0?????????????1??2112??10????001??00?00?????
???11??
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Baru_huberi

00010??00?????0?000010000?00?01?0000??0? ??????????????????????????????????
???0000000101000100100001???0??001???1?
2?1???11021020??10?1????????????????
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Baru_wickeni

00010??00010??0000001000?001?0110000100???0010?1101000001?0?1??100010??
?0????001100?????????0??0?000000100100001?0000?0100010010000100100?0010?0111
10100020?001120011??00110000?????????????11021120??1001??0?110100000100010
01101100??
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Borealosuchus_acutidentatus

00000?00010??0?0001?00?0000?0110000000???0000?01000?00001???????1000000??
?000?????10????0?????1??0??0????????????001?001?300120000000?00110?0000????
0??00????0?????????????????00??
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Borealosuchus_griffithi

00000?00010??000001?000?00000110100000???00000010??0001??1?1?01?000?010
0011?1?0?1????00??0?000??000010101?00001[01]0013300010010??0?0010??0000??
101??0?1??11?1120?1??0?0?000?????????????100210100?00?00?001?010010??000
01?11000?????0?????0??1??????0?010021?0?1?10?????1????????????????????
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Borealosuchus_formidabilis

00000?00010??0?0001?000?000?01100000001001000?00100000001?0?1?01000000?
?000??00110000101130100000000010001000001100033001200100000101000000?0110
000000??00011200100000000000?????0?????01002120?1??0000?00110100111?00101
011000?00000?0?1000001001100001011011??11110?00100100001000001??????????
?10002??

Borealosuchus_sternbergii

00000?00010??00000120000000?0110000000100100000000000000010?0110010000000
?0001100110000101100100000000010001000001[01]001[03]3000100100000001[01]00000
0?[01]1100000012011011200101?00000000?001??0?00111002110?1??0000?001201001
01?00100011000?0??0?00??10101??0?0?0101?0?1?????????00?000001000??????
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0000111011110011000110121110000000010001001[01]0010013200[01]1101000000101
00[01]10?0[01]10[012]0000110001112011101110000001001110??1?0011021021??000110
00120[12]00111?00[01]011110011111010011111100111100100101111010110110100011
10111100011101110010023111211

Caiman_gasparinae

000????0?010??1?0001?000??01?0?????????????????0??21020011?1??211?0?????????
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Caiman_latirostris

010011100010??10000010100001?002[01]0000001100001012002[01]01101112111010200
0011101?110011000110121110000000010001001100[12]00132000010100000011010001
0?0[01]10000001100011120111011100000010011110?1?0011021121??000110001212001
11?0000111000111110[01]00111101001111001000101?1??0110110100?1110111?????
1011[01]0010023111211

Caiman_lutescens_MACN

????110?0020????????????????????????1001????????001??2102001101?????????????????
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UCMP_39978

0100??0??????1?00011000??111?0????0???0? ?????? ???? ???? ???? ???? ???? ???? ????
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00000?1000?1120001??11000??
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Caiman_wannlangstoni

010111100010??0?00001010?001??1110010001??001002002001001????1?010?0??01?
??????001100?110121?100000?00?1??????????1????3200001000100??????????1110010
00000??0011120?0?????00?00??
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Caiman_yacare

000010100010??10000[01]10000001?00210010001000001002002001001112111010[12]00
00111011110011000110121110000000010001001100100132000[01]10100000001010001
0?001000000110001112011101110000001001110?01?0011021021??00011[01]00120[12]0
0111?00001111001111100001??11100111100000010111??1110110100011101111100??
1011[01]001?0?3111211

Ceratosuchus_burdoschi

00000??00011100?00001010?001?0001101000???00000????000001????1???101?00??
??????00?1?00??????110000?000?1000?????0320003200001010?0000?0?10101??0?01
00000??0????12?????????????00??????????????????1101210?0??0????0?1?????????0??1
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??1?????

Crocodylus_acutus

00100??00010??10000010001001?010000000011011011020000000010001110100000010
?[12]0000001100001000201000000000100101001001001310002000000000010010000?11
112[01]000020110112000000001000000101111001?0111021020??00010?0011020000001

Crocodylus_niloticus

00000??00010??10000010001001?01000000001101[01]0111200000000100011101000000
10?2000000110000100020100000000010010100100[12]0013100020010000000100[01]000
0?01112[01]00002011011200000000[01]000000101112101?0111021020??00010?0011020
0000110010011011000000110100000100111010011101110?0101000110111120010
011100001113111000

Crocodylus_novaeguineae

00010??00010??10000010001000?010000000011010010020000000010001110100000010
?10000001100001000201000000000100101001002001310002001000001010000100?1111
2100002011011200000000000000001111110?1?0111021020??00010?00110100000110010
011011000000110?????????????????????1?0?1?????????0?????????????????0111000011
13111000

Crocodylus_palustris

00000??00010??10000010101001?010000010011010[01]101200000000100011101000000
10?[12]000000110000100020100000000010010100000000101000200100000001000000?
[01]1102[01]000020110112000000001000000101112101?0111021020??00010?001101000
0011001001101100000011011000010000101001110?1??1110?01010001101111200??01
1100001112111000

Crocodylus_porosus

00010??00010??10000010[01]0100[01]?010000000011010[01]10[01]200000000100011101
00010010?[12]000000110000100020100000000010010100100[12]00131000200100000001
0000000?11112[01]00002011011200000000[01]000001101112101?0111021020??00010?0
0110200000010010011011000[01]00110100000100[01]00010011102110?11100010100001
01111200??011000001112111000

Crocodylus_rhombifer

00100??00010??10000010001000?010000010011010010120000000010001110100000010
?[12]0000001100001000201000000000100101001001001010002001000000010010000?11
11210000201101120000000000000000101111001?0111021020??00010?001101000000100
100110110000001101100001001110100111011101110001010001101111110?01110000
1112111000

Crocodylus_siamensis

00010??000111110000010001000?010000010011011110120000000010001110100010000
?20000001100001000201000000000100101001001001310002001000000011000000?1110
21000020110112000000001000000101112101?0111021020??00010?00110200000010010
011011000000010??000010001001000110?1???1110?01010001101111210??0110000011
12111000

Crocodylus_thorbjarnarsoni

00000??00010??0000001000?000?01100000001???1010120??110001????1?01?00??000
?1????00110000100?20?00?0000??10?10?000002001310002001000000010000000?1111
200000????011200001?001?0000??1?????????11021020??0?10?0?11020000??10?10
?111110?0100110??
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Crocodylus_palaeindicus

00000??00010??1000001010?00?????0????00????0[01]101??000000010??01101000000
1??2000?0111000??000?01000000000100101000?0100?110002001000000010000000?01
1021000?2?1?01120000??001?00?????????????????110?1020??00010?0?110100000?10?
1001100110????????????????????????????1???1???1?10?????????1101????????????????
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Dadagavialis_gunai

00000??000?0?????00??0?1?100?01000101?0?0??0021021?????????1????????111?01???

Gavialis_browni

00000??00000??100??1?2?1?100?1100010?0??002?021??0001???0010?11??1??
??????111100?00000?01??0??????????010??0??0??701120000001010000?1100?0101
0?001?0??011210?0??0??10??
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Gavialis_gangeticus

00000??00000??11000122010101?110001010000000021011001100010002001013110100
?00001111100000000001000011111101001000014111270112000000101100001100?0101
0000100000011210001?000010110000110?01?201103040?31?0100?01110210000201000
011000?000001001000001000011111110110100010000110000010110010010100000010
210?0000

Gavialis_lewisi

??00??00000????????????10??100010?00?0?0021??001000010??0010?3110100
?00001111100?000000?100001101111001??????????7??12??000101?00000?00?0111
00001?00?0011212001?30101011?????????????1?????0??1?01?0?01110?10000201000
01?0??0??
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Gavialosuchus_eggenburgensis

00000??00010??1?0001?001??00?10000100?0?0001?02100000001?0??1?01110001??
??1??101100?????0??10000000001000??0??03101?2411120000?00?10100?000?????0
?????0200????????????????0??
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Globidentosuchus_brachyrostris

0000??00010??10000??01?0001?0??10010?0?0??000112102001001?0?????1?200?00?
??????????1?0??????????0????????????????????000?000002?00010?0100?0?????001110??
0????????????12????????????????????????????????????11021001??11?????0?120100111??0?0?
?10001?111??
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Gnatusuchus_pebasensis

0?000??100?0??1?0?0?01010?0?????1?0001000?0??0000120020010011??????1?0?0??0?
?0?????????1?0?010120?00?001000100010????0?0000?000001000100?0?????1?0?????0??
0?000??0001120100001100?10?????????????????0100?20?1??0??000120?00111?00001
?1100?0?0??
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Gryposuchus_colombianus

00000??00000??1100012001?000?0100010000?0??0021011001100?10?0200100311110?
?0??011?0200000000001000011101111001000?2211?2701120000??101000000100?0111
00000?0?0?0?12??????????0?0??0?00?0?01001103030?20?001??0011?1?000000?000
0111?0?0000100??
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Gryposuchus_croizati

00000??000?0??100001??01????????????????0?0??02100?1?1?00?1?0??00?113??0??
?????1??1?0??????0??1?0?0??11??111?0010?1?01??7?1120000??1?0????????????
?????1??00?11????????????1?1?????????????????1103030?21?0????00????????????
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Gryposuchus_neogaeus

00000??00000??1?00012101?????????0?0?0?????002?0?0?0?1?0001??02??0?????????0

??????1102?00????00?1?00011111111001000?2211?27?1?20000001????????????
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01?0????0??
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Gryposuchus_pachakamue

00000?00000??1?00012001?000?0100010100???001101000110001????0011?1?1?110?
?000??1?01000?0000?010?0?01101111???011?2111?2711120000001010000?0100?0???
0???100?000112???0??000?101????0?? ???????1103030?20?0?00?00111100000201010
0111???0??
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Ikanogavialis_gameroi

00000?00000??1?0001?101?000?01000?0100???00110110?1?0001?0?0010?31?????
?0????11?1?0?????0??1?0?0?1?1?0??1???0??0?501?2701120000????010000??100?0?00
00001?0?000112???01?000?0?11????????????????1?3040?30? ???????1?????0???????
?1??
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Jiangxisuchus_nankangensis

0000100000?0????00001000?000?0100000000???000?10101000001?0111?1?00??010
?000?00011?000?00?2?1000000?00?000??0?00110000100?10010000?002?000000?11?0
00000??1?01120010010000000? ??????? ???????11021020??10?10?001?01??00? ??????
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??11???

Kambara_implexidens

00000?000110??1?00001001000??100000000???001?020010000010?01110100000000
?000000011000000010?100000000010000?0000010013100020010000? ??????0?0?00?0110
10100000010?120000002?11000????1?0?0??1?01?1021020??000??00110100?00?0?000
?1?0110000??1??
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Kambara_murgonensis

00000?0001?0??1?0000100??00?01000000?0???001??2001000?0?0??1??1?00??0??
?100??0011?0?????10?0?0?????????????????0?0? ??????? ?0?? ??????????????????
????????????12????????1????????????????????11??12??0????????1??1?0?????0?1??
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Kambara_tarina

00?00??00110??1000001001?000?01000?0000???000?12101000001??????1?000?0??
?1????0021?00??0010010000?000100?0?00000?00121000200?0000?00100?0000?0111
0?00?????01120?0?0?2?1100?0??????????????1102102????00??001?01?00?01001??
?110??
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Kentisuchus_spenceri

00000?00000??1?00001001?001?01[12]0000100???0011020001001010????1001?0000?
00??????111100?????????????0?000001000?00000?1011210012000000001?100?0000?01
1020000?2???0?12???0????100?0????????????????????????????????????
1001?100?0??
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Kuttanacaiman_iquitosensis

00?0110000?0??1?00001010?0?????0001000???0000121????1?011?2????1???????
?0????????1????10121?000000000?000?????00?0000?200001000100?00??10?????00??
0???01??0001120111??1100??0????????????????1?2?121???00?????1??1???????????

?1?0??
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Leidyosuchus_canadensis

000010000010??00000110000000?010000000010000010101001000010?011101000?0000
?0010100110000101100000100000100010[01]000100003300000000000000[01]0[01]001
0?01100000000000011200100020000000??11010?001?1002100?0?0000?00110100110
101?01?10000?00?000????0??001??????0?????
?????????1111??

Mecistops_cataphractus

00000?00010??10000110010000?010000000011010000020010000010001110100000010
?10010001100001000201000000000100101001011011310002000000001010000100?1[01]
1111101020110112000000000000001101111001?0111021120??10010?001102000000100
00011011001000110100100100011010001101110111000101000110?111200?01110000
01121110?0

Mekosuchus_inexpectatus

????0?00010??0?0001?00????0??120101?021??101??10??00??0??1??000000??
?1????0021????0010??0?0?0?00?000?????00?0000?????1??0?0?0?????????????1??
??????0100?????????????????0?????????????????01021120??0010?1010100110??000?1
0000110001?0110?????????110010??11??1?????0?0????????????????????????????
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Mekosuchus_sanderi

?0??0????010????????????????????01??1?2????101??20010000110?0?1??100000??
?1????012?00?0?0010010?0????????????????????????100?1?010?001??????00?????
??1????0100?????????????????0??
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Mekosuchus_whitehunterensis

?0??0????0????????????????????010??02???001??0????????????????????????
???0????100?1?010??01??????0??????
???01021120??001??10101011101?0?0?
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Melanosuchus_niger

010011100010??10000010100001?00[12]000100011000010120020010011?211101010000
11201?11001100011012111000000001100010010001001020000100000000000100010?00
000000011000111201110110100000100111[01]?0??0011021021??00011000120100111?0
00011100011110110110111001111001?001?111??0110210100011101111000??101100
0100231112?1

Moroccosuchus_zennaroi

00000?00010??1000001001?001?01000000001??001?0211?0001010?011001000??010
?00010101100011000??1000000000100??100?00?011?1000200?0000?01100?0000?01??
?????02?1?011200001?001000?????0?????????1102120?1??000?00110200000?100??
?10000?0?????????????????????????????????????1?????10????????????????????
??111???

Mourasuchus_amazonensis

000010101011001?0?01?011?0100?121101000???002?12002001111?????1?010300?00?
?01?????011001110100110010??01110??0010??00??0001??0?00?0?0110??10?00?0
0??0?0000?0112?????????0?00?0?1??1110?????11?3?02???10?????0?1202?0??????0?
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Mourasuchus_arendsi

000011101011001?0101?011?01?1?121101000?0002?12102001[01]11??211?01?30??0
01101?110011000110100110010000111010??0000?30003??0001??0??0?000?1??010?1?
100?000??0?01120??????????00?001113211?01??030??????0????0?1??0?0??????
?????0????010?1????11????110???100?1???1????????????01????????????1????????
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Mourasuchus_atopus

00?011101?????1?010????1??0????1?1101000?0002?????????????????1?0103000??
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00?0??0000011202110?11100?0?????????????????1103002??100?10001??100110201001
11100111??001101??1110????????????
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Necrosuchus_ionensis

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??11021021??000??000????????????
??1??1??0?????????01?10111100????????
??111???

Osteolaemus_tetraspis

00010??00010??10010000000000?01000001001101001002000001001?001110101000010
?200000021001010002000000000001000100011010002100020010000000211[01]0011011
1020000120110112000000301000000101110?11?0111021020??10010?001101011000000
10011011000000110100000100001000001101110111000102000?10111110100111[01]1
000102111100

Paleosuchus_palpebrosus

10000??00010??10000010000000?0100[01]000001100001002101002001?1??1101020000
11101?1100200001101211100000000010001001111[01]00?320000101100000111100010?
011000000110001112001100110000001001110?01?0011021021??10012100120101111?0
0001110000?111010010011110110000100110121??011001012101110111110??101111
110022111211

Paleosuchus_trigonatus

00000??00010??10010010000000?10001000001000001002101002001?1??110102000011
101?110020000[01]101211100000000010001001111000?320000101100000111100010?01
1000000110001112011100110000001001110?01?0011021021??10012100120101111?000
01111000?111010010011110110000100110121??0110?10121011101111100??10111111
1022111211

Paratomistoma_courti

00000??00000?????????????????00?010001010?1?0?001??2000100001?011??????????
?????1?1?1?0?????????????00000001000?????????????????2??0????????????????
?????????????????????????????????????01010??11?????0?????????????1?01000??00010
?1?000?0??
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Penghusuchus_pani

00000??000?0?????00?????1?001?01200000001????000102?????0?01?????0101?00001??
??????1111000?1??0201000000?001?0001??????????501120000000010100?0000?0100
000000????001213001?00100000????011?????????1100130?20?00?0?0012?000?00?????0?
?????10?0????????1000??11?0?1111011??211??0110?????0?011110010????????????
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Piscogavialis_jugaliperforatus

00000??00000??1?00012101?00?????0?101001????0001020001100010?01001111101010

?00000110200000000301000011111111?010?0?1501?271112000000101000000100?0111
1000100000011210?11?2?0000?1?000?0????0?1103040?21?00?0?0011010001010????
???1???0????0??
???01???

Planocrania_datangensis

10000??00010??0?00001001?0??????0000000???001?0000000001?011101?00000??
??????0??0??0??0??????0?00?0??1?0?0??0?2?00??3000100?2000?0?100?0000?????
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Planocrania_hengdongensis

???00?00010????????????????????????????????0000000???000??000000001?011??1?000??
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0110?0?????????????????????????????????????1????????????????????????????
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Procaimanoidea_utahensis

10000??00010??0?00001010?0100?120100000???0000120000000010??11101010000??
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00000?0?0?011200010?10000000?????????????????1110200?0?000?0?11110000??1001
010000??10000??
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Protocaiman_peligrensis

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Purussaurus_brasiliensis

01000??10020??1000001110?0110?1210010001??0010121020010010?211101020000?1
1011110011100?001211100000000110001000001200022000010?0?00?0?1???0010?00??
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110000?1?????????????????????????????????1??1?????????????????1?1101???
??111???

Purussaurus_mirandai

01000??10020??1000001110??101?1110010?0?00001012001??1001????1??1?0000??
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Purussaurus_neivensis

000010000020??1000001010?0110?1210010001??001012001001001??2111010200001?
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Quinkana

[01]0010?00????0000001001000[01]?01?0?00??0??0?????????????????????0?1??10001
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Siquisiquesuchus venezuelensis

00000?00000??1?0001??01????????????????????????????110?????100?1????????1?1??????
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0111?????????0??
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Stangerochampsa mccabei

00000?00010??1?00101011??101?120100000???0000?1001000001??2111?10101?001
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Thecachampsa antiquus

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Thecachampsa sericodon

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Thoracosaurus isorhynchus

00000?00000??1?0001??01?000?0100000010???0011001000000010?00000111110100
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Thoracosaurus neocesariensis

00?00??0?000??1?000??01??00?0?00? ?????? ????00?001001000010??0?????????????
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Tomistoma cairense

00000?00010??100001??0??00?????0?0??00?0?00110200?0001010??10?0100100??
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Tomistoma dowsoni

00000?00000??1000012001?000?01000101001??001?020000000010?01?????????00?0?
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Tomistoma_lusitanica

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Maomingosuchus_petrolica

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Tomistoma_schlegelii

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Toyotamaphimeia_machikanensis

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Trilophosuchus_rackhami

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Tsoabichi_greenriverensis

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Ultrastenos_willisi

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Voay_robustus

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Wannaganosuchus_brachymanus

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Theriosuchus_pusillus

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- +[/196 5 +[/109 6 +[/176 7 +[/3 8 +[/138 9
- +[/103 10 +[/254 11 +[/254 12 +[/18 13 +[/45 14
- +[/72 15 +[/5 16 +[/40 17 +[/2 18 +[/81 19
- +[/2 20 +[/292 21 +[/255 22 +[/244 23 +[/197 24
- +[/211 25 -[/100 26 -[/100 27 -[/100 28 -[/100 29
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-[/100 300	-[/100 301	-[/100 302	-[/100 303	-[/100 304
-[/100 305	-[/100 306	+[/100 307	-[/100 308	-[/100 309
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-[/100 320	-[/100 321	+[/100 322	+[/100 323	-[/100 324
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Ancstates

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-200	-201	-202	-203	-204	-205	-206	-207	-208	-209
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-220	-221	-222	-223	-224	-225	-226	-227	-228	-229

-230 -231 -232 -233 -234 -235 -236 -237 -238 -239
-240 -241 -242 -243 -244 -245 -246 -247 -248 -249
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-270 -271 -272 -273 -274 -275 -276 -277 -278 -279
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-290 -291 -292 -293 -294 -295 -296 -297 -298 -299
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-310 -311 -312 -313 -314 -315 -316 -317 -318 -319
-320 -321 -322 -323 -324 -325 -326 -327 -328 -329

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xgroup

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+0 +1 +2 +3 +4 +5 +6 +7

+8 +9 +10 +11 +12 +13 +14 +15

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+24 +25 +26 +27 +28 +29 +30 +31

+32 +33 +34 +35 +36 +37 +38 +39

+40 +41 +42 +43 +44 +45 +46 +47

+48 +49 +50 +51 +52 +53 +54 +55

+56 +57 +58 +59 +60 +61 +62 +63

+64 +65 +66 +67 +68 +69 +70 +71

+72 +73 +74 +75 +76 +77 +78 +79

+80 +81 +82 +83 +84 +85 +86 +87

+88 +89 +90 +91 +92 +93 +94 +95

+96 +97 +98 +99 +100 +101 +102 +103

+104 +105 +106 +107 +108 +109 +110 +111

+112 +113 +114 +115 +116 +117 +118 +119

+120 +121 +122 +123 +124 +125 +126 +127

+128 +129 +130 +131 +132 +133 +134 +135

+136 +137 +138 +139 +140 +141 +142 +143

+144 +145

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9. Dataset : Walter et al., supplementary dataset (modified Rio & Mannion, 2021 – discrete and redescrptised characters; .tnt)

nstates 16 ;

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330 146

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Bernissartia_fagesii

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Acresuchus_pachytemporalis

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Acynodon_iberoccitanus

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000????0?10?000????0????0???
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Agaresuchus_fontisensis

10100000?100000?0?????????000010000000??1000001000?001?0100010100????00111
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Aktiogavialis_caribesi

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Alligator_mcgrewi

0010?0[01]00000101?0[01]000?????00000?000010??0001000010?0101?1000000001?000
0101201?[01]000010?21110101010001001?11002100011011010000000001100010000002
0003200[01]0100000000010100111100110000012000011201110011000000?001110??1?0
01111220?1??1001000111000010001001010000?011000100011100??1100000101?1???
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Alligator_meffferdi

1010?000001???0100010?????000010000010??1?01000010?0101?1200000001?1?00101
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Alligator_mississippiensis

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Alligator_olseni

001??0?0010??0001000????000010000010??1001000010?0110?120100000??0?00101
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Alligator_prenasalis

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Alligator_sinensis

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Allodaposuchus_precedens

101000?011000?1?0????????000010000010??0000001000?001?0110000?001??00111
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Allognathosuchus_polyodon

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Allognathosuchus_wartheni

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Arambourgia_gaudryi

001??000000??0?0??1??????10000??00010??0?00001010?0110?120100001000100?0
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Argochampsia_krebsi

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????0??????1????00????101??1?1?????????????????0?????0100?????1????????????????
?????0?????????????????????????????????001???

Asiatosuchus_depressifrons

10100000[01]10????0001?1??10?00000??00010??10000010010000?0120000001????000
0010010000010?01110100010100?00111001100001000001000000000100000000110013
10001001000010020000000?011010000020010112001?????1000?0?001111001?1111021
110??10010?00110100000?00110011000?00?????????????1??1110000111?21??11110?0
????000101110100?????????????????101???

Asiatosuchus_germanicus

101??000100?????000?10111?00000??00010??0000001000?000?0100000000??0?00001
1101?000010?0111010001000??0????0011000010002010010000??1??0?0000000000010
0000010000100200?0000?0?1010000??0?????120?000?000?????????????????1102110
?1??0000?0011010000??10010?110?????????????10?????????????????????1?????100???
?00?101111010?????????????????111???

Asiatosuchus_nanlingensis

?????????????????????0??
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??????000???10?112
0??000?0?00110??0000?1010?0110?????????????0????????????????????????????
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Australosuchus_clarkae

100?000000000??0?0?????????00000??00010??00000010010000?01000000001?0?000?1
01010000010?011?011100001??1????0011100?110000?1000000000?00?????001001310
0011010?000001??0000??100000002001?????????????????0?????1?????????1102102
0??100??001??100?00?0?0?????????????????????????????1????????????????????
?????101?????????????????????????101???

Baru_darrowi

??1?1??????00????0?????????00000??00?????000001?0000000?0120000100????00101
?????????????????1??100000???000000001010
0000000000?1020000010?011110[01]00?????011200??0??10??0?????????????1??21
12????10????001????00?????????11??
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Baru_huberi

??1?0??????0?????????????????00010??00?????0?000010000?00?01?0000??0?????????
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00100100001?????0001????1?2?1???1102102
0??10?1??
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Baru_wickeni

??0?0???1?00????00?1?????00010??00010??0000001000?001?0110000100????0010?
1101000001??0?1??100010????0????001100???????0??0?000000100100001?0000?010
0010010000100100?0010?011110100020?001120011??00110000?????????????1102112
0??1001??0?11010000010001001101100????????????????????????????????????
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20000000010?01110100000000?0???10011000100010010010?0000100???000031000030
100001201000010000000?0111100000200001120010??000??000??1?1??????1102110
?0??0000?001??1?11??0?000010010?0??????0??1??110010??11?11????110????
??001101110100????????????????101???

*Brachychamps*_montana

100000001100001100000??0?00000??00010??1000101011?0101?1101000001?0?00001
20011000011?1111010100000?0111100110001001111100000000010000020?013000310
000100010000110100010?1001000001?000011200010010000000?0?1110?01?10110?112
1??1?010?0?12010001??01001110000?0??????001110?101000?0011????????????00
0000010111????????????????0241111??

*Brochuchus*_pigotti

100000000000000100?0??????00010??00010??0?00001000?000?1100000100????00101
211?0000010?01110101000110?0????001100101000201000000000100?00001001001210
002001000001010000000?1010210000201111120010??30100000??1110????0?110?102
????0????0?1102000000????0?1??110????????????????????1??????1??1??11?0????
??001????11????????????????????111???

*Caiman*_brevirostris

????0??????????0??????????010011100??0??1000001010??01?0?20001?0????001??
??????1??????????????10????????????0011?????????1?????????00?000?0?????0?00?20
0?010?0100?000??????????????????0?1000??12??1?????0?0??????0??????1100112
1??0001??001??????11??001????????????????????????????????1??1??????0????
????????????????????????????????111???

*Caiman*_crocodilus

10[01]0?0[01]00000001000[01][01]1?11[01]1000011[01]00010??10000[01]10000001?00000
00000110000100200[12]001001112111010200001110111100110001101211100000000010
001001[01]0010013200[01]1101000000010100[01]10?0[01]10[012]00001100011120111011
10000001001110??1?0011021021??00011000120[12]00111?00[01]011110011110100111
11100111100100010111101011011010001110111100011101110010023111211

*Caiman*_gasparinae

??1100?0100????????????????000?????0?010??1?0001?000??01?0????????????????0??
21020011?1??211?0????????????????11001100??????????0?00?0?????0?????01?001?20
0?010????0??1?10????????????
??
????????????????0????????????????????

*Caiman*_latirostris

101[01]0000000011100010?011?1010011100010??10000010100001?002[01]00000011000
01012002[01]011011121110102000011101?1100110001101211100000000010001001100[
12]001320000101000000110100010?0[01]10000001100011120111011100000010011110?
1?0011021121??00011000121200111?000011100011110[01]00111101001111001000101
?1??0110110100?1110111??????1011[01]0010023111211

*Caiman*_lutescens_MACN

?????0?0100????????????????????110?0020????????????????????1001????????001??
2102001101????????????????????0011????????????????????????????????????
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*Caiman*_wannlangstoni

00????0?0000????0?????????010111100010??0?00001010?001??1110010001????00100
2002001001????1?010?0?01????????001100?110121?100000?00?1??????????1???320
0001000100?????????111001000000????0011120?0?????00?00????????????????

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Caiman_yacare

10100000[01]0000[01]1000[01]01??1[01]?000010100010??10000[01]10000001?002100100
01000001002002001001112111010[12]00001110111100110001101211100000000100010
01100100132000[01]101000000010100010?00100000011000111201110111000000100111
0?01?0011021021??00011[01]00120[12]00111?0000111100111100001??1110011110000
0010111??1110110100011101111100??1011[01]001?0?3111211

Ceratosuchus_burdoschi

100??0?0?110??00?????????00000??00011100?00001010?001?0001101000????00000
????000001??1?1??101?00?????????00?1?00?0??110000?000?1000?????032000320
0001010?0000?0?10101??0?0100000??0????12????????????00?????????????????1101210
?0??0??0?1?????????0??1??
??

Crocodylus_acutus

100101001000001000111??10?00100??00010??10000010001001?0100000000110110110
20000000010001110100000010?[12]00000011000010002010000000001001010010010013
100020000000000010010000?11112[01]000020110112000000001000000101111001?01110
21020??00010?0011020000001001001101100001011010000010011001001110?1??1110
001010001101110200??011000001111111000

Crocodylus_affinis

10[01]00[01][01]000[01]0000000100?1??00000?000010??1000001000?000?012000000?
?0?0001[01]20000000010?011101000000?0?10?010011000000002?100000000010010001
001[01]000[01]10001000000010020000000?011011000020000112001000000000000??111
10?1?0111021110??00010?00110100000010[01]10011000?00000110??0??1?????????
??0?????????????????001101??0100?????????????????11???

Crocodylus_anthropophagus

??0?????????0????000?1?????00000??00?111100000010001?0????00000?0?11010?1??
200?????0??????1??10?0??0??2?????00?1000010002?000000?0?1101010?00?10?1310
0020010000000100????????11?2?0????011??1?????????0?000?????????????1102102
0??10?10?0?11010000??10110?110110??00?1??0??1??????10??1?????????????????
??0??101??

Crocodylus_intermedius

100100[01]000[01]000100011?????00100??00010??10000010001000?0120000[01]00110
100110200000000010001110100000010?20000001100000000201000000000100101000001
001310002001000000010010000?11112[01]000020110112000000000000000111111001?1
111021120??00010?00110100000010010011011000010110??000010011001001110?1???
1110?01010?????????????????011100001112111?00

Crocodylus_johnstoni

10000000010000100011110[01]0000000?00010??10000110001000?01000[01]0[01]00110
10011020010000010001110100000110?[12]00000011000110000010000000001001010110
110012101020000000010[01]0000[01]00?11111[01][01]0002011011200000000000000111
112101?1111021120??00010?0011020000001001001101100000011010000010000101001
110?1??1110?010000011011112000?011100001112111100

Crocodylus_megarhinus

100000000000??1000?????????00000??00010??10000010000000?0100010100??0?00101
20010000010?01110100010010?20000001100001000201000000000100001011001001110
002001000000020000000?11111000002011011200000000100000?1?111??1??111102112
0??00010?00110100001?0?110011011000?????????????????????????????????????
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Crocodylus_mindorensis

1001?000101000100011?????00010??00010??10000010001001?0100000000110100110
20000000010001110100000010?20000001100001000201000010000100101001002001210
002001000000010000100?11112100002011011200000000000000111111001?011102102
0??00010?00110100000110010011011000000110????? ??????????????1?0?1????????0??
?????????????????011000001112111000

Crocodylus_moreletii

10010100100000100010????10?00100??00010??10000010001001?0100000000110100101
20000000010001110100000010?1000000110000100020100000000100101001003001110
00200000000001000000?111121000020110112000000001000000101111001?011102102
0??00010?00110100000110010011011000000110?????1?????????????1?0?1????????0??
?????????????????011000001112111000

Crocodylus_niloticus

10000000000000100010100[01]0100000?00010??10000010001001?01000000001101[01]
011120000000010001110100000010?2000000110000100020100000000010010100100[12]
0013100020010000000100[01]0000?01112[01]00002011011200000000[01]0000001011121
01?0111021020??00010?00110200000110010011011000000110100000100111010011101
11011110?0101000110111120010011100001113111000

Crocodylus_novaeguineae

10010000100000100010????11?00010??00010??10000010001000?0100000000110100100
20000000010001110100000010?1000000110000100020100000000100101001002001310
002001000001010000100?1111210000201101120000000000000001111110?1?011102102
0??00010?00110100000110010011011000000110????? ??????????????1?0?1????????0??
?????????????????011100001113111000

Crocodylus_palaeindicus

1011000010[01]000?000?0??1???00000?00010??1000001010?00?????0?0????00????0[0
1]101??000000010??11010000001??2000?0111000??000?01000000000100101000?010
0?110002001000000010000000?011021000?2?1?01120000??001?00?? ???????????????11
0?1020??00010?0?110100000?10?1001100110? ?????? ??????????????1?1??1??1?1
0?????????1101?????????????????????111???

Crocodylus_palustris

1001000000000011?001010110000000?00010??10000010101001?010000010011010[01]1
0120000000010001110100000010?[12]00000011000010002010000000001001010000000
101000200100000001000000?[01]1102[01]000020110112000000001000000101112101?0
111021020??00010?0011010000011001001101100000011011000010000101001110?1???
1110?01010001101111200??011100001112111000

Crocodylus_porosus

10[01]10[01][01]0[01]0000[01]10001010000100010??00010??10000010[01]0100[01]?01000
0000011010[01]10[01]20000000010001110100010010?[12]00000011000010002010000000
0010010100100[12]00131000200100000001000000?11112[01]00002011011200000000[0
1]000001101112101?0111021020??00010?00110200000010010011011000[01]001101000
00100[01]00010011102110?1110001010000101111200??011000001112111000

Crocodylus_rhombifer

1000?00?[01]0000010001010011100100??00010??10000010001000?01000001001101001
0120000000010001110100000010?[12]000000110000100020100000000010010100100100
1010002001000000010010000?11112100002011011200000000000000101111001?01110
21020??00010?001101000000100100110110000001101100001001110100111011101110
001010001101111110??011100001112111000

Crocodylus_siamensis

10010[01]001[01]000010001010010?00010??000111110000010001000?010000010011011

110120000000010001110100010000?2000000110000100020100000000010010100100100
1310002001000000011000000?11102100002011011200000001000000101112101?01110
21020??00010?00110200000010010011011000000010?000010001001000110?1????1110
?01010001101111210??011000001112111000

Crocodylus_thorbjarnarsoni

101001001000101?0010?????00000?000010??0000001000?000?01100000001????10101
20??110001????1?01?00?000?1????00110000100?20?00?0000??10?10?000002001310
002001000000010000000?1111200000??011200001?001?0000???1????????1102102
0????0?10?0?11020000??10?10?111110?0100110????? ??????????????????????
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Dadagavialis_gunai

?0????????????????1?????????00000?0000?0????00?0?1?100?01000101?0????00210
21????????1????????111?01????????????0?????????????????????????????????271
1120000001010000?0?00??0?0?001????0????????????????0?????0? ??????????????3??
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Deinosuchus_riograndensis

1001?1?02010??02010??1?????????0??01??0??100000?000?00001100100000?1??00101
0001?001010?210?01?100?100?0??111011100? ???????00?00?00?1?? ???000013000030
0000010?00?001??0000?????0????????1??1????????????00??????????????????1002102
??000??00100210?11?10001?111??0??010????????????????????0?1??1?????0????
??????1????????????????????????????10????

Diplocynodon_darwini

0000?0[01]00[01]0?001?111?0?010?00000?000010??10[01]0012000?000?0020000000??
?000?100010000010??1110101000000?011?1001100000011001000000?0?1??0100??010
001?300011010000?00110000????11?????0?0?0?0112011?0?2?000?00??????????????1
0021020??10010?0011010011?01001011010?00000?010001001?0?1000000111?1?????
1001000000?101110000?????????????112100201

Diplocynodon_deponiae

0?0?????0[01]0????0?0?????11?00000?000010??001001?00?000?0120?00000????000
?10100001001??[01]11??10100000?0?1?00021?0????????00?0????0??????0????0?0??
??300?11010000?00110????????1??????0????011120?01?2?00????????????????100
2102????0010?0?1??000??0??1?1?0?????????????????????????????????1??1??????0
??????0??10111000?????????????0?2101211

Diplocynodon_hantoniensis

10[01]000[01]0[01]10000000010?????000110000010??0001012000?000?0100000000??
?00111010[01]0000010??1110101000000?011010111000010110010000000001000100000
10000030001101010000011000010?01100000011001111201100120000000???1110??1?0
?10021020??1001[01]000110100100101001110010?10? ??????00?????1?0100000011?21?
??0?0?????00110111000????????????????1002??

Diplocynodon_muelleri

10????0?0010?????1?????00?010000010??1101?01?000?0100?00100????001?1
01000000010?2?1????100??0?011?????1?0?01011??10?0000???10?0?0?0?0?00??30
0??10?0000?00110??00??1100?000????1011200100?0??00?00????? ?????????10?2?02
1????0????0?1????????????0??100?????????????????????????????????1??????????
??0??101??00????????????????????1112??

Diplocynodon_ratelii

1010?000000?00000??0?0??000110000010??10010010000000?0100000100100100110
00000000010?1110101000000?0110?002100000011001000000000100000010010001030
001101000000011000000?111010000110010112011001200000001001110?11?111002102

0??00010?001101000000010010110?0??0?????????????1??0100000?11??1??????0????
??001101111200?????????????????100???

Diplocynodon_remnensis

?????0????0?????0010?????000110000010??100001?000?000?01000101001????000?1
11010000010?2111010000000?0??0100110000?011011000000000100010000010001030
001?010000000110?000??01??0??00?000[01]01120110002000000?????1??0????0110021
00?0??0010?00110100101?00001110010??0??? ?????????????????????????????????0??
??1002??

Diplocynodon_tormis

10000000010?0????0?????????000010000010??1?1101?000?000?0100000100????00000
0100000001??11101?10??000??1101001100?01?????????0??000?00?0?????0?000?03?
0?????000??001?0?0000??1??0??????????????120?1?????????????0?1110??1?011??02
?????????????1??1?0??
?????????????????01??

Dollosuchoides_densmorei

1000?0000110000?0?????????00000??00010??1?0001?001?001?0100000000????00100
2000100?0?????????1?????????0?????????1?0??000??1??0??0??1????000?1111?210
0120000000011100?0000?01102?000?????01120000??00000? ??????????????????1103?20
?10?0?0?00110200000100?100110????0????? ??????????????0????????????????????
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Eocaiman_cavernensis

?????????????1????01?????????0000111000?0?????????????00?????????????00?????????
2000000?0?????1??102?00?????????????1?????????????0?0?0?????????????1????20
000?00000000?10?00111001000000?00??0?12?????1?????????????????????112102
1??00??00110100?11??
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Eocaiman_palaeocenicus

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??????0?0???1110102
1??0?0??001101?00??0?001110000?? ?????????????????????????????????????
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Eogavialis_africanum

10[01]110[01]0[01][01][01]000?01?0?????000000?00000??100001?001?000?0100000?0
010000011020001100010?01001111010100?0??1111110000000020100001101110000100
001[23]011271112000000101000000000?01112000000000011210000000000011??00?0?
??0?1103030?30?0000?001101000001110000110?0?0?????????????????????1?????
?????????????????0?????1?????????????????????000???

Eosuchus_lerichei

1?0????0?010000000?????????00000??00000??1?00012001?000?01001000101?0?00010
000?0000010?0100?100100010?000?000110000110020100000000?100000000002000370
112000000000110000100?01000000001000011200000000000000????0? ??????????11030?0
?21?00?0?00???1????11101?1????????????
?????????11?????????????????????????011???

Eosuchus_minor

1????????0????????0?0????????00000??00010??100001?001?000?0100000010??0?00010
101?1000010?0?00?100100?0?????0?10110000?100201000001000100000000001000370
1120000001001100?0000?0110000000000?112?000??000?001??0?1?0??0111103120
?21?00?0?0011010000??00000110010?00????? ??????????1?0001?11?1??1?????0????
??0?0100110?????????????????????1010???

Eothoracosaurus_mississippiensi

101??00001[01]????01?????0??00000??00000??1?0001?001?000?01?00?01?0?000000
10010?100001????0??1?1?????????????1?0100?00000??10000?0?01000000000120002
7?1020000001010000?000??0?000000??0?????1 12?0?01?000?000????0?????10030
30?2??0????0?1001?001??10?0??1?010?????? ?????? ?????? ??????1??1?????1??
????00????????????????????????000???

Euthecodon_arambourgi

1001?0000000????0?????????00010?00010??0?00012101?000?01000000001101001?0
21010000010??1110100000010?1??0000110010100020100000?0?????00001?001270
0020000??000?11??0?0????0?2000?02011??????????????0?0??1? ??????11?????
??
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Gavialis_browni

?0???000111?0?1?1?????????00000??00000??100??1?2?1?100?1100010?0?0??002?0
21????0001????0010?11??1?????????11100?00000?01??0? ???????010?? ???????70
1120000001010000?1100?01010?001?0??011210?0??0??10??????????????????????
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Gavialis_gangeticus

10[01]010[01]00110[01][01]00200101000100000??00000??11000122010101?11000101000
0000021011001100010002001013110100?00001111000000000010000111111010010000
14111270112000000101100001100?01010000100000011210001?000010110000110?01?2
01103040?31?0100?01110210000201000011000?00000100100000100001111111011010
0010000110000010110010010100000010210?0000

Gavialis_lewisi

?0???000000?0111??1?????????00?00000??00000??00000??00000??00000??00000??
??001000010??0010?3110100?00001111100?000000?100001101111001??????????7?
?12????000101?00000?00?011100001?00?0011212001?30101011????? ???????1?????
??1?01?0?01110?1000020100001?0??0? ?????? ?????? ?????? ?????? ?????? ??????
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Gavialosuchus_eggenburgensis

100?1000111????00?????????00000??00010??1?0001?001??00?10000100?0????001?0
2100000001????1?01110001????1????101100?????0??10000000001000?0?03101?241
1120000?00?10100?000?????0?????0200????? ?????? ?????? ?????? ?????? ??????
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Glen_Rose_form

?????0?0010?10110?????????000010000000??0000000000?0111?1200000001?0?10100
00000000100?0?110100000?????????100??0?0? ?????? ?0?010000000100?0000001?00
000010000000010000000?010000000010?0010000001?00000?1??0?1?0??????0102120
?20?0000?000??????1??????????????00????????????????????????????1??????????
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Globidentosuchus_brachyrostris

???????0100?????????????????0000??00010??10000?0?1??001?0??10010?0????00011
2102001001??????1?200?00??????????1?0?????????0????????????????000?00002?
00010?0100??????001110??0? ?????? ??????12????? ?????? ?????? ?????? ??????
1??11?????0?120100111??0?0??10001?111??????????????????????????????????
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Gnatusuchus_pebasensis

00????0?0000????0?0?????????0?000??100?0??1?0??01010?0????1?0001000????00001

20020010011??????1??0??????0??????1?0?010120?00?001000100010????0??000?00
0001000100?????1??????0??0??00??0001120100001100?10??????0100?20
?1??0????00120?00111?0001?1100??0??????0??????0??????0??????0??????0
????????????????????????????????????

Gryposuchus_colombianus

?0??0?00??0??0??10?0??0??00000??00000??1100012001?000?0100010000????00210
11001100?10?0200100311110??0??011?0200000000001000011101111001000?2211?270
1120000??101000000100?011100000?0?0?0?12??????0??0?0??0?00?0??01001103030
?20?001?0011?1?000000?0000111?0??0000100?????0??????0??????0??????0??????0
????????????????????????????????????

Gryposuchus_croizati

??11????1??????11????????00000??000?0??100001??01??????????????0?????0210
0?1?1?00?1????00?113??0?????????1??1??????0??1??0??11??111??010?1?01??7?
1120000??1?????????????????????1??00?11??????0??1?1??????0??????01103030
?21?0??00??
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Gryposuchus_neogaeus

1?1110?00110??0?10??????00000??00000??1?00012101????????0??0??0??002?0
??0?1?0001??2????????????0??????1102?00???00?1?0001111111001000?2211?27?
1?20000001???01??????0??????0????
?????????????110100?0??0?0?001?0??0??????0??????0??????0??????0??????0
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Gryposuchus_pachakamue

?00010?0111?[01]0??101??????00000??00000??1?00012001?000?0100010100????001
101000110001????0011?1??110??000??1?01000?0000?010?0?01101111??011?2111?2
711120000001010000?0100?0??0??100?000112??0?000?101????0??????011030
30?20?0?00?001111000002010100111??0?0??0????????????????????????????
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Hassiacosuchus_haupti

[01]01??000?10?????00100??11?10000??00010??000?0?01010?001?01201010001?0?000
?010??0000010?21110101000000?01?1100110?0??1?1??0?000?0?0??0??????0??
2000010?0100?00??10?????0??
?0?????000?0?1?010101?010??0100??0??????0??10?0?????????????1??1?????0??
????00??111?0?????????????????3111111

Hylaeochamps_a_vectiana

?0??0?1000?00?1????????00000??00000??00000?????1100?120101000????0011?
01001001000?0?00??10?00?0?????10110010???0?0110110000100010?????????60
??0??0?0?000100011?0?01?12?0100?0??0?12?0001?0000010????10?0??????????
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Iharkutosuchus_makadii

0010?0?01????00?0????????00000??00010??1000001011?1100?12010010????0?010
?10100200????0?????00000?01??00?0010?0?0103001101?100?000?00???033000160
01010?020000011001000?01112001000?0?01120001??00000101??1?1??????0?104110
?1??0?00?000????0011?00?00000000??0?????0?????0?????0?????0?????0????
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Ikanogavialis_gameroi

?0??0?010111?0??02????????00000??00000??1?0001?101?000?01000?0100????00110
110?1?0001??0?0010?31?????0?????11?1?0??0??0??1??0?1?1?0??1?????501?270
1120000??010000??100?0?0000001?0?000112??01?000?0?11?????????????1?3040

Lohuecosuchus_megadontos

0010?0?00000100?0??0?????000010100010??0000001000?000?111?0?100????00111
11??000[01]00??011001000000010100?10011010??010301010000?00?00?100000010011
20000000000000020000000?0111200000??10011200?01?00000000???1?????????11021
020??10?10?000????0000000?1??11010?00??00?????????????????????????????
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Maomingosuchus_petrolica

1000?0[01]00[01]0??0??0?0?0?0?????00000?000010??1000011001?000?01000000001????
01102?000000010?01110100000100?000??0011000?00?0?010000000001000010010?001
?310112000000000110000[01]00?0110000000201001120000??30000000?0??1?0????0?1
10?020?2??00?0?0?1202000001?1?100110????000000??????00111000001???1?????
????????0??001??1????????????????1011??

Mecistops_cataphractus

100110000000001000111101[01]100000?000010??10000110010000?01000000001101000
0020010000010001110100000010?100100011000010002010000000001001010010110113
10002000000001010000100?1[01]111110102011011200000000000001101111001?01110
21120??10010?0011020000001000001101100100011010010010001101000110111011110
00101000110?111200??0111000001121110?0

Mekosuchus_inexpectatus

??00????????????0?010?????????????0??00010??0?0001?00??0?0??120101?021??101??
?10????00?????1?000000?????1????0021????0010?0?0?0?00?000?0??00?000???
??1????0?0?????????????1????????0100?????????????0?????????????0102112
0????0010?1010100110??000?10000110001?0110??????????110010??11??1?????0????
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Mekosuchus_sanderi

?????0?0?00????0?????????????0??0??010?????????????????????????????01??1?2????101??
20010000110?0?1??100000?????1????012?00?0?0010010?0?0?????????????????????010
0?1?010?001????????00?????????1????0100?????????????0?????????????????????
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Mekosuchus_whitehunterensis

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?0??
0?1?010?001????????0???0102112
0????001??10101011101?0?0??????10?000??110????????????????????????????????
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Melanosuchus_niger

00010000100011100010100111010011100010??10000010100001?00[12]00010001100001
0120020010011?21110101000011201?110011000110121110000000011000100100010010
200001000000000000100010?00000000011000111201110110100000100111[01]?0??00110
21021??00011000120100111?00001110001111011011011001111001?001?111??0110
210100011101111000??1011000100231112?1

Morccosuchus_zennaroi

??1100?0[01]11?????0000?????00000?000010??1000001001?001?01000000001????001
?0211?0001010?011001000??010?00010101100011000??1000000000100??100?00?011?
1000200?0000?01100?0000?01??????02?1?011200001?001000?????0?????0?????11021
20?1?000?000110200000?100??10000?0?????????????????????????????1?????10??
??111???

Mourasuchus_amazonensis

1110?0100??0?????????????000010101011001?0?01?011?0100?121101000????002?1

2002001111????1?010300?00??01????011001110100110010??01110????0010??00????
0001??0?00?0?0110??10?00?00??0?0000?0112??????0?00?0?1??1110?????11?3?02
???10?????0?1202?0??????0?????011????????????????????????????????
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Mourasuchus_arendsi
?1??0?0?00??1[01]2????????000011101011001?0101?011?01?1?121101000????002
?12102001[01]11??211?01?30??001101?110011000110100110010000111010?0000?300
03??0001??0??0?000?1??010?1?100?000??0?01120??????????00??001113211?01??0
30?????0??0?1????0????????????0????010?1????11??110??100?1??1??????
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Mourasuchus_atopus
????????????10??1?01????00?011101????1?010???1??0????1?1101000????002??
??????????????1?0103000????????????????????????????????1?010?0?03?000??1
?001??0??000??11??10??01?00?0??0000011202110?1100?0??????????????1103002
???100?10001??10011020100111100111????????????????????????????????
??001101??1110????????????????????

Navajosuchus_mooki
0?0??????0?0??000??011??000010000010??0?00001000?000?0120110000????000?[
01][12]000000010?2?110101000????0??110011?????012111000?0000?1000?01??0020
00320000100010000010?00010??110000012000??12?0?10?10??0??0??1?????????11
11210?1??101100011100011000100??1??0??010001????????????????????????
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Necrosuchus_ionensis
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??1????????????????0????????????
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1??000??00??1??1??0??????
??01?10111100????????????????111???

Osteolaemus_tetraspis
101000000000[01]10001[01]1011[01]000010??00010??10010000000000?0100000100110
1001002000001001?001110101000010?2000000210010100020000000000100010001101
0002100020010000000211[01]0011011102000012011011200000030100000101110?11?0
111021020??10010?001101011000000100110110000001101000001000010000011011101
111000102000?10111110100111[01]1000102111100

Paleosuchus_palpebrosus
1000?00000?0011000101011110000??00010??10000010000000?0100[01]000001100001
002101002001?1??110102000011101?1100200001101211100000000010001001111[01]00
?320000101100000111100010?011000000110001112001100110000001001110?01?00110
21021??10012100120101111?00001110000?11101001001110110000100110121??0110
01012101110111110??101111110022111211

Paleosuchus_trigonatus
10[01]000[01]000?00[01]1000100011110000??00010??1001001000000?100010000100
0001002101002001?1??110102000011101?110020000[01]10121110000000001000100111
1000?320000101100000111100010?011000000110001112011100110000001001110?01?0
011021021??10012100120101111?0000111000?11101001001110110000100110121??
0110?10121011101111100??10111111022111211

Paratomistoma_courti
?????0?0010????0????????00000??00000????????????00?010001010?1?0?001??
2000100001??011??????????0????1?1?1??0??0????????0?0000001000????????
??2????0??01010??11??????0

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Penghusuchus_pani

10??00?0111?00100????0001100000??000?0??000?0??1?001?0120000001??00010
2?????0?01????0101?00001????????1111000?1??020100000?001?0001?????????50
1120000000010100?0000?0100000000??001213001?00100000??011??????1100130
?20?00?0?0012?000?00????0?????10?0??????1000?11?0?1111011??211?0110????
??0?011110010????????????????000???

Piscogavialis_jugaliperforatus

1011?000101000002?0????0??00000??00000??1?00012101?00?????0?101001??00010
20001100010?01001111101010?0000011020000000030100001111111?010?0?1501?271
112000000101000000100?01111000100000011210?11?2?0000?1??000?0????0?1103040
?21?00?0?0011010001010??????1??0?????0?????????????????????????????????
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Planocrania_datangensis

101??0?0?10?????1????????10000??00010??0?00001001?0?????0000000??001?0
000000001??011101?00000?????????0??0??0??0?????0?00?0??1??0?????02?00?30
00100?2000?0?100?0000????????????????12?0?????????0????????????????110????
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Planocrania_hengdongensis

1????000?00????1??0????????00??00010?????????????0?????0000000??0000??
?000000001??011??1??000?????????0??0??00010?1?00??0?????0??????1??30
0?000?2000??10000?0????????????????112?????????00??????????????110?112
0??10????????????????????000110?0????????????????????????????1??????????
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Portugalosuchus_azenhae

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0100000001??00001101000100????010?????????????????0?0?0??1????0??????????
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Procaimanoidea_utahensis

0?00?0?0?100?0??0?0????????10000??00010??0?00001010?0100?120100000??00001
20000000010??11101010000?????0??1?00110001001211100000000?00010000001000020
00010110000?????0?1?10?01000000?0?0?011200010?10000000????????????1110200
?0??000??0?11110000??1001010000??10000????????????????????????????
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Protocaiman_peligrensis

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Purussaurus_brasiliensis

10000110010011?000?01?????01000??10020??1000001110?0110?1210010001??00101
21020010010?211101020000?11011110011100?0012111000000001100010000012000220
00010?0?00?0?1????010?00??0??0?000??1?????????????0????????????1100102
1??0000100012010011??010?1110000?1????????????????????????????1??1????????
??1?1101????????????????????111???

Purussaurus_mirandai

?????????????0?????????????01000??10020??1000001110??101?1110010?0????00101
2001??1001????1??1??0000??0??1??1?0?? ?????? ?????? ??????0??00000200?2??
0001??0000?????1?0010?00??0??0??0?111202?10? ???0? ?????? ?????? ??????11?2?02
????0?0?001202?0????11?01?100???? ?????? ?????? ?????? ?????? ?????? ??????
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Purussaurus_neivensis

10000010000001100?001????000010000020??1000001010?0110?1210010001????00101
2001001001??2111010200001??01111001110010012111000000001000100?00?1000020
0001000?0000010100010?00100000010000111202010111000001001110??1?0?????????
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??0?11????????????????????????????????

Quinkana

??11[01]?????????????0??????????[01]0010?000? ?????0000001001000[01]?01?0?00?00??
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01]0012[13]001[012][01]0[01][012]0[01]000?2??0000??0?00000?2011?????????????????
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Shamosuchus_djadochtaensis

?0??0000010????01????????????00000??00000??0?????000?0101?100000000????00110
011?0000110?00100100000001001??100?101?000????1000000000000010?????????????00
00010?0?00?101?0?1????01?????????????010000001?00000?1?????0??????????????1?0
?????01??0?0?????1?1?00?0??000?????????????0??0??0?1?1?1?1?????1?????
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Siquisiquesuchus_venezuelensis

10?????0?11?????????????????00000??00000??1?0001??01????????????????????????110
?????100?1?????????1?1?????????????????2?00?0?0?03?1??0??11?11???????????????????
11200?0??1?10000?1?????1?10?????????????12?????????????00?????????????????1103040
?30?0?????0?????00?????????0111?????????0????? ?????? ?????? ?????? ?????? ??????
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Stangerochampsia_mccabei

0000?0000100000?001?0??1??00000??00010??1?00101011??101?120100000????0000?
1001000001??2111?10101?0010011?10011?0??1??111100000??00?000?0200002000320
0001000100000001?1110?00010000012?00011200110011000000????? ??????0?1101110
?0??1001000110100011??100??10?00?010100? ?????? ??????010000001??1??0?????????
001??10111100?????????????????0111??

Thecachampsia_antiquus

?0?1?0?0101?????0?????????00000??00010??100001?001?001?0000010100????00110
201?1000010?010?0111001??0??????10?1?00? ?????? ?????? ?????? ??????000012000210
1120000000010000?0?00?0?0?2000002001??12????? ?????? ?????? ?????? ??????1102020
?20?00?????0???
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Thecachampsia_sericondon

100??0001100000?0?????????00000??00010??100001?001?001?1000010100????00010
101?1000010?01010111001110?010101011000102?0201001000000100001000012010210
1120010??011000000100?01012000002001011213000000000010?00110????1?110?20
?20?0??????1?01?00?????0???
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Theriosuchus_pusillus

?0????0?0?10?00?0?0?????1??00010?00000??000000000000??000001000????10100

010?0000100?111111000000??01?1?0011??0?00030101000000?000010??030000030
000000100000000100100?01??1??????0??0100100000000000?0??1??????1102210
?20?000?000????1101?010??000????????????????????????????????1????0??0??????
??0?00?11????????????11????010011?

Thoracosaurus_isorhynchus

1000?000011?00?11????????00000?00000??1?0001??01?000?0100000010????00110
01000000010?00000111110100?000??10110000?00030100000000110000000013010270
1120100000010000?0100??1?0??????????0?1210001?00000?0??????????????????
??1?1?????1??????????
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Thoracosaurus_neocesariensis

??11?0?0[01]11????0??????????00?00?0?000??1?000??01??00?0?00??????????00?
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??11??1????01??0?0?0????0????????????
??1?1?????1??????????
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Tomistoma_cairense

?0???000001?0000????????00000?000010??100001??0??00?????0?0?00??0?00110
200?0001010??10?0100100????0????00120000?00100100000000100001?????????71
1120000?0001000000100?11?0?????0?0?01121000??00000000??0?0?????????030?0
?20?00?0?001????00??0001?011010?0????????????????????????????????????
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Tomistoma_dowsoni

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20000000010?01????????00?0????????1111000?0??????00?0000011100??0??101?371
1120000??101?00??0100??1????00??1????????????????1??000?0??1??????????
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Tomistoma_lusitanica

1001?000010????0?0????????00000?000010??100001?001?000?11?00?0100????00110
211????0001??010?01?100111??01????101200?01?0?02010?000?000100?01000012011211
1?200?0000?1??00?01????01????????0??0112030000000?0?0??????????????1102020
?20?00??0012?10000?00?0??110????????????????????????????????????
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Tomistoma_schlegelii

100110001[01]0000100[01]01000[01][01]100000?000010??10000120010001?0100000001
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1012011310012000000001010000000?11000000002011011210000000000000101101001
?201103030?20?0010?00110200000200010011000?0000000010000100001010011?0111
0101100000100011011110001011100000022101000

Toyotamaphimeia_machikanensis

10100000000?000000010010??00000?000010??1?00012001?000?0100000000????00100
21??1?0001????0101100001?0?0001?1011000?1??0201000000001110001001000010350
012000000000?00?0100?01000000002011?1120?01?0?0??00?????????????????0??0
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10001101110010????????????????000???

Trilophosuchus_rackhami

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21011000110?0111110000010?1??0000110001100100000000000000?0?0??????????
0?0????0?01??1000?011001112?000001100112??0?????0?0?00?101110?01?01???????

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Tsoabichi_greenriverensis

[01]0[01]??000?00?????????????11100000??00010??0?1000100??000?0110100000????0
01?12101001001????11?1?1??????01????00?1????????????????????????????????01?00
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UCMP_39978

??100??????0011?0????????????0100????0??????1?00011000??111?0??0??0?????????
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00010000000001010?010?001000000?1000?1120001??11000? ??????????????????????
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Ultrastenos_willisi

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20010000010?11????????????????1000?00210000000100100000000100001?????????????
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Voay_robustus

101000001000000000100?1??100010??000211100000010000000?010000000110111101
[12]0010010010?01110101010010?10?000011001010002010000000001000010000010000
10002001000000010000000?111020000020110112000?00301000001101111001?0011021
020??10010?001101010001100100110110100?0110?????????????????0?1??1?1??01?0??
????00110111100????????????????????1?????

Wannaganosuchus_brachymanus

000??0?0110?????0??0??11100000??00010??100010100??0101?120101000??0?000?1
10????0001????1?01?1????0?????????0011?0??1?????????0??0????????000002000320
00010?0100?0000??1010????0100000?????????1????00?0????00????????????1101210
?0??0?0100?12?1?00????????1?????0?????????????1????????????????1??1??0?10????
000??101110000????????????????????11?????

Wannchampsus_kirpachi

????????0010??100?????????00000??00000?? ???????000?0100?1?0000?00????10000
010100001????0111011000000??[01]1??10021?0??0?1?2?1000000000000010????????0??
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Ccode

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- [/1 10 -[/1 11 -[/1 12 -[/1 13 -[/1 14
- [/1 15 -[/1 16 -[/1 17 -[/1 18 -[/1 19
- [/1 20 -[/1 21 -[/1 22 -[/1 23 -[/1 24

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-[/1 60 -[/1 61 -[/1 62 -[/1 63 -[/1 64
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-[/1 80 -[/1 81 -[/1 82 -[/1 83 -[/1 84
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-[/1 130 -[/1 131 -[/1 132 -[/1 133 -[/1 134
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-[/1 140 -[/1 141 -[/1 142 -[/1 143 -[/1 144
-[/1 145 -[/1 146 -[/1 147 -[/1 148 -[/1 149
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Snout_length_in_dorsal_view,_ratio_of_anteroposterior_snout_length_(measured_from_level_of_anterior_orbital_margin,_to_antermost_point_of_rostrum),_to_total_skull_length_(measured_from_posteriormost_level_of_quadrate_condyle_to_antermost_point_of_rostrum)
?_0.5_>_0.5;

{1
Skull_proportions_ratio_of_mediolateral_rostrum_width_at_the_level_of_the_anterior_orbita
l_margin_to_mediolateral_width_across_anterior_margin_of_the_cranial_table <_3 ?_3;

{2 External_naris_mediolateral_width_to_anteroposterior_length_ratio ?_1 >_1_;

{3
External_nares_anterior_margin_thickness_ratio_of_distance_between_anterior_margin_of
_nares_and_anterior_margin_of_rostrum_to_maximum_anteroposterior_length_of_external
nares_in_dorsal_view <_0.5 ?_0.5_;

{4
Rostral_depth_ratio_of_maximum_dorsoventral_height_of_the_maxilla_to_mediolateral_wid
th_of_the_maxilla_at_the_5th_maxillary_alveolus <_0.5 ?_0.5_;

{5
Interorbital_distance_ratio_of_minimum_mediolateral_width_between_orbits_to_maximum_
mediolateral_width_across_anterior_cranial_table <_0.5 ?_0.5_;

{6
Infratemporal_fenestra_size_ratio_of_maximum_anteroposterior_infratemporal_fenestra_len
gth_to_maximum_anteroposterior_length_of_the_cranial_table <_0.8 ?_0.8_;

{7
Cranial_table_shape_ratio_of_maximum_anteroposterior_cranial_table_length_(measured_f
rom_the_level_of_the_frontal-
postorbital_suture)_to_maximum_mediolateral_width_(measured_at_the_level_of_the_ant
erior_table_corner) <_1 ?_1_;

{8
Cranial_table_shape_minimum_angle_subtended_by_the_posterolateral_cranial_table_mar
gin_and_sagittal_axis_of_skull <_10 >=_10 =_0_(parallel);

{9
Supratemporal_fenestra_size_ratio_of_maximum_anteroposterior_supratemporal_fenestra_
length_to_anteroposterior_cranial_table_length_(measured_from_the_level_of_the_frontal-
postorbital_suture) <_0.5 ?_0.5_;

{10
Supratemporal_fenestra_shape_ratio_of_maximum_mediolateral_width_to_maximum_ant
eroposterior_length ?_1 >_1_;

{11
Incisive_foramen_size_ratio_of_maximum_mediolateral_width_to_the_mediolateral_width_o
f_the_rostrum_at_the_premaxilla-maxilla_suture <_0.3 ?_0.3_;

{12
Suborbital_fenestra_shape_ratio_of_maximum_mediolateral_width_to_maximum_ant
eroposterior_length: ?_0.5 >_0.5_;

{13
Choana_shape_ratio_of_maximum_mediolateral_choanal_width_to_maximum_ant
eroposterior_length <_2 ?_2_;

{14
Pterygoid_proportions_of_ptyerygoid_wing:_maximum_mediolateral_width_to_maximum_ant
eroposterior_length_ratio ?_3 <_3_;

{15

Basioccipital_tubera_ratio_of_maximum_mediolateral_width_of_basioccipital_tubera_to_maximum_mediolateral_width_of_the_occipital_condyle <_2 ?_2;

{16 Number_of_maxillary_alveoli <_18 18-22 >_22;

{17

External_mandibular_fenestra_shape_ratio_of_anteroposterior_length_(between_anterior_and_posterior_limits)_to_dorsoventral_height_(between_dorsal_and_ventral_limits) <_2.5 ?_2.5;

{18

External_mandibular_fenestra_shape_minimum_angle_subtended_by_dorsal_margin_of_fenestra_and_the_horizontal <_25 ?_25;

{19

Articular_retroarticular_process_ratio_of_anteroposterior_length_(measured_from_the_transverse_ridge_to_the_posteriormost_tip_of_articular)_to_the_mediolateral_width_across_the_glenoid_fossa <_1.5 ?_1.5;

{20

Scapular_blade_anteroposterior_are_of_dorsal_end_(at_maturity):_angle_subtended_by_anterior_and_posterior_margins ?_35 <_35;

{21 Scapula-

coracoid_ratio_of_maximum_proximodistal_coracoid_length_to_maximum_proximodistal_scapula_length <_1.0 ?_1;

{22

Coracoid_shape_ratio_of_maximum_expansion_of_distal_coracoid_to_maximum_proximodistal_coracoid_length <_0.5 ?_0.5;

{23

Ulna_length_ratio_of_maximum_proximodistal_ulna_length_to_maximum_proximodistal_humeral_length <_0.7 ?_0.7;

{24

Femur_length_ratio_of_maximum_proximodistal_femur_length_to_maximum_proximodistal_humeral_length_(at_maturity) <_1.2 ?_1.2;

{25

Ischial_blade_shape_ratio_of_maximum_expansion_of_distal_ischial_blade_to_maximum_proximodistal_length_of_ischium <_0.5 ?_0.5;

{26 Rostral_ornamentation,_canthi_rostralii absent present;

{27

Rostral_ornamentation,_development_of_anterolaterally_directed_ridges_on_the_lateral_surface_of_the_rostrum_(at_maturity) absent present;

{28 Rostral_ornamentation,_dorsal_boss_on_sagittal_axis absent present;

{29

Rostral_ornamentation,_anteroposteriorly_orientated_preorbital_ridges_extending_from_the_anterior_corner_of_the_orbit_(at_maturity) absent present;

{30 Rostral_ornamentation,_transverse_ridge_between_the_orbits_(i.e._spectacle) absent present;

{31 Rostral_ornamentation,_morphology_of_the_transverse_orbital_ridge_(i.e._spectacle) low,_lacking_a_posterior_fossa tall,_with_deep_posterior_fossa;

{32

Rostral_ornamentation:_anterior_extent_of_transverse_bridge_between_orbits_(i.e._spectacle) posterior_to_anterior_orbital_margin level_with_or_anterior_to_anterior_orbital_margin_;

{33

Rostral_ornamentation,_extensive_fossa_extending_anteriorly_from_the_frontal_to_the_posterior_margin_of_the_external_naris absent present;

{34 Prefrontal,_prominence_at_anteromedial_orbital_margin not_thickened hypertrophied,_forming_rounded_protuberances;

{35

Cranial_table_ornamentation,_fossa_on_the_sutural_intersection_of_the_postorbital,_frontal_and_parietal absent present;

{36 Skull_table_morphology

posterolateral_edges_directed_ventrolaterally_from_the_sagittal_axis planar_across_entire_length,_or_lateral_edges_directed_dorsolaterally_<20_across_entire_length lateral_edges_directed_dorsolaterally_?_20_along_entire_length;

{37 Cranial_table_ornamentation posterolateral_and/or_posterior_margin_of_squamosal_?at_upturned_to_form_a_discrete_eminence_(i.e._a_squamosal_horn);

{38 Cranial_table_ornamentation,_squamosal_horn_position restricted_to_posterior_end_of_skull_table extends_anteriorly_along_the_whole_lateral_margin_of_the_skull_table_;

{39

Cranial_table_ornamentation,_direction_of_squamosal_horn_expansion_from_cranial_table dorsally_only dorsally_and_laterally;

{40 External_nares,_orientation projects_anterodorsally dorsally;

{41

External_nares,_development_of_bony_excrescence_(ghara)_in_reproductively_mature_males absent present;

{42 External_nares,_thin_crest_circumscribing_narial_margin absent present;

{43 Premaxilla,_notch_posterolateral_to_naris absent present;

{44 Premaxilla,_fossa_on_the_lateral_margin_of_the_naris absent present;

{45 Nasals,_external_contact_with_naris present absent;

{46 Nasals bisect_nares_completely protrude_partially_into_posterior_narial_margin_excluded_internally_from_posterior_narial_margin;

{47 Nasals,_contact_with_premaxillae present_with_overlap_present,_point_contact absent;

{48 Premaxilla-maxilla_suture,_anterior_limit_relative_to_posterior_margin_of_external_naris posterior_to_level_with_or_anterior_to_;

{49 Premaxilla,_posterior_extent_of_dorsal_process terminating_level_with_or_anterior_to_the_third_maxillary_alveolus extending_posterior_to_third_maxillary_alveolus;

{50 Maxilla,_linear_array_of_pits_(cecal_recesses)_on_lateral_margin_of_narial_canal absent present;

{51 Maxilla, posterior extent relative to anterior margin of postorbital bar terminates anterior to the level of the postorbital bar level with or posterior to the postorbital bar;

{52 Lacrimal, sutural contact with nasal present absent;

{53 Maxilla, posterior process in the lacrimal absent present;

{54 Maxilla, posterior process extends between lacrimal and prefrontal absent present;

{55 Maxilla, posterior process extends between nasal and lacrimal absent present;

{56 Lacrimal, mediolateral width in relation to prefrontal equal to or greater than twice the maximum prefrontal width less than twice the maximum prefrontal width;

{57 Lacrimal, anteroposterior length relative to that of prefrontal longer equal in length shorter;

{58 Prefrontals, sutural contacts (at maturity) separated by frontal and nasals at maturity prefrontals meet medially;

{59 Frontal, anterior process morphology forms an acute, ?v? shape that extends anteriorly into posterior margins of nasals forms broad sutural contact with the nasals or prefrontals;

{60 Frontal, position of tip of anterior process relative to anterior tip of prefrontal posterior or at the same level anterior;

{61 Frontal, position of tip of anterior process relative to anterior orbital margin anterior level with or posterior;

{62 Jugal, anterior extent relative to anterior tip of frontal anterior to or level with frontal posterior to frontal;

{63 Prefrontal, linear sulcus adjacent to medial orbital margin absent present;

{64 Jugal, suture with lacrimal long, widely separating maxilla from orbital margin point contact, narrowly separating maxilla from orbital margin jugal-lacrimal contact absent, maxilla contributes to orbital margin;

{65 Prefrontal pillar morphology dorsal half of pillar narrow, less than twice minimum anteroposterior length equal to or greater than twice minimum anteroposterior length;

{66 Prefrontal pillar, morphology of medial processes, long axis orientation dorsoventrally anteroposteriorly;

{67 Prefrontal pillar internal morphology solid with pneumatic recess;

{68 Prefrontal pillar, morphology of medial process at base of pillar wide constricted;

{69 Frontal, ornamentation, midsagittal crest on fused frontals absent present;

{70 Orbit, ornamentation, protuberance on the frontal-prefrontal suture intersection with the orbit absent present;

{71 Orbit, dorsomedial margin ?ush with skull surface upturned projecting into orbit;

{72 Orbit, position of posterior margin (measured at the level of the postorbital-frontal suture) relative to posterior margin of suborbital fenestra posterior to or at the same level anterior;

{73 Orbit, lateral-
most_margin_relative_to_the_lateral_margin_of_the_maxilla_at_the_level_of_alveoli_3?6
lateral_level_with_or_medial;

{74 Frontoparietal_suture, intersection_with_supratemporal_fenestra_(at_maturity)
deep_intersection, postorbital-parietal_suture_not_exposed_on_skull_table
frontoparietal_suture_incipiently_contacts_supratemporal_fenestra, postorbital-
parietal_suture_slightly_visible
frontoparietal_suture_does_not_intersect_supratemporal_fenestra, postorbital-
parietal_contact_fully_exposed_on_skull_table;

{75 Frontoparietal_suture, shape_between_supratemporal_fenestrae concavo-convex
straight;

{76 Supraoccipital, exposure_on_dorsal_skull_table present absent;

{77 Supraoccipital, extent_of_exposure_on_skull_table
small, mediolateral_width_across_dorsal_supraoccipital_exposure_less_than_half_that_alo
ng_the_posterior_margin_of_the_parietal moderate, medio-
lateral_width_across_dorsal_supraoccipital_exposure_more_than_half_to_equal_that_along
_the_posterior_margin_of_the_parietal
large, such_that_the_parietal_is_excluded_from_the_posterior_edge_of_skull_table;

{78 Supraoccipital, posterolateral_tuberosities_in_dorsal_view not_visible visible;

{79
Supraoccipital, acute_process_projecting_posteriorly_from_the_midline_of_the_cranial_tabl
e absent present;

{80 Supratemporal_fenestra, morphology_of_fenestral_rim_(at_maturity)
with_fossa, dermal_bones_of_skull_roof_do_not_overhang_rim
dermal_bones_overhang_rim_supratemporal_fenestra_completely_closed;

{81
Skull_table_morphology, acute_dorsal_indentation_on_the_supraoccipital_(and_sometimes
_the_parietal) absent present;

{82 Parietal, sagittal_crest_between_supratemporal_fenestrae absent present;

{83 Supratemporal_fenestra, shallow_fossa_at_anteromedial_corner present absent;

{84 Parietal, medial_wall_of_the_supratemporal_fenestra_with_one_or_more_foramina
absent present;

{85 Parietal, recess_communicating_with_pneumatic_system present absent;

{86 Supratemporal_fenestra, posterior_wall
quadrate_forms_entire_ventral_margin_of_orbitotemporal_canal_(no_parietal-
squamosal_contact)
quadrate_partially_forms_ventral_margin_of_orbitotemporal_canal_(parietal_and_squamosa
l_narrowly_separated)
quadrate_excluded_from_ventral_margin_of_orbitotemporal_canal_(parietal_and_squamosa
l_in_contact);

{87 Supratemporal_fenestra, posterior_wall squamosal-
parietal_suture_passes_medially_to_the_orbitotemporal_foramen, little_to_no_development
_of_fossa_medial_to_orbitotemporal_foramen squamosal-
parietal_suture_intersects_dorsal_margin_of_orbitotemporal_foramen, large_medial_fossa
squamosal-

parietal_suture_intersects_dorsal_margin_of_orbitotemporal_canal,_medial_fossa_extends_over_entire_width_of_posterior_supratemporal_fenestra_wall;

{88 Postorbital,_morphology_of_postorbital_bar
anteroposteriorly_expanded,_elliptical_in_cross_section
columnar_and_slender,_circular_in_cross_section;

{89
Postorbital,_protuberance_on_the_dorsolateral_margin_of_the_postorbital_bar_(at_maturity)
present absent;

{90 Postorbital_bar,_orientation_laterally_inclined,_greater_than_or_equal_to_20
(bar_visible_in_dorsal_view) slightly_inclined_to_vertical,_lateral_inclination_<_20
(not_visible_in_dorsal_view);

{91 Postorbital_bar ?ush_with_dorsolateral_margin_of_jugal
dorsolateral_margin_of_jugal_raised_to_form_ridge,_with_sulcus_separating_it_from_postor
bital_bar;

{92 Jugal,_posterodorsal_jugal_foramen,_at_base_of_postorbital_bar
absent_or_small,_diameter_less_than_half_the_minimum_mediolateral_width_of_the_jugal_
arch large,_equal_to_or_greater_than_half_the_minimum_jugal_arch_width;

{93 Orbit,_dorsal_pro?le_of_jugal_forming_posteroventral_margin
convex_or_straight,_continuous_with_the_dorsal_margin_of_the_lower_temporal_bar
posteroventrally_sloping,_gradually_descending_into_the_lower_temporal_bar
strongly_convex_with_a_step_anterior_to_the_lower_temporal_bar_
abruptly_angled_ventrally,_creating_a_near_vertical_margin_descending_toward_the_posto
rbital_bar_(i.e._a_notch);

{94 Jugal,_ventral_margin_of_jugal_arch concave straight;

{95 Jugal,_ventrolateral_sulcus_on_jugal_and_maxilla,_at_level_of_the_jugal-maxilla_suture
absent present;

{96 Jugal,_ventrolateral_foramina_adjacent_to_the_jugal-maxilla_suture
small,_less_than_half_the_diameter_of_the_last_maxillary_alveolus_(and_usually_numerou
s)
large,_equal_to_or_greater_than_half_the_diameter_of_the_last_maxillary_alveolus_(usuall
y_2?3_foramina);

{97 Infratemporal_fenestra,_dorsal_margin_shape triangular broadly_curved,_oval-shaped_;

{98 Infratemporal_fenestra,_dorsal_extent_of_quadratejugal
reaches_dorsal_angle_of_fenestra does_not_reach_dorsal_angle_of_fenestra;

{99
Postorbital,_posteroventral_process_in_quadratejugal_at_dorsal_corner_of_the_infratempor
al_fenestra absent present;

{100 Postorbital,_morphology_of_posteroventral_process_in_quadratejugal
narrow_with_acute_?V?_shaped_tip broad,_blunt_tip;

{101 Infratemporal_fenestra,_posterior_angle quadratejugal_forms_posterior_angle
quadratejugal-jugal_suture_lies_at_posterior_angle;

{102 Quadratejugal,_development_of_spina_quadratejugalis_(at_maturity) prominent
greatly_reduced_or_absent;

{103 Quadratojugal, _position_of_spina_quadratojugalis
low, _near_posterior_angle_of_infratemporal_fenestra
high, _between_posterior_and_dorsal_angles_of_infratemporal_fenestra;

{104
Postorbital, _medial_contact_with_quadrate_at_dorsal_corner_of_the_infratemporal_fenestra
absent present;

{105
Postorbital, _medial_contact_with_quadratojugal_at_dorsal_angle_of_infratemporal_fenestra
absent present;

{106 Squamosal, _anterior_divergence_of_dorsal_and_ventral_rims_of_lateral_groove
absent present;

{107 Squamosal, _shape_of_the_lateral_cranial_table_edge, _dorsal_to_the_otic_aperture
vertical, _dorsal_and_ventral_edges_equally_expanded_laterally
bevelled, _ventral_edge_projects_further_laterally_than_dorsal_edge;

{108
Squamosal, _angle_between_dorsal_pro?le_of_the_paroccipital_process_and_dorsal_margi
n_of_the_cranial_table <_10_(approximately_horizontal) 10-50 >_50;

{109 Squamosal, _posterolateral_prongs
absent, _or_very_short, _barely_exceeding_the_level_of_the_posterior_wall_of_the_cranial_t
able_behind_supratemporal_fenestrae
long, _exceeding_the_level_of_the_posterior_margin_of_the_cranial_table, _less_than_half_a
nteroposterior_cranial_table_length
long, _greater_than_or_equal_to_half_anteroposterior_cranial_table_length;

{110 External_auditory_meatus, _position_of_ventral_margin
ventral_to_the_level_of_the_dorsal_margin_of_infratemporal_fenestra
level_with_or_dorsal_to_the_dorsal_margin_of_the_infratemporal_fenestra;

{111 Quadrate, _sutural_contact_with_squamosal_posterior_to_external_auditory_meatus
present
absent, _exoccipital_separates_squamosal_and_quadrate_posterior_to_external_auditory_m
eatus;

{112
Squamosal, _descending_lamina_extending_anteriorly_over_quadrate_ramus_from_parocci
pital_process absent present;

{113 Quadrate-squamosal_suture, _intersection_with_external_auditory_meatus_(EAM)
extends_dorsally_along_posterior_margin_of_EAM_(suture_separated_from_posterior_marg
in)
extends_only_to_posteroventral_corner_of_EAM_(suture_incipiently_contacts_posterior_ma
rgin);

{114 External_auditory_meatus, _posterior_margin_shape straight invaginated;

{115 Quadrate, _foramen_aereum_size
small, _diameter_less_than_half_dorsoventral_height_of_medial_hemicondyle
large, _equal_to_or_greater_than_half_dorsoventral_height_of_medial_hemicondyle_;

{116 Quadrate, _foramen_aereum_position_on_posterior_quadrate_ramus
dorsomedial_corner dorsal_surface_;

{117 Quadrate_condyle, _notch_on_the_dorsal_articular_border
absent_or_small, _restricted_to_dorsomedial_edge_of_quadrate_articular_border

large, as an extensive indentation of the dorsal articular_1408
inset from dorsomedial edge of the condyle;

{118 Quadrate condyle shape, dorsal and ventral margins
subparallel across length (sub-rectangular condyle) medially tapering constricted at mid-
length ventrally re?ected medial hemicondyle;

{119 Quadratojugal, extent over lateral surface of posterior quadrate ramus
covers entire lateral surface notch in quadratojugal, exposing quadrate ventrolaterally;

{120 Quadrate, posterior ramus length
distance between posterior margin of quadrate condyle and the level of the anterior_
margin of the occipital condyle, less than quadrate condyle mediolateral width
equal to or greater than quadrate condyle mediolateral width;

{121 Exoccipital, extent on dorsal surface of quadrate ramus
small, not reaching articular border of quadrate condyle
large, extending to border of quadrate condyle;

{122 Exoccipital, posterior projection of the paroccipital process absent present;

{123

Quadrate, paroccipital process, distance between distal tip of paroccipital process and
distal end of the quadrate condyle
less than the maximum mediolateral width of the quadrate condyle
equal to or greater than the maximum mediolateral width of the quadrate condyle;

{124 Exoccipital, paroccipital process dorsal margin squamosal-exoccipital suture sub-
horizontal dorsolaterally directed;

{125 Lateral carotid foramen, proximity to metotic foramen
separated (positioned ventral to metotic foramen) adjacent to the metotic foramen ;

{126 Exoccipitals, contact with basioccipital tubera absent present;

{127 Exoccipitals, posteroventral inclination
absent, occiput vertical and not visible in dorsal view
present, occiput inclined posteriorly, visible in dorsal view;

{128 Basioccipital, orientation of lateral margins of ventral basioccipital plate
parallel or ventrally convergent ventrally divergent ;

{129

Basioccipital, dorsoventral height of ventral plate exposed below occipital condyle relat
ive to occipital condyle height greater or equal in height shorter;

{130 Basioccipital and ventral portion of exoccipital (otoccipital), orientation (at maturity)
inclined anteriorly vertical;

{131 Basioccipital, sagittal crest on ventral plate present absent;

{132

Basioccipital, concavity on ventral margin, posterior to median eustachian foramen
absent present;

{133 Lateral eustachian foramina, position relative to medial eustachian foramen dorsal
lateral (at same level);

{134

Basisphenoid, dorsoventral exposure ventral to basioccipital, in posterior view (at matu
rity) little to no exposure large exposure;

{135 Pterygoid, shape_of_posterior_process_ventrolateral_to_basioccipital
tall, long_axis_orientated_dorsoventrally dorsoventrally_short, no_discernible_long_axis;

{136 Incisive_foramen, intersection_of_premaxilla-maxilla_suture separated_by_inter-
premaxillary_suture intersecting_at_posterior_margin_ intersecting_at_lateral_margin_;

{137 intersecting_at_lateral_margin_
absent_(anterior_margin_around_2nd_or_3rd_alveolus)
present_(projects_between_or_abuts_?rst_premaxillary_teeth);

{138 Incisive_foramen, posterior_margin rounded
invaginated_by_anterior_process_of_premaxilla_(spade-shaped_foramen);

{139 Premaxilla, number_of_teeth_early_in_post-hatching_ontogeny five four;

{140 Premaxilla, size_of_the_three_most_posterior_alveoli
penultimate_alveolus_is_the_largest
penultimate_and_antepenultimate_alveoli_are_largest_and_similar_in_size
antepenultimate_alveolus_is_largest alveoli_are_same_size;

{141
Premaxilla, posterior_extent_on_palate, relative_to_number_of_maxillary_alveoli, in_ventr
al_view '0' '1' '2' '3' '4' 5_or_more;

{142
Premaxilla, position_of_the_penultimate_premaxillary_alveolus_relative_to_the_antepenulti
mate_alveolus posterolateral_or_in_the_same_line posteromedial;

{143
Premaxilla, position_of_the_last_premaxillary_alveolus_relative_to_the_penultimate_alveolu
s posterior_or_posterolateral posteromedial;

{144 Premaxilla, alveolar_spacing_(at_maturity) all_alveoli_equally_separated
second_alveolus_separated_from_the_?rst_and_close_to_the_third;

{145 Premaxilla-maxilla_suture, shape_on_palate_in_ventral_view horizontal
posteriorly_bowed, with_one_rounded_apex posteriorly_bowed, with_one_acute_apex_
posteriorly_bowed_with_two_or_more_apices;

{146 Maxilla, number_of_the_largest_alveolus '3' '5' '4' 4_and_5 '6' '7'
maxillary_alveoli_gradually_increase_in_diameter_posteriorly_toward_penultimate_alveolus
homodont;

{147 Maxilla, interalveolar_distances_between_alveoli_1?10
less_than_or_equal_to_diameter_of_?rst_maxillary_alveolus
greater_than_the_diameter_of_the_?rst_maxillary_alveolus;

{148 Maxilla, shape_of_the_lateral_pro?le_between_alveoli_1_to_5 flaring_posteriorly
straight;

{149 Maxilla, shape_of_the_toothrow_posterior_to_the_first_six_alveoli
laterally_convex_or_linear laterally_concave_;

{150 Occlusion_pattern all_dentary_teeth_occlude_lingual_to_maxillary_teeth_
partial_interlocking_occlusion, with_at_least_one_pit_between_maxillary_teeth_5and8, all_
other_dentary_teeth_occlude_lingually
all_dentary_teeth_occlude_in_line_with_maxillary_teeth_;

{151 Occlusion_pattern
4th_dentary_tooth_occludes_in_notch_between_premaxilla_and_maxilla_early_in_ontogeny
occludes_in_a_pit_between_premaxilla_and_maxilla no_notch_early_in_ontogeny;

{152 Maxilla,_diastema_between_alveoli_5_and_6 absent present;

{153 Maxilla,_diastema_between_alveoli_6?8 absent present;

{154 Maxillary_and_dentary_alveoli,_shape all_circular_in_cross-section
posterior_alveoli_mediolaterally_compressed all_alveoli_mediolaterally_compressed;

{155 Dentary_and_maxillary_teeth,_shape_behind_alveoli_12?13 pointed_to_slightly_blunt
globular molariform,_multicusped;

{156 Maxillary_and_dentary_tooth_carinae smooth serrated;

{157 Maxilla,_position_of_alveoli_relative_to_maxillary_palate_separating_toothrows
ventral_or_at_the_same_level dorsal;

{158 Maxilla,_size_of_foramen_for_palatine_ramus_of_cranial_nerve_V
small_or_absent,_less_than_half_diameter_of_6th_maxillary_alveolus
large,_equal_to_or_greater_than_half_diameter_of_6th_maxillary_alveolus;

{159 Palatine,_anterior_process_shape rounded_or_quadrangular
wedge_shaped_(i.e._forms_a_?V?_shape_anteriorly);

{160 Palatine,_invagination_of_anterior_process absent present;

{161
Palatine,_anterior_process_position_relative_to_anterior_margin_of_suborbital_fenestra
anterior_to,_and_at_the_level_of_more_than_two_full_alveoli
anterior_to_and_at_the_level_of_two_or_fewer_full_alveoli
at_the_same_level_or_posterior_to_anterior_margin_of_suborbital_fenestra;

{162
Palatine,_palatal_bar,_lamina_projecting_into_suborbital_fenestrae_from_anterolateral_mar
gin absent present;

{163 Palatine,_palatal_bar,_orientation_of_posterolateral_margin_realtive_to_sagittal_axis
sub-parallel_($<40^\circ$) flared_($>40^\circ$);

{164 Palatine,_ventrolateral_?ear-
shaped?_process_projecting_from_base_of_prefrontal_pillar absent present;

{165 Suborbital_fenestra,_position_of_anterior_margin_relative_to_anterior_orbital_margin
anterior_to level_with,_or_posterior_to;

{166 Suborbital_fenestra,_anteromedial_margin,_intersection_of_maxilla-palatine_suture
at_anteromedial_margin at_anterior_corner;

{167
Suborbital_fenestra,_anterolateral_margin_width,_distance_from_medial_edge_of_the_tooth
row_to_fenestral_margin narrow,_less_than_or_equal_to_one_alveolus_width
broader_than_one_alveolar_width_(usually_at_least_twice_alveolar_width);

{168 Suborbital_fenestra,_lateral_margin_shape straight projecting_medially_into_fenestra_;

{169 Suborbital_fenestra,_contribution_of_maxilla_to_medial_projection
absent,_projection_entirely_formed_by_ectopterygoid present;

{170 Suborbital_fenestra,_posterolateral_margin_shape_at_ectopterygoid-
pterygoid_suture_intersection straight bowed_anteromedially;

{171 Suborbital_fenestra,_posterior_margin,_intersection_of_palatine-pterygoid_suture
at_posterior_corner on_the_posteromedial_margin_;

{172 Ectopterygoid, anterior extent relative to maxillary alveoli reaches the level of two or fewer alveoli more than two alveoli;

{173

Ectopterygoid, anterior extent relative to anteroposterior length of suborbital fenestra less than two thirds of fenestra length
equal to or greater than two thirds of fenestra length;

{174

Ectopterygoid, contact with maxillary toothrow, forming the medial wall of at least one maxillary alveolus absent, ectopterygoid-maxilla suture anteromedially orientated and separated from toothrow margin absent, ectopterygoid-maxilla suture parallel and adjacent to medial toothrow margin present;

{175

Ectopterygoid, morphology of anterior maxillary ramus on lateral suborbital fenestra wall acute, tapering to a single point forked;

{176 Ectopterygoid, anterior maxillary ramus contacts suborbital fenestra separated from the suborbital fenestra by the maxilla;

{177 Ectopterygoid, position relative to maxillary alveoli restricted to medial side forming posterior and lateral margins;

{178 Maxilla, non-dentigerous posterior process between jugal and ectopterygoid short, less than anteroposterior length across last three maxillary alveoli
long, equal to or greater than anteroposterior length across last three maxillary alveoli
;

{179 Ectopterygoid, dorsal extent along medial surface of postorbital bar large, extends dorsal to level of ventral orbital margin
small, level with or ventral to level of ventral orbital margin;

{180 Ectopterygoid, morphology of posterior process on the medial jugal surface acute, extends beyond level of posterior margin of postorbital bar
acute, terminating before posterior margin of postorbital bar rounded;

{181

Jugal, extent of ectopterygoid and maxilla on medial surface, anterior to the postorbital bar minimal, visible jugal extensive, covering medial surface of jugal;

{182 Quadratojugal, anterior process on medial surface of lower temporal bar present absent (or very modest);

{183 Jugal, morphology of medial foramen anterior to postorbital bar small foramen large recess;

{184 Ectopterygoid-ptyergoid suture, shape (at maturity) straight kinked (i.e. with 'flexure');

{185 Ectopterygoid, posterior extent on pterygoid ?ange reaches posterior tip
does not reach posterior tip;

{186 Choanae, palatine participation present, forms anterior margin of choanae absent, choanae entirely surrounded by the pterygoids;

{187 Choanae, position of anterior margin anterior to posterior margin of suborbital fenestra

level_with_posterior_margin_of_suborbital_fenestra
posterior_to_posterior_margin_of_suborbital_fenestra;

{188

Choanae,_position_of_posterior_margin_relative_to_posterior_edge_of_pterygoid_?ange
anterior_to_or_at_the_same_level_as_the_posterior_edge_of_pterygoid_?ange
posterior_to_posterior_edge_of_pterygoid_flange;

{189 Choanae,_shape circular_or_elliptical sub-triangular,_tapering_posteriorly sub-
rectangular_(long-axis_orientated_mediolaterally) sub-triangular,_tapering_anteriorly;

{190 Choanae,_anterior_margin_shape linear_o_curved invaginated;

{191 Choanae,_direction_of_choanal_projection_(at_maturity) posteroventrally
ventrally_to_anteroventrally;

{192 Choanae,_septum present absent;

{193 Choanae,_external_projection_of_septum
absent,_septum_remains_recessed_within_choanae
present,_septum_approaches_external_margin_of_choanae;

{194 Choanae,_ornamentation_of_margins
unornamented,_margins_(usually)_?ush_with_pterygoid_surface
elevated,_forming_a_wall_restricted_to_the_posterior_and_posterolateral_margins
elevated_forming_a_wall_which_extends_to_the anterolateral_(but_not_anterior)_margins_
of_the_choanae elevated,_forming_a_wall_which_completely_circumscribes_the_choanae;

{195 Choanae,_morphology_of_posterior_wall
not_notched,_or_with_broadly_rounded_notch_ acutely_notched;

{196 Pterygoid,_surface_lateral_and_anterior_to_choanae flush
depressed_to_form_?neck?;

{197

Pterygoid,_ornamentation_lateral_to_choanae,_anteriorly_directed_ridges_on_the_pterygoid
_extending_from_the_lateral_margins_of_the_choanae absent present;

{198 Pterygoid,_bulbous_differentiated_bullae_(at_maturity) absent present;

{199

Quadrate,_ventral_surface,_attachment_scar_for_posterior_mandibular_adductor_muscle,_
morphology linear_crest ventrally_directed_knob;

{200 Basisphenoid,_exposure_between_basioccipital_and_pterygoids_in_ventral_view
not_or_poorly_exposed,_basisphenoid_anteroposteriorly_short
largely_exposed,_basisphenoid_anteroposteriorly_long;

{201 Jugal,_posterior_extent_relative_to_basioccipital_tubera
extends_beyond_level_of_posterior_margin_of_basioccipital_tubera_
level_with_or_anterior_to_posterior_margin_of_basioccipital_tubera;

{202 Basisphenoid_rostrum,_posteroventrally_directed_ridge_on_lateral_margins absent
present;

{203

Basisphenoid,_exposure_on_the_lateral_braincase_wall,_anteroventral_to_the_trigeminal_f
oramen absent present;

{204 Basisphenoid,_sulcus_on_anterior_braincase_wall,_lateral_to_basisphenoid_rostrum
present absent;

{205 Laterosphenoid,_orientation_of_capitate_process_anterior_margin
perpendicular_to_the_sagittal_plane directed anterolaterally_from_the_sagittal_plane;

{206 Laterosphenoid,_lateral_laterosphenoid_bridge_over_cavum_epiptericum absent
present;

{207 Laterosphenoid,_lateral_laterosphenoid_bridge_morphology
short_process,_which_does_not_suture_to_the_pterygoid_ventrally
robust_process,_which_sutures_to_the_pterygoid_ventrally;

{208 Laterosphenoid,_caudal_laterosphenoid_bridge_over_cavum_epiptericum absent
present;

{209 Laterosphenoid,_caudal_laterosphenoid_bridge_morphology
short_ventrally_directed_strut
long_ventral_process_joining_with_extra_process_of_the_quadrate
hypertrophied_wall,_which_bisects_the_foramen_ovale;

{210
Laterosphenoid,_ascending_process_of_the_pterygoid_forming_ventral_portion_of_lateral_laterosphenoid_bridge absent present;

{211 Epipterygoid present absent;

{212 Epipterygoid,_retraction_from_the_cavum_epiptericum
epipterygoid_overhangs_cavum_epiptericum epipterygoid_isolated_from_cavum_epiptericum;

{213 Prootic,_exposure_on_external_braincase_wall
small,_little_to_no_exposure_dorsal_and_ventral_to_the_trigeminal_foramen
large_exposure_ventral_to_trigeminal_foramen_only
extensive_exposure_dorsal_and_ventral_to_trigeminal_foramen;

{214 Quadrate-
pterygoid_suture,_path_on_lateral_braincase_wall_between_basisphenoid_exposure_and_foramen_ovale ventrally_deflected straight;

{215 Dentary,_anteriormost_teeth strongly_procumbent,_approaching_sub-horizontal
project_dorsally_or_steeply_anterodorsally;

{216 Dentary,_alveoli_3_and_4 confluent separate;

{217 Dentary,_dorsoventral_height_at_the_level_of_alveoli_1?4_relative_to_alveoli_11?12
at_same_level_or_higher lower;

{218 Dentary,_numerical_position_of_largest_alveolus_posterior_to_4_th_dentary_alveolus
13_and/or_14 13_and/or_14_and_a_posterior_series 10,_11_and/or_12
no_differentiation_posterior_to_4th_alveolus posterior_to_14;

{219 Dentary,_shape_of_dorsal_profile_between_4_th_and_10_th_alveoli_in_lateral_view
linear curved deeply_curved;

{220 Mandibular_symphysis,_posterior_extent,_adjacent_to_number_of_full_dentary_alveoli
<_6 6-8 9-12 13-20 >_20;

{221 Splenial,_participation_in_symphysis
full_participation,_dorsal_and_ventral_to_Meckelian_fossa
partial_participation_by_splenial_rostral_tip_no_participation;

{222 Splenial,_position_of_anteriormost_tip_relative_to_Meckelian_fossa ventral dorsal;

{223 Splenial, anterior extent in dentary symphysis adjacent to 1 full alveolus 2 to 3 alveoli 4 to 7 alveoli > 7 alveoli;

{224 Splenial, shape of splenial-dentary suture adjacent to dentary toothrow (in dorsal view) constricted, laterally concave (narrow ?V?-shape) straight (wide ?V?-shape);

{225 Dentary symphysis, shape of posterior margin of symphyseal surface in medial view dorsal lobe extends further posterior than ventral lobe dorsal and ventral lobes subequal in extent, or ventral lobe projects further posterior than dorsal lobe;

{226 Dentary, orientation of posteriormost alveoli in a straight line in a laterally curved line;

{227 Dentary, posterior process between angular and splenial on ventral side of the mandible absent present;

{228 Splenial, anterior perforation for mandibular ramus of cranial nerve V (i.e. foramen intermandibularis oralis) present absent;

{229 Splenial, posterior perforation(s) for mandibular ramus of cranial nerve V absent present;

{230 Splenial, number of posterior perforations for mandibular ramus of cranial nerve V one two;

{231 Splenial, shape of dorsal profile straight (anterodorsally inclined) concave (abruptly dorsally inclined at posterior end);

{232 Splenial, anterior process within the dentary, medial to the posterior toothrow absent present;

{233 External mandibular fenestra absent present;

{234 External mandibular fenestra, size narrow slit, no discrete fenestral concavity on angular dorsal margin, foramen intermandibularis caudalis not visible moderate discrete concavity on angular dorsal margin, foramen intermandibularis caudalis not visible large, most of foramen intermandibularis caudalis visible;

{235 Surangular-dentary suture, intersection with external mandibular fenestra anterior to posterodorsal corner at posterodorsal corner;

{236 Surangular-angular suture, intersection with external mandibular fenestra (at maturity) at posterodorsal angle at posterior margin passes broadly along ventral margin;

{237 Dentary, acute posterior process in the angular ventral to the external mandibular fenestra present absent;

{238 Angular and surangular margins ?ush with lateral surface of mandible margins everted forming flange;

{239 Angular, fossa for M. pterygoideus ventralis visible on posterolateral surface of the mandible not visible on posterolateral surface;

{240 Surangular, relative length of the anterior processes unequal, ventral process <75% anteroposterior length of dorsal process (measured from surangular foramen) sub-equal, ventral process ?75% length of dorsal process;

{241

Surangular, anterodorsal process (spur) lingual to posterior most dentary alveoli, between splenial and dentary present absent;

{242 Surangular, anterodorsal process (spur), anterior extent

not reaching 1 full alveolus reaching 1?2 alveoli reaching 3 or more alveoli;

{243 Surangular, ascending process on lateral wall of glenoid fossa present absent;

{244 Surangular, posterior extent on lateral margin of retroarticular process

reaches posterior tip pinches out anterior to posterior tip;

{245 Surangular, sulcus on dorsal margin lateral to glenoid fossa absent present;

{246 Surangular-articular suture, shape in glenoid fossa

straight, oriented anteroposteriorly bowed laterally;

{247 Articular, position of foramen aerum at medial margin of retroarticular process

inset from medial margin of retroarticular process;

{248 Articular, lamina extending from posterior edge of foramen aerum absent present;

{249 Articular, orientation of retroarticular process projects posteriorly

projects posterodorsally;

{250 Articular, dorsal extent of retroarticular process

at the same level or ventral to posterior edge of articular

dorsal to posterior edge of articular fossa;

{251 Articular, sharp longitudinal crest on dorsal surface of retroarticular process

absent present;

{252 Articular, lingual foramen for articular and alveolar nerve

perforates surangular only perforates surangular-articular suture;

{253 Articular, anterior process on posterior wall of adductor chamber absent present;

{254 Articular, position of anterior process on posterior wall of adductor chamber

dorsal to lingual foramen ventral to lingual foramen;

{255 Surangular-

angular suture, lingual intersection with articular in the ?oor of the adductor chamber

at ventral tip dorsal to ventral tip;

{256

Angular, anterior extent relative to foramen intermandibularis caudalis (FIC) (in medial

view) extends anteriorly beyond half the anteroposterior length of the FIC

terminates at, or posterior to the anteroposterior mid-length of the FIC;

{257 Splenial, acute posterior process separating angular and coronoid present absent;

{258

Foramen intermandibularis medius (FIM), anteroposterior length relative to foramen intermandibularis caudalis (FIC) short, less than 25% FIC length

long, equal to or greater than 25% FIC length;

{259 Coronoid, position of foramen intermandibularis medius (FIM) (at maturity)

on coronoid-splenial suture entirely within coronoid;

{260

Coronoid,_anterior_extent_relative_to_level_of_anterior_margin_of_foramen_intermandibularis_caudalis_(FIC) anterior at_the_same_level_or_posterior;

{261 Coronoid,_orientation_of_dorsal_profile inclined_anteriorly_across_entire_length horizontal_towards_posterior_end;

{262

Coronoid,_prominent_medioventral_lamina_extending_over_inner_(medial)_surface_of_Meckelian_fossa present absent;

{263 ProAtlas,_acute_anterior_process

present,_anterolateral_margin_of_proAtlas_prominently_concave
absent,_anterior_margin_of_proAtlas_straight_or_convex;

{264 ProAtlas,_dorsal_keel present absent;

{265 Atlas_intercentrum,_shape_in_lateral_view wedge-shaped plate-shaped;

{266 Atlantal_rib,_dorsal_margin_shape straight,_or_with_modest_process
with_prominent_process;

{267 Atlantal_rib,_thin_medial_lamina_at_proximal_end absent present;

{268 Atlantal_rib,_proximal_articular_facet_for_opposing_atlantal_rib absent present;

{269

Odontoid_process:_mediolateral_width_across_axial_rib_facets,_relative_to_mediolateral_width_across_axial_tubercula_facets narrower subequal;

{270 Axial_rib,_tuberculum_shape short_and_broad,_equal_in_size_to_capitulum
long_and_acute,_narrower_than_capitulum;

{271 Axial_rib,_tuberculum,_contact_with_axial_diapophysis
absent,_or_occurs_late_in_ontogeny present_early_in_ontogeny;

{272 Axis,_neural_spine,_anterior_half_of_dorsal_margin_in_lateral_view_(at_maturity)
horizontal slopes_such_that_it_faces anterodorsally;

{273 Axis,_neural_spine,_posterior_half dorsally_inflexed_to_form_crest
continuous_with_anterior_half,_not_crested;

{274 Axis,_neural_spine,_shape_of_distal_end dorsoventrally_thick dorsoventrally_thin,_rod-like;

{275 Axis,_lateral_process_(diapophysis)_on_neural_arch_lateral_margin absent present;

{276 Axis,_hypapophysis_position located_towards_centre_of_centrum
toward_anterior_end_of_centrum;

{277 Axis,_hypapophysis_shape un-forked forked;

{278 Prominent_cervical_hypapophyses present absent;

{279

First_postaxial vertebra_(Cv3),_anteroposterior_length_at_the_distal_end_of_the_neural_spine long,_greater_than_or_equal_to_half_the_length_of_the_non-condylar_centrum
short,_dorsal_tip_acute_and_less_than_half_the_length_of_the_non-condylar_centrum;

{280 Cervical_centra amphicoelous_(both_articular_surfaces_concave)
procoelous_(anterior_articular_surface_concave,_posterior_articular_surface_convex);

{281 Posterior_cervical_vertebrae_(C7?C9),_anterior_extent_of_hypapophyses_(C7?C9)
level_with,_or_anterior_to_the_level_of_anterior_margin_of_the_prezygapophyses
posterior_to_the_level_of_anterior_margin_of_prezygapophyses;

{282 Cervical_rib_8,_length_in_proportion_to_cervical_rib_9
long,_greater_than_half_the_length_of_cervical_rib_9
short,_equal_to_or_less_than_half_the_length_of_cervical_rib_9;

{283 Hypapophyseal_keels,_posterior_retention_until_10th_postatlantal_vertebra_(Dv2)
11th_postatlantal_vertebra_(Dv3) 12th_postatlantal_vertebra_(Dv4);

{284 Dorsal_centra amphicoelous procoelous;

{285
Dorsal_vertebrae,_maximum_mediolateral_width_across_both_transverse_processes_at_ve
rtebrae_7-10 equal_to_or_greater_than_twice_the_equivalent_width_on_DV1
less_than_twice_the_equivalent_width_on_DV1;

{286 Dorsal_vertebrae,_fusion_of_the_diapophysis_and_parapophysis,_occurrence
anterior_to_or_on_the_12th_dorsal_vertebra_on_the_13th_dorsal_vertebra;

{287 Presacral_vertebrae,_maximum_mediolateral_width_across_prezygapophyses sub-
equal_throughout increases_posteriorly_throughout_presacral_vertebrae;

{288 Sacral_vertebra_1,_anterior_extent_of_sacral_rib_capitulum
anterior_to_tuberculum_(visible_in_dorsal_view)
at_the_same_level_as_tuberculum_(obscured_in_dorsal_view);

{289 Sacral_vertebra_2,_posterior_extent_of_ribs
extend_beyond_level_of_posterior_extent_of_postzygapophyses
terminate_level_with_or_anterior_to_level_of_postzygapophyses;

{290 Caudal_vertebra_1,_centrum opisthocoelous_or_procoelous biconvex;

{291 Caudal_centra,_posterior_to_?rst_caudal_vertebra procoelous
amphicoelous_or_opisthocoelous;

{292 Caudal_vertebrae,_number_with_transverse_processes ?rst_15_or_fewer 16_to_20_
21_or_more;

{293 Caudal_vertebrae,_articular_surfaces_of chevrons_posterior_to_the_?rst
open,_or_partially_fused completely_fused;

{294 Hyoid,_shape_of_dorsal_projection_(cornu) plate-shaped rod-shaped;

{295 Hyoid,_?are_of_dorsal_projection_(cornu) absent present;

{296 Interclavicle_flexure
minimal_dorsoventral_flexure,_minimum_angle_between_anterior_and_posterior_ends_<15
moderate_dorsoventral_flexure,_minimum_angle_15?25
severe_dorsoventral_flexure,_minimum_angle_>_25;

{297 Interclavicle,_shape_of_anterior_end_(at_maturity) plate-shaped rod-shaped;

{298 Scapula,_deltoid_crest_shape thin,_with_sharp_margin wide,_with_broad_margin;

{299 Scapulocoracoid_synchondrosis closes_very_late_in_ontogeny
closes_early_in_ontogeny;

{300 Scapulocoracoid_facet,_shape_anterior_to_glenoid_fossa_(at_maturity)
uniformly_narrow broad_immediately_anterior_to_glenoid_fossa,_tapering_anteriorly;

{301 Humerus, proximal margin of deltopectoral crest
straight, emerging smoothly from proximal end of the humerus
concave, emerging abruptly from proximal end of humerus;

{302 Humerus, axial rotation of the proximal epiphysis relative to the distal epiphysis
small, ventral surface of the proximal epiphysis not visible in medial view
large, ventral surface exposed in medial view;

{303
Humerus, scarring on proximodorsal surface for M. teres major and M. dorsalis scapulae (at maturity) two muscle scars
single muscle scar (M. teres major and M. dorsalis scapulae insert on common tendon);

{304 Ulna, shape of olecranon process narrow and sub-angular wide and rounded;

{305 Ulna, proximal diaphysis curved straight;

{306 Ilium, preacetabular process shape acute, pointed anteriorly
broad, rounded anteriorly;

{307 Ilium, dorsal outline of postacetabular process convex, no dorsal indentation
broadly concave with a small indentation
strongly concave, with an acute indentation (?wasp-waisted?);

{308 Ilium, posterior margin of the postacetabular process
deep, anteroposterior length to dorsoventral height ratio < 1
shallow, length to height ?1;

{309 Ilium, postacetabular process projects posteriorly posterodorsally;

{310 Cerebrum, posterodorsal outline anterior to optic lobe flat with sharp step;

{311
Medial pharyngeal sinus, ratio of ventral length (measured from ventral tip to junction with basisphenoid diverticulum) to dorsal length (measured from basisphenoid diverticulum to dorsal tip) ?2 < 2;

{312 Keratinised buccal cavity present absent;

{313 Integumentary sensory organs, distribution on body cranial only
cranial and postcranial;

{314 Ventral scales, follicle gland pore present absent;

{315 Ventral collar scales not enlarged relative to other ventral scales
in 1?2 enlarged rows;

{316
Tail dorsal scalation, number of transverse scale rows from the level of the cloacal vent to the point of convergence of paired mid-dorsal crests into a single longitudinal crest > 13 ?13;

{317 Palpebral, number of ossifications one two or more;

{318 Palpebral, size in relation to orbit
small, covering no more than half the area of the orbit
large, covering more than half the orbit (usually completely concealing it);

{319 Tongue, lingual osmoregulatory pores large, 1?2 mm small, < 1 mm;

{320 Postoccipital osteoderms, number of rows two or more one;

{321 Nuchal_osteoderms grade_continuously_into_dorsal_shield
differentiated_from_dorsal_shield;

{322 Number_of_nuchal_osteoderms four_six_eight_or_more;

{323 Dorsal_osteoderms,_maximum_number_in_the_middle_transverse_row_(at_maturity)
two_four_six_eight_ten;

{324 Dorsal_osteoderms,_longitudinal_midline_keel absent_present;

{325 Dorsal_midline_osteoderm_shape_rectangular,_width_to_length_ratio_>_1
approximately_square,_width_to_length_ratio_?_1;

{326 Dorsal_midline_osteoderms,_anterolateral_process present_absent;

{327 Ventral_osteoderms absent_(or_poorly_developed) present,_single_ossification
present,_paired_ossification;

{328 Tail_armour
partial_covering_(usually_?_10_transverse_rows_of_contiguous_osteoderms_posteriorly_fro
m_the_level_of_caudal_vertebra_one) tail_completely_encased_in_osteoderms;

{329 Limb_armour
forelimbs_and_hindlimbs_lack_osteoderms,_or_weakly_armoured_with_patches_of_poorly_
developed_osteoderms densely_covered_in_well-formed_osteoderms;

;

;

Ancstates

-0	-1	-2	-3	-4	-5	-6	-7	-8	-9
-10	-11	-12	-13	-14	-15	-16	-17	-18	-19
-20	-21	-22	-23	-24	-25	-26	-27	-28	-29
-30	-31	-32	-33	-34	-35	-36	-37	-38	-39
-40	-41	-42	-43	-44	-45	-46	-47	-48	-49
-50	-51	-52	-53	-54	-55	-56	-57	-58	-59
-60	-61	-62	-63	-64	-65	-66	-67	-68	-69
-70	-71	-72	-73	-74	-75	-76	-77	-78	-79
-80	-81	-82	-83	-84	-85	-86	-87	-88	-89
-90	-91	-92	-93	-94	-95	-96	-97	-98	-99
-100	-101	-102	-103	-104	-105	-106	-107	-108	-109
-110	-111	-112	-113	-114	-115	-116	-117	-118	-119
-120	-121	-122	-123	-124	-125	-126	-127	-128	-129
-130	-131	-132	-133	-134	-135	-136	-137	-138	-139
-140	-141	-142	-143	-144	-145	-146	-147	-148	-149
-150	-151	-152	-153	-154	-155	-156	-157	-158	-159
-160	-161	-162	-163	-164	-165	-166	-167	-168	-169

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-280 -281 -282 -283 -284 -285 -286 -287 -288 -289
-290 -291 -292 -293 -294 -295 -296 -297 -298 -299
-300 -301 -302 -303 -304 -305 -306 -307 -308 -309
-310 -311 -312 -313 -314 -315 -316 -317 -318 -319
-320 -321 -322 -323 -324 -325 -326 -327 -328 -329

;

xgroup

;

agroup

;

taxcode

+0 +1 +2 +3 +4 +5 +6 +7
+8 +9 +10 +11 +12 +13 +14 +15
+16 +17 +18 +19 +20 +21 +22 +23
+24 +25 +26 +27 +28 +29 +30 +31
+32 +33 +34 +35 +36 +37 +38 +39
+40 +41 +42 +43 +44 +45 +46 +47
+48 +49 +50 +51 +52 +53 +54 +55
+56 +57 +58 +59 +60 +61 +62 +63
+64 +65 +66 +67 +68 +69 +70 +71
+72 +73 +74 +75 +76 +77 +78 +79
+80 +81 +82 +83 +84 +85 +86 +87
+88 +89 +90 +91 +92 +93 +94 +95

+96 +97 +98 +99 +100 +101 +102 +103
+104 +105 +106 +107 +108 +109 +110 +111
+112 +113 +114 +115 +116 +117 +118 +119
+120 +121 +122 +123 +124 +125 +126 +127
+128 +129 +130 +131 +132 +133 +134 +135
+136 +137 +138 +139 +140 +141 +142 +143
+144 +145

;

blocks 0;

tshrink

;

APPENDIX 2: Supplementary information and data for Chapter 2

1. Supplementary Table of worldwide Diplocynodon occurrences

2. Summary table of values presented in Figure 1

	Number of occurrences	Percentage out of total entries	Percentage out of total entries with evidence
Paleocene	3	0,017751479	/
Eocene	37	0,218934911	/
Oligocene	28	0,165680473	/
Miocene	101	0,597633136	/
Without evidence (only	66	0,390532544	/
With evidence (figured or	102	0,603550296	/
Material is figured	75		0,735294118
Material is described	96		0,941176471
Based on articulated	24		0,235294118
Based on several	11		0,107843137
ATTRIBUTIONS			
	Number of occurrences	Percentage out of total entries	Percentage out of total entries where the genus level is reached
Only referred at genus level	93	0,550295858	/
Genus level + only	49		0,52688172
Genus level + disarticulated	46		0,494623656
			Percentage out of total entries where the species level is reached
Species level reached	76	0,449704142	/
species level + only	17		0,223684211
species level reached +	15		0,197368421
species level reached +	10		0,131578947
species level +	41		0,539473684
TYPE	Number of occurrences	Percentage out of total entries with evidence	Percentage out of total entries based on disarticulated material
Based on articulated	24	0,235294118	/
Comprising several	11	0,107843137	/
Based on disarticulated	91	0,538461538	/
Including teeth	64		0,703296703
Including osteoderms	46		0,505494505
Including cranial	30		0,32967033
Including mandible	38		0,417582418
Including postcranium	27		0,296703297
Only jaw	11		0,120879121
Only osteoderms	3		0,032967033
Only teeth	19		0,208791209
Only parts of the skull	6		0,065934066
Only postcranium (except	3		0,032967033

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APPENDIX 3: Supplementary information and data for Chapter 3

1. *Dataset modifications*

We used a modified version of Chabrol et al. (2024) dataset for the phylogenetic analysis, the latter expanded from the parent Rio & Mannion (2021) dataset. Modifications of the latter dataset by Walter et al. (2025; Chapter 1) were implemented here, which include the addition of *Deinosuchus riograndensis* Colbert, 1954 and *Borealosuchus griffithi* Wu, 2001. *Diplocynodon tormis* was removed following Walter et al. (Chapter 2). *Diplocynodon darwini* was rescored based on the complete sample of specimens seen in collections (see Appendix 4 for a complete list) and scores differing from the previous version of the datasets are indicated here. Other *Diplocynodon* species were rescored for some characters, and a justification is provided.

List of modifications and updates of scores in the dataset of Chabrol et al. (2024)

32. Rostral ornamentation, morphology of the transverse orbital ridge (i.e. spectacle): low, lacking a posterior fossa (0); tall, with deep posterior fossa (1).

Diplocynodon remensis: 1 > 0

The spectacle is only known from the best-preserved specimen CE 0001. The bridge is however low and does not bear any posteriorly excavating fossae, as in all other *Diplocynodon* species where present, and in contrast to other crocodylian species scored as state (1) (e.g. *Caiman latirostris*)

41. External nares, orientation: projects anterodorsally (0); dorsally (1).

Diplocynodon darwini: 1 > 0

Diplocynodon deponiae: 0 > 1

Diplocynodon ratelii: 1 > 0

Diplocynodon remensis: 1 > 0

The external nares of *Diplocynodon* species actually project anterodorsally in all adult specimens that preserve the relevant region in 3 dimensions. Only *D. deponiae* differs from this condition.

43. External nares, thin crest circumscribing narial margin: absent (0); present (1).

Diplocynodon darwini: 0/1 > 0

44. Premaxilla, notch posterolateral to naris: absent (0); present (1).

Diplocynodon muelleri: 1 > 0

Diplocynodon ratelii: 1 > 0

47. Nasals, bisect nares completely (0); protrude partially into posterior narial margin (1); excluded internally from posterior narial margin (2) (ORDERED).

Diplocynodon deponiae: ? > 2

Diplocynodon muelleri: ? > 2

Diplocynodon remensis: ? > 2

The only species not bearing state (2) among *Diplocynodon* is *D. ratelii*. State (2) was observed in all other species preserving the relevant region.

57. Lacrimal, mediolateral width in relation to prefrontal: equal to or greater than twice the maximum prefrontal width (0); less than twice the maximum prefrontal width (1).

Diplocynodon darwini: 0 > 1

58. Lacrimal, anteroposterior length relative to that of prefrontal: longer (0); equal in length (1); shorter (2) (ORDERED).

Diplocynodon darwini: 2 > 0/1

Diplocynodon deponiae: 2 > 1

The lacrimal and the prefrontal are always sub-equal in length in specimens of *Diplocynodon deponiae* that preserve both bones. Deformation sometimes flattens the bones and uproots the sutures, but the respective size of the elements remains comparable (e.g. SMF-Me 2609; HLMD-Be 147). We therefore rescore the taxon to (1). *Diplocynodon darwini* is instead scored polymorphic here, after observation of state (0) in some specimens (HLMD-Me 236; HLMD-Me 7500; SMF-Me 2748; SMNK-PAL 6517) and (1) in others (HLMD-Me 233; HLMD-Me 10496).

73. Orbit, position of posterior margin (measured at the level of the postorbital-frontal suture) relative to posterior margin of suborbital fenestra: posterior to or at the same level (0); anterior (1).

Diplocynodon darwini: ? > 0

75. Frontoparietal suture, intersection with supratemporal fenestra (at maturity): deep intersection, postorbital-parietal suture not exposed on skull table (0); frontoparietal suture incipiently contacts supratemporal fenestra, postorbital-parietal suture slightly visible (1);

frontoparietal suture does not intersect supratemporal fenestra, postorbital-parietal contact fully exposed on skull table (2) (ORDERED).

Diplocynodon remensis: 1 > 0

As in all other *Diplocynodon* species, the frontoparietal suture enters the supratemporal fenestra, and the parietal-postorbital suture is not exposed on the skull table (Martin et al., 2014). This morphology is mediolaterally deformed in the best-preserved specimen CE 0001, but recognised in MNHN F BR 13105, MNHN F BR 13106 and MNHN BR 2622.

76. Frontoparietal suture, shape between supratemporal fenestrae: concavo-convex (0); straight (1).

Diplocynodon darwini: 0 > 1

77. Supraoccipital, exposure on dorsal skull table: absent (0); present (1).

Deinosuchus riograndensis: 0 > 1

Borealosuchus griffithi: 0 > 1

Both taxa scores were changed to state (1) to accommodate the inversion of the character definition by Chabrol et al. (2024).

78. Supraoccipital, extent of exposure on skull table: small, mediolateral width across dorsal supraoccipital exposure less than half that along the posterior margin of the parietal (0); moderate, mediolateral width across dorsal supraoccipital exposure more than half to equal that along the posterior margin of the parietal (1); large, such that the parietal is excluded from the posterior edge of skull table (2) (ORDERED).

Diplocynodon darwini: 1 > 0

90. Postorbital, protuberance on the dorsolateral margin of the postorbital bar (at maturity): present (0); absent (1)

Diplocynodon deponiae: ? > 1

SMF-Me 2609 shows the absence of this feature in the species.

91. Postorbital bar, orientation: laterally inclined, greater than or equal to 20° (bar visible in dorsal view) (0); slightly inclined to vertical, lateral inclination < 20° (not visible in dorsal view) (1).

Diplocynodon deponiae: ? > 0

SMF-Me 2609 preserves the postorbital bar that is not severely deformed. It is rather slender dorsoventrally oriented. Character state (0) seems appropriate here.

105. Postorbital, medial contact with quadrate at dorsal corner of the infratemporal fenestra: absent (0); present (1).

Diplocynodon darwini: ? > 0

108. Squamosal, shape of the lateral cranial table edge, dorsal to the otic aperture: vertical, dorsal and ventral edges equally expanded laterally; (0) bevelled, ventral edge projects further laterally than dorsal edge (1).

Diplocynodon hantoniensis: 1 > 0

This character shows some degree of variation, where an intermediate morphology can be observed: the ventral margin is slightly more exposed laterally than the dorsal margin.

Diplocynodon hantoniensis bears the latter condition, otherwise observed in other *Diplocynodon* species scored for the primitive condition (such as *D. darwini*, *D. deponiae*, or *D. remensis*). Since this condition is clearly different from state (1) observed in longirostrine taxa, and similar to congeneric species scored (0), we hereby rescore the taxon as (0).

115. External auditory meatus, posterior margin shape: straight (0); invaginated (1).

Diplocynodon darwini: 0 > 1

116. Quadrate, foramen aereum size: small, diameter less than half dorsoventral height of medial hemicondyle (0); large, equal to or greater than half dorsoventral height of medial hemicondyle (1).

Diplocynodon deponiae: ? > 0

The foramen aërum is small in *D. deponiae*, as can be observed on the left side of HLMD-Be 147.

123. Exoccipital, posterior projection of the paroccipital process: absent (0); present (1)

Diplocynodon deponiae: ? > 0

Three specimens of *D. deponiae* lack the posterior projection described in this character (HLMD-Be 147; SMF-Me 2609; HLMD-Me 7496). State (0) is appropriate here.

129. Basioccipital, orientation of lateral margins of ventral basioccipital plate: parallel or ventrally convergent (0); ventrally divergent (1).

Diplocynodon darwini: ? > 0

130. Basioccipital, dorsoventral height of ventral plate exposed below occipital condyle relative to occipital condyle height: greater or equal in height (0); shorter (1).

Diplocynodon darwini: ? > 0

132. Basioccipital, sagittal crest on ventral plate: present (0); absent (1).

Diplocynodon darwini: ? > 0

133. Basioccipital, concavity on ventral margin, posterior to median eustachian foramen: absent (0); present (1).

Diplocynodon darwini: ? > 0

138. Incisive foramen, anterior margin intersection with premaxillary tooth row: absent (anterior margin around 2nd or 3rd alveolus) (0); present (projects between or abuts first premaxillary teeth) (1).

Diplocynodon darwini: ? > 0

Diplocynodon ratelii: 1 > 0

First hand study of specimens studied by Rio & Mannion (2021) did not show the state (1) as scored in the authors dataset. Instead, we recognise the state (0) in MNHN SG 13728, MNHN SG 539, NHMB 4005 and NHMB 6507. We therefore rescore the character as (0) for the taxon. *Diplocynodon darwini* is newly scored for this character.

139. Incisive foramen, posterior margin: rounded (0); invaginated by anterior process of premaxilla (spade-shaped foramen).

Diplocynodon darwini: ? > 0

146. Premaxilla-maxilla suture, shape on palate in ventral view: horizontal (0); posteriorly bowed, with one rounded apex (1); posteriorly bowed, with one acute apex (2); posteriorly bowed with two or more apices (3).

Diplocynodon darwini: ? > 0

156. Dentary and maxillary teeth, shape behind alveoli 12–13: pointed to slightly blunt (0); globular (1); molariform, multicusped (2) (after Salas-Gismondi et al. 2015 [198]).

Change state 0 to “pointed to blunt” (state 1 should be only for globidonts)

Diplocynodon hantoniensis: 1 > 0

159. Maxilla, size of foramen for palatine ramus of cranial nerve V: small or absent, less than half diameter of 6th maxillary alveolus (0); large, equal to or greater than half diameter of 6th maxillary alveolus (1).

Diplocynodon darwini: ? > 0

168. Suborbital fenestra, anterolateral margin width, distance from medial edge of the toothrow to fenestral margin: narrow, less than or equal to one alveolus width (0); broader than one alveolar width (usually at least twice alveolar width) (1).

Diplocynodon darwini: ? > 1

169. Suborbital fenestra, lateral margin shape: straight (0); projecting medially into fenestra (1).

Diplocynodon darwini: ? > 0

172. Suborbital fenestra, posterior margin, intersection of palatine-pterygoid suture: at the posterior corner (0); on the posteromedial margin (1).

Orientalosuchus naduongensis: 1 > 2

Dongnanosuchus hsui: 1 > 2

Mekosuchus inexpectatus: 1 > 2

Trilophosuchus rackhami: 1 > 2

These taxa scores were modified following changes reported in Chabrol et al. (2024), but that as a likely mistake were not implemented in the discrete version of the dataset.

184. Jugal, morphology of medial foramen anterior to postorbital bar: small foramen (0); large recess (1).

Diplocynodon darwini: ? > 1

Diplocynodon deponiae: 0 > 1

A large anterior medial foramen is here newly recognised in *D. darwini*. *D. deponiae* is rescored as having an enlarged foramen (1), following the respective descriptions of Delfino & Smith (2012) and first-hand study of several specimens.

185. Ectopterygoid-pterygoid suture, shape (at maturity): straight (0); kinked (i.e. with 'flexure') (1).

Diplocynodon darwini: 0 > 1

190. Choanae, shape: circular or elliptical (0); sub-triangular, tapering posteriorly (1); sub-rectangular (long-axis orientated mediolaterally) (2); sub-triangular, tapering anteriorly (3).

Diplocynodon deponiae: ? > 1

Diplocynodon muelleri: 0 > 1

The choanae are split in two in the holotype specimen of *D. muelleri* (Spa 4), but the lateral margins are well preserved and taper posteromedially (1). This condition is similar to all other *Diplocynodon* species, including *D. deponiae* that is here newly scored for this morphology.

192. Choanae, direction of choanal projection (at maturity): posteroventrally (0); ventrally to anteroventrally (1).

Diplocynodon darwini: ? > 0

193. Choanae, septum: absent (0); present (1)

Diplocynodon deponiae: 1 > 0

194. Choanae, external projection of septum: absent, septum remains recessed within choanae (0); present, septum approaches external margin of choanae (1).

Diplocynodon darwini: ? > 0

Diplocynodon hantoniensis: 1 > 0

Diplocynodon ratelii: 1 > 0

Diplocynodon muelleri: ? > 0

196. Choanae, morphology of posterior wall: not notched, or with broadly rounded notch (0); acutely notched (1).

Diplocynodon darwini: ? > 0

230. Splenial, posterior perforation(s) for mandibular ramus of cranial nerve V: absent (0); present (1).

Diplocynodon hantoniensis: 0/1 > 0

This binary character was previously scored polymorphic in *D. hantoniensis*, because of the absence of the foramen in some specimens and definite presence in NHMUK OR 30394.

Given the latter evidence, we choose here to score the taxon as having a posterior foramen for the mandibular ramus of cranial nerve V (1). The scoring of the dependent character 231 was not altered (0).

233. Splenial, anterior process within the dentary, medial to the posterior toothrow: absent (0); present (1)

Diplocynodon deponiae: ? > 0

242. Surangular, anterodorsal process (spur) lingual to posterior most dentary alveoli, between splenial and dentary: absent (0); present (1).

Deinosuchus riograndensis: 1 > 0

Diplocynodon darwini: ? > 0

Deinosuchus riograndensis score was changed to state (0) to accommodate the inversion of the character definition by Chabrol et al. (2024).

243. Surangular, anterodorsal process (spur), anterior extent: not reaching 1 full alveolus (0); reaching 1–2 alveoli (1); reaching 3 or more alveoli (2) (ORDERED).

Diplocynodon hantoniensis: 1 > 2

The spur described in this character reaches at least 3 alveoli in the specimens NHMUK OR 25178 and CAMSM TN 904, despite the latter being incomplete (Rio et al., 2020). We therefore rescore the taxon to state (2).

249. Articular, lamina extending from posterior edge of foramen aerum: absent (0); present (1).

Diplocynodon darwini: 0 > 1

256. Surangular-angular suture, lingual intersection with articular in the floor of the adductor chamber: at ventral tip (0); dorsal to ventral tip (1).

Diplocynodon darwini: 0 > 1

266. Atlas intercentrum, shape in lateral view: wedge-shaped (0); plate-shaped (1).

Diplocynodon ratelii: ? > 0

First-hand observation of the specimen NMB Ph 4110 indicates that the intercentrum is wedge-shaped in *D. ratelii*.

271. Axial rib, tuberculum shape: short and broad, equal in size to capitulum (0); long and acute, narrower than capitulum (1).

Diplocynodon darwini: ? > 0

281. Cervical centra: amphicoelous (both articular surfaces concave) (0); procoelous (anterior articular surface concave, posterior articular surface convex) (1).

Diplocynodon remensis: ? > 1

289. Sacral vertebra 1, anterior extent of sacral rib capitulum: anterior to tuberculum (visible in dorsal view) (0); at the same level as tuberculum (obscured in dorsal view).

Diplocynodon darwini: ? > 1

301. Scapulocoracoid facet, shape anterior to glenoid fossa (at maturity): uniformly narrow (0); broad immediately anterior to glenoid fossa, tapering anteriorly (1).

Diplocynodon darwini: ? > 1

308. Ilium, dorsal outline of postacetabular process: convex, no dorsal indentation (0); broadly concave with a small indentation (1); strongly concave, with an acute indentation (“wasp-waisted”) (2) (ORDERED).

Diplocynodon ratelii: 2 > 1

The dorsal indentation of the postacetabular process is not “wasp-waisted” in *D. ratelii*, as a more acute constriction defines the latter morphology. This region of the ilium however

exhibits a variable indentation corresponding to the intermediate state, as observed first-hand in MNHN SG 13728 or NHMB SG 10514. We therefore rescore the taxon to state (1).

318. Palpebral, number of ossifications: one (0); two or more (1).

Diplocynodon darwini: ? > 0

319. Palpebral, size in relation to orbit: small, covering no more than half the area of the orbit (0); large, covering more than half the orbit (usually completely concealing it) (1).

Diplocynodon darwini: ? > 0

326. Dorsal midline osteoderm shape: rectangular, width to length ratio > 1 (0); approximately square, width to length ratio < = 1 (1).

Diplocynodon muelleri: 1 > 0

Although described as “more squared than *D. ratelii*”, the dorsal midline osteoderms of *D. muelleri* are primarily rectangular in shape (Piras & Buscalioni, 2006).

328. Ventral osteoderms: absent (or poorly developed) (0); present, single ossification (1); present, paired ossification (2)

Diplocynodon ratelii: ? > 2

D. ratelii was previously scored as unknown for this character. It is however diagnostic of the genus, and paired ossifications are reported for the latter species (e.g. NMB Ph. 4052)

List of modifications and updates of scores in the dataset of Walter et al. (2025; Chapter 1)

Where possible, corresponding characters from the above dataset were rescored for consistency in the dataset of Walter et al. (2025; Chapter 1).

Ch. 6.

Diplocynodon deponiae: 0 > ?

Diplocynodon hantoniensis: 1 > ?

Diplocynodon ratelii: 0 > ?

Diplocynodon remensis: 0 > ?

Ch. 7.

Diplocynodon remensis: 0 > ?

Ch. 21.

Diplocynodon darwini: 0 > 1

Diplocynodon remensis: 0 > ?

Ch. 25.

Diplocynodon darwini: ? > 1

Diplocynodon ratelii: ? > 1

Diplocynodon remensis: 0 > ?

Ch. 30.

Diplocynodon darwini: ? > 0

Diplocynodon ratelii: 0 > ?

Ch. 31.

Diplocynodon darwini: ? > 0

Diplocynodon ratelii: 0 > ?

Ch. 51.

Diplocynodon darwini: 0 > 1

Diplocynodon deponiae: ? > 1

Diplocynodon remensis: 0 > 1

Ch. 52.

Diplocynodon hantoniensis: 0 > 1

Ch. 54.

Diplocynodon darwini: 0 > 1

Ch. 55.

Diplocynodon darwini: ? > 0

Ch. 58.

Diplocynodon darwini: ? > 0

Ch. 61.

Diplocynodon darwini: ? > 1

Diplocynodon hantoniensis: 1 > 0

Ch. 65.

Diplocynodon darwini: 0 > 1

Diplocynodon hantoniensis: 0 > 1

Ch. 80.

Diplocynodon hantoniensis: 1 > 0

Diplocynodon ratelii: 1 > 0

Ch. 84.

Diplocynodon deponiae: 0 > 1

Ch. 85.

Diplocynodon hantoniensis: ? > 1

Ch. 101.

Diplocynodon darwini: 0 > 1

Ch. 102.

Diplocynodon muelleri: 0 > ?

Diplocynodon deponiae: 0 > ?

Ch. 121.

Diplocynodon darwini: ? > 1

Diplocynodon remensis: 1 > 0

Ch. 123.

Diplocynodon muelleri: 0 > ?

Ch. 125.

Diplocynodon darwini: 0 > 1

Diplocynodon hantoniensis: 0 > 1

Diplocynodon deponiae: 0 > 1

Ch. 142.

Diplocynodon deponiae: 1 > ?

Ch. 150.

Diplocynodon ratelii: 0 > 1

Ch. 215.

Diplocynodon darwini: ? > 0

Diplocynodon deponiae: ? > 0

Diplocynodon hantoniensis: ? > 0

Diplocynodon muelleri: ? > 0

2. Supplementary figures

Figure S1

Articulated adult specimen of *Diplocynodon darwini*. A, HLMD-Me 20336 exposed ventrally (scale bar = 10 cm); B, close-up view of ventral armor made of bipartite osteoderms; C, close-up view of the bipartite osteoderms organisation; D, close-up view of the medial side of the splenial and dentary (arrow points at the anterior tip of the splenial passing ventral to the Meckelian groove). E, close-up view of the anterior part of the tail bearing dorsal osteoderms (scale bar = 10 cm).

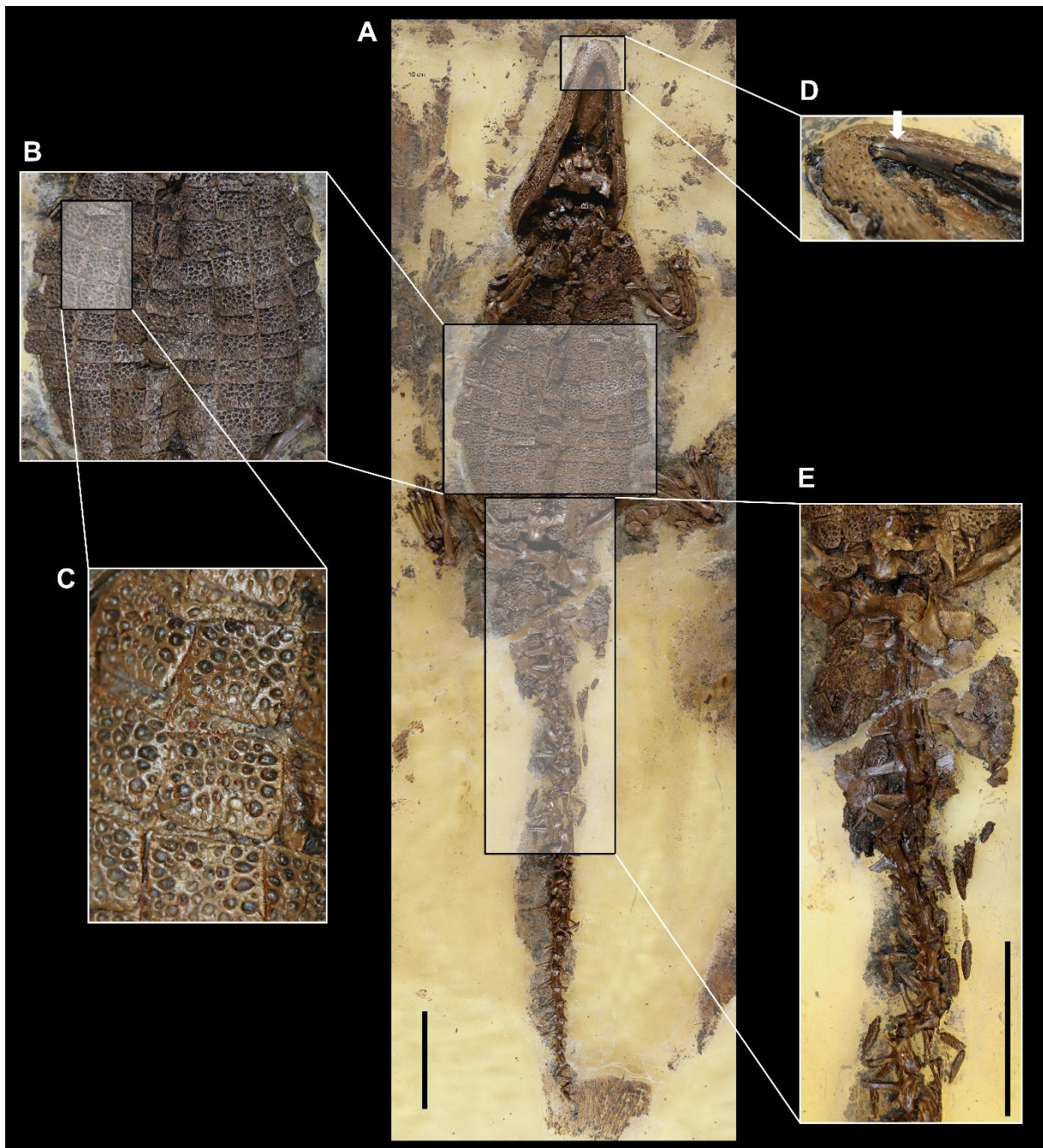


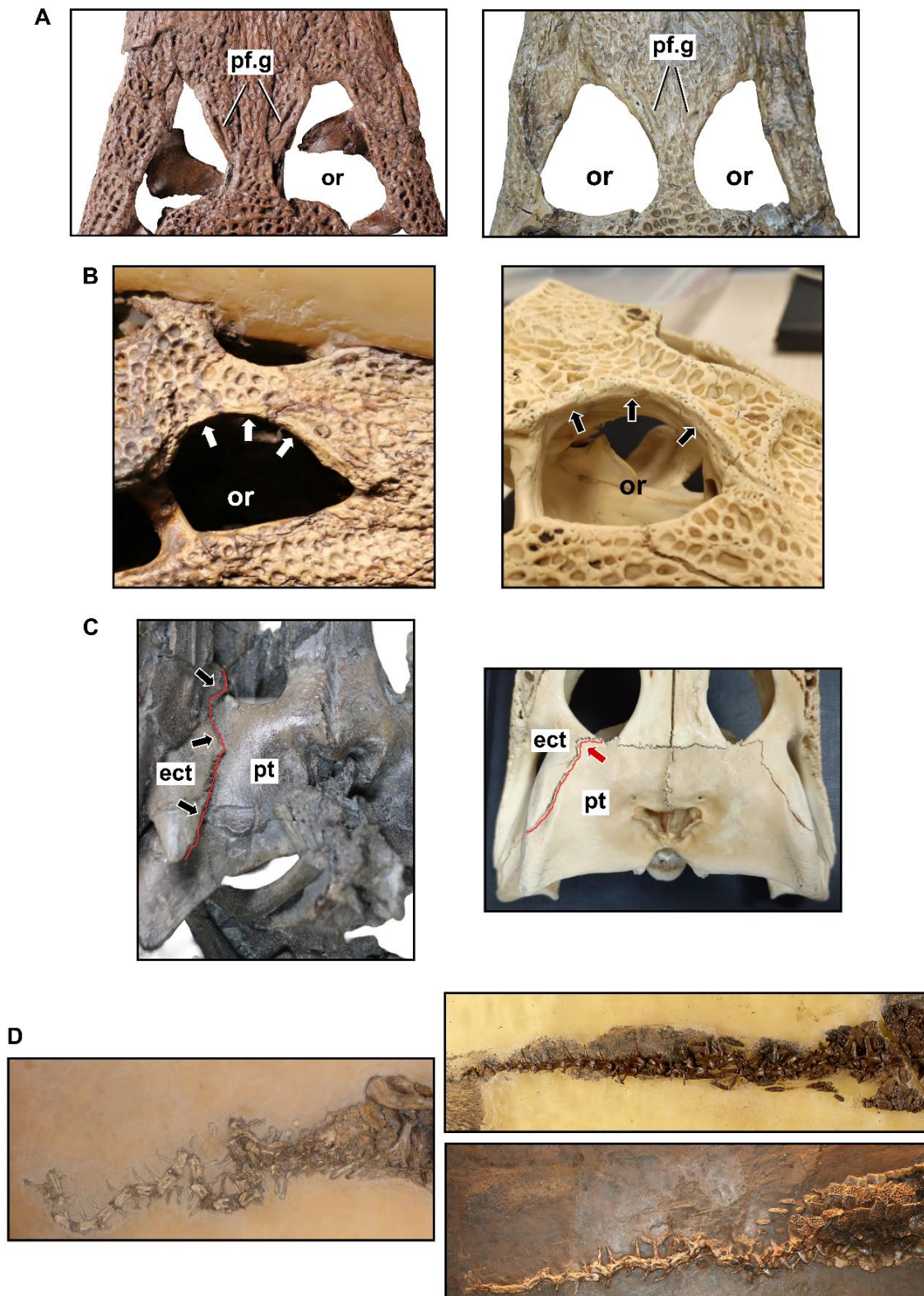
Figure S2

Articulated sub-adult specimen of *Diplocynodon darwini*. A, HLMD-Me 10262 exposed dorsally (scale bar = 3 cm). B, close-up view of the ultimate caudal vertebrae bearing osteoderms (scale bar = 3 cm); C, close-up view of the skull in dorsal view (scale bar = 3 cm); D, close-up view of the pelvic girdle and first caudal vertebrae (scale bar = 1.5 cm).



Figure S3

Diagnostic characters of *Diplocynodon darwini*. A, presence of prefrontal grooves/sulci (left, GMH XXXVI-524-1966; right, SMF-Me 900); B, orbital margin is flush with the skull surface (left, HLMD-Me 7500; right *Caiman yacare* with the “upturned” orbital margin condition); C, retention of the ectopterygoid-ptyergoid flexure (left, HLMD-Me 7571; right, *Caiman yacare* showing the same condition in situ); D, lack of osteoderm coverage on the posterior part of the tail (left, HLMD-Me 7500; top right, HLMD-Me 20336; bottom right, HLMD-Me 236).



3. Dataset: Walter et al., supplementary dataset (modified Walter et al. (2025; Chapter 1); .tnt)

xread

219 128

Bernissartia_fagesii

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Acynodon_adriaticus

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Acynodon_iberoccitanus

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Agaresuchus_subjuniperus

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Albertochampsa_langstoni

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Alligator_mcgrewi

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Alligator_mefferdi

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Alligator_mississippiensis 01011001?[0

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Alligator_olseni

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Alligator_prenasalis

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Alligator_sinensis

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Alligator_thomsoni

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Allodaposuchus_precedens

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Allognathosuchus_polyodon

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Allognathosuchus_wartheni

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Arambourgia_gaudryi

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Arenysuchus_gascabadiolorum

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Asiatosuchus_germanicus

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Australosuchus_clarkae

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Borealosuchus_acutidentatus

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Brachyuranochampsia_eversolei

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Brochuchus_pigotti

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Caiman_brevirostris

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Caiman_crocodilus

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Caiman_latirostris

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Caiman_wannlangstoni

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Caiman_yacare

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Centenariosuchus_gilmorei

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Ceratosuchus_burdoshi

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Chinatichampsus_wilsonorum

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Crocodylus_acer

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Crocodylus_affinis

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Crocodylus_megarhinus

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Crocodylus_niloticus

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Crocodylus_porosus

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Crocodylus_rhombifer

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Deinosuchus_riograndensis

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Deinosuchus_schwimmeri

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Diplocynodon_darwini

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Diplocynodon_deponiae

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Diplocynodon_hantoniensis

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Diplocynodon_muelleri

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Diplocynodon_ratelii

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Diplocynodon_remensis

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Diplocynodon_tormis

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Dollosuchoides_densmorei

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Dongnanosuchus_hsui

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Eoalligator_chunyii

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Eocaiman_cavernensis

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Eocaiman_itaboraiensis

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Eocaiman_palaeocenicus

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Eogavialis_africanum

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Eosuchus_lerichei

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Eosuchus_minor

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Eothoracosaurus_mississippiensis

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Euthecodon_arambourgii

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Gavialis_gangeticus

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Gavialis_lewisi

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Gavialosuchus_eggenburgensis

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Globidentosuchus_brachyrostris

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Gnatusuchus_pebasensis

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Gryposuchus_colombianus

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Hassiacosuchus_haupti

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Maomingosuchus_petrolica

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Mecistops_cataphractus

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Melanosuchus_niger

01111001?1?0010000010101111100110001112212101100211210101111201102011001??
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103000101100100110210001002000012000110-?2011001000000110000001

Mourasuchus_amazonensis

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Mourasuchus_arendsi

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Mourasuchus_atopus

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Navajosuchus_mooki

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Necrosuchus_ionensis

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Orientalosuchus_naduongensis

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Osteolaemus_osborni

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Osteolaemus_tetraspis

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Pachycheilosuchus_trinquei

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Paleosuchus_palpebrosus

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Paleosuchus_trigonatus

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Paratomistoma_courti

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Pietraroiasuchus_ormezzanoi

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Piscogavialis_jugaliperforatus

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Planocrania_datangensis

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Planocrania_hengdongensis

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Procaimanoidea_kayi

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Procaimanoidea_utahensis

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Prodiplocynodon_langi

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Protoalligator_huiningensis

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Protocaiman_peligrensis

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Purussaurus_brasiliensis

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Purussaurus_mirandai

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Purussaurus_neivensis

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Quinkana_spp

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Rimasuchus_lloydi

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Shamosuchus_djadochtaensis

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Stangerochampsia_mccabei

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111001012101111100?110200?0?2100102101010??1?1?0100110010001??000012?0?01022 -
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Thecachampsia_antiqua

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Thoracosaurus_macrorhynchus

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Thoracosaurus_neocesariensis

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Tomistoma_cairense

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Tomistoma_lusitanica

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1001??1110010000003??000012??0?0?-?-011001[0 1]?00?01??0000?1

Tomistoma_schlegelii

21000001?0010100010110001111110110001013011011122?1040000010020000000201000
01001200000011021000010101000001101000100100100000110000111110000110101221010010
101011001011110010000003111000013000000-0-0110010000000100000?1

Toyotamaphimeia_machikanensis

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Trilophosuchus_rackhami

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Tsoabichi_greenriverensis

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Voay_robustus

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Wannaganosuchus_brachymanus

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cnames

- {0 Fused_proatlas_shape boomerang-shaped strap-shaped block-shaped;
- {1 Proatlas_process with_anterior_process without_anterior_process;
- {2 Proatlas_dorsal_keel with_dorsal_keel without_dorsal_keel;
- {3 Atlas_intercentrum_shape wedge-shaped plate-shaped;

{4 Dorsal_margin_of_atlantal_rib_process smooth dorsal_process;

{5 Atlantal_ribs_lamina without_lamina with_lamina;

{6 Atlantal_ribs_articular_facets without_facets with_facets;

{7 Axial_rib_tuberculum_tip broad_dorsal_tip acute_dorsal_tip;

{8 Axial_rib_tuberculum_diapophysis contact_late_in_ontogeny contact_early_in_ontogeny;

{9 Axis_neural_spine_shape horizontal_anteriorly slopes_anteriorly;

{10 Axis_neural_spine_crested not_crested;

{11 Posterior_half_of_axis_neural_spine_wide narrow;

{12 Axis_neural_arch_lacks_diapophysis bears_diapophysis;

{13 Axial_hypapophysis_location_center_of Centrum anterior_end_of_Centrum;

{14 Axial_hypapophysis_shape without_deep_fork with_deep_fork;

{15 Hypapophyseal_keels_presence 11th_vertebra_behind_atlas 12th_vertebra_behind_atlas 10th_vertebra_behind_atlas;

{16 Third_cervical_vertebra_hypapophysis prominent not_prominent;

{17 Neural_spine_on_third_cervical long short;

{18 Cervical_and_anterior_dorsal_centra lack_deep_pits_ventrally bear_deep_pits_ventrally;

{19 Presacral_centra amphicoelus procoelus;

{20 Anterior_sacral_rib_capitulum broadly_visible_in_dorsal_view obscured_in_dorsal_view;

{21 Scapular_blade_shape flares_dorsally sides_sub-parallel;

{22 Deltoid_crest_of_scapula very_thin_with_sharp_margin very_wide_with_broad_margin;

{23 Scapulocoracoid_synchondrosis closes_late_in_ontogeny closes_early_in_ontogeny;

{24 Scapulocoracoid_facet_shape narrow_anterior_to_glenoid_fossa broad_anterior_to_glenoid_fossa;

{25 Proximal_edge_of_deltopectoral_crest_of_humerus not_concave concave;

{26 M._teres_major_and_M._dorsalis_scapulae_insertion separately single_insertion_scar;

{27 Olecranon_process_of_ulna_shape narrow_and_sub-angular wide_and_rounded;

{28 Ulna_shape proximal_extremity_equal_to_distal proximal_extremity_wider_than_distal;

{29 Interclavicle_shape without_dorsoventral_flexure with_moderate_dorsoventral_flexure with_severe_dorsoventral_flexure;

{30 Anterior_end_of_interclavicle_flat rodlike;

{31 Iliac_anterior_process_prominent virtually_absent;

{32 Dorsal_margin_of_iliac_blade__ rounded_with_smooth_border rounded_with_modest_dorsal_indentation rounded_with_strong_dorsal_indentation narrow_with_dorsal_indentation rounded_dorsal_tip_deep;

{33 Supraacetabular_crest narrow broad;

{34 Limb_bones_form robust slender;

{35 M._caudofemoralis_single_head double_head;

{36 Dorsal_osteoderms_keel not_keeled keeled;

{37 Dorsal_midline_osteoderms_shape rectangular nearly_square;

{38 Number_of_contiguous_dorsal_osteoderms_per_row_ four six eight ten;

{39 Nuchal_shield grades_continuously_into_dorsal_shield_with_four_nuchal_osteoderms six_nuchal_osteoderms eight_nuchal_osteoderms_in_two_parallel_rows;

{40 Ventral_armor_absent single_ventral_osteoderms paired_ventral_osteoderms;

{41 Anterior_margin_of_dorsal_midline_osteoderms_with_anterior_process without_anterior_process;

{42 Ventral_scales_pores have_follicle_gland_pores lack_follicle_gland_pores;

{43 Ventral_collar_scales_not_enlarged single_enlarged_row two_parallel_enlarged_rows;

{44 Median_pelvic_keel_scales_along_tail two_parallel_rows single_row merge_with_lateral_keel_scales;

{45 Alveoli_size_of_dentary_teeth_3_and_4_same_size_and_confluent 4_larger_than_3_and_separated 3_and_4_are_nearly_the_same_size_and_separated;

{46 Anterior_dentary_teeth strongly_procumbent project_anterodorsally;

{47 Dentary_symphysis_extension fourth_and_fifth_alveolus sixth_through_eight_alveolus eighth_to_twelfth_alveolus twelfth_to_sixteenth beyond_the_sixteenth;

{48 Dentary_curvature_between_fourth_and_tenth_alveoli gently deeply linear;

{49 Largest_dentary_alveolus_caudal_to_fourth 13_or_14 between_11_and_14_and_a_series_behind_it 11_or_12 no_differentiation behind_14 10;

{50 Splenial_with_anterior_perforation_for_cranial_nerv_V existent lacking;

{51 Mandibular_ramus_of_cranial_nerv_V only_anterior single_perforation_posterior double_perforation_posterior;

{52 Mandibular_symphysis_size splenial_participates_ splenial_excluded,_anterior_tip_of_splenial_ventral_to_Meckelian_groove splenial_excluded,_anterior_tip_of_splenial_dorsal_to_Meckelian_groove deep_splenial_symphysis,_splenial_forms_wide_V deep_splenial_symphysis,_splenial_forms_narrow_V splenial_reaches_mandibular_symphysis_but_does_not_touch_other_splenial;

{53 Coronoid_position_for_foramen_intermandibularis_medius bounding_posterior_half_of_foramen_completely_surrounding_foramen obliterates_foramen_;

{54 Coronoid_superior_edge sloping_strongly_anteriorly almost_horizontal;

{55 Coronoid_inferior_process lapping_over_inner_surface_of_meckelian_fossa remains_on_medial_surface_of_mandible;

{56 Coronoid_perforation imperforate
perforation_posterior_to_foramen_intermandibularis_medius;

{57 Splenial_process separates_angular_and_coronoid no_process_between_angular_and_coronoid;

{58 Angular-surangular_suture_with_ext.mand._fenestra contacting_fenestra_at_posterior_angle
passing_along_ventral_margin_of_fenestra;

{59 Surangular_anterior_processes unequal sub-equal_to_equal;

{60 Surangular_spur_on_lingual_tooth_row spur_for_at_least_one_alveolus_length no_spur;

{61 External_mandibular_fenestra absent present_as_narrow_slit
present_with_discrete_concavity_on_angular_dorsal_margin present_and_very_large;

{62 Surangular-dentary_suture_intersection_with_ext._mand._fenestra
anterior_to_posterodorsal_corner at_posterodorsal_corner;

{63 Angular_anterior_tip_to_foramen_intermandibularis_caudalis
towards_anterior_end_of_foramen_not_towards_anterior_end_of_foramen;

{64 Surangular-angular_suture_lingually_meets_articular at_ventral_tip dorsal_to_tip;

{65 Surangular_at_lateral_wall_of_glenoid_fossa continuing_to_dorsal_tip truncated;

{66 Articular-surangular_suture_form simple
articular_bears_anterior_lamina_dorsal_to_lingual_foramen
articular_bears_anterior_lamina_ventral_to_lingual_foramen
articular_bears_lamina_above_and_below_foramen;

{67 Lingual_foramen_for_articular_artery perforates_surangular_entirely
perforates_surangular/angular_suture;

{68 Foramen_aerum_position at_lingual_margin_of_retroarticular_process
set_in_from_margin_of_retroarticular_process;

{69 Retroarticular_process_projection posteriorly
posterodorsally,_not_higher_than_the_posterior_edge_of_the_articular_fossa
projects_posterodorsally,_higher_than_the_posterior_edge_of_the_articular_fossa;

{70 Surangular_extension posterior_end_of_retroarticular_process
pinched_off_anterior_to_tip_of_retroarticular_process;

{71 Surangular-articular_suture_orientation_within_glenoid_fossa anteroposteriorly
bowed_strongly_laterally;

{72 Articular-surangular_connection sulcus_between_articular_and_surangular
articular_flush_against_surangular;

{73 Hyoid_cornu_dorsal_projection_form flat rodlike;

{74 Hyoid_cornu_dorsal_projection_lateromedial narrow_with_parallel_sides flared;

{75 Lingual_osmoregulatory_pores small large;

{76 Tongue with_keratinized_surface without_keratinized_surface;

{77 Teeth_and_alveoli_of_maxilla/dentary_form circular_in_cross-section
posterior_teeth_laterally_compressed_all_teeth_compressed_;

{78 Maxillary_and_dentary_teeth_serration smooth_carinae serrated
with_neither_carinae_nor_serrations;

{79 Naris_projection anterodorsally dorsally posterodorsally;

{80 External_naris_and_nasal_interaction external_naris_birsected_by_nasals
nasal_contacts_external_naris_without_bisection nasal_excluded_externally_from_naris
nasal_and_premaxilla_not_in_contact;

{81 Naris_shape circular_or_key-hole_shaped wider_than_long
anteroposteriorly_long_and_tear-drop-shaped;

{82 External_naris_of_reproductively_mature_males similar_to_that_of_females
with_bony_excrescence;

{83 External_naris_opening flush_with_dorsal_surface_of_premaxilla circumscribed_by_thin_crest;

{84 Premaxilla_surface_lateral_to_naris smooth with_deep_notch;

{85 Number_of_teeth_in_premaxilla_early_in_ontogeny five four;

{86 Incisive_foramen_size small large_and_more_than_half_the_greatest_width_of_premaxillae
large_and_intersects_premaxillary-maxillary_suture;

{87 Incisive_foramen_position situated_far_from_premaxillary_tooth_row
abuts_premaxillary_tooth_row projects_between_first_premaxillary_teeth;

{88 Dorsal_premaxillary_process short long_behind_3th_maxilla_tooth;

{89 Dentary_tooth_four_early_in_ontogeny in_notch_between_premaxilla_and_maxilla
in_pit_between_premaxilla_and_maxilla;

{90 Dentary_teeth_position all_teeth_lingual_to_maxillary_teeth
occlusion_pit_between_seventh_and_eighth_maxillary_teeth
dentary_teeth_in_line_with_maxillary_tooth_row;

{91 Largest_maxillary_alveolus third fifth fourth four_and_five_the_same_size six
maxillary_teeth_homodont maxillary_alveoli_gradually_increase_in_diameter;

{92 Maxillary_tooth_row_form_posterior_to_first_six_maxillary_alveoli medially_curved_or_linear
broadly_curved_laterally;

{93 Dorsal_surface_of_rostrum curves_smoothly bears_medial_dorsal_boss;

{94 Canthi_rostraliai_at_maturity absent_or_very_modest very_prominent;

{95 Preorbital_ridges_at_maturity absent_or_very_modest very_prominent;

{96 Antorbital_fenestra present absent;

{97 Vomer_position_anterior entirely_observed_by_premaxilla_and_maxilla
exposed_on_palate_at_premaxillary-maxillary_suture;

{98 Vomer_position_posterior entirely_observed_by_maxillae_and_palatines
exposed_on_palate_between_palatines;

{99 Surface_of_maxilla_within_narial_canal imperforate with_linear_array_of_pits;

{100 Medial_jugal_foramen_size small very_large;

{101 Maxillary_foramen_for_cranial_nerve_V_size small_or_not_present very_large;

{102 Ectopterygoid_contact_with_maillary_toothrow_forming_medial_wall_of_at_least_1_mx_alveolus absent_and_ectpt-mx_suture_anteromedially_orientated_and_separated_from_toothrow_margin absent_ans_ectopt-mx_suture_parallel_and_adjacent_to_medial_toothrow_margin present;

{103 Maxilla_termination_in_palatal_view anterior_to_lower_temporal_bar comprises_part_of_the_lower_temporal_bar;

{104 Penultimate_maxillary_alvelous_size less_than_twice_the_diamater_of_the_last_one more_than_twice_the_diamater_of_the_last_one;

{105 Prefrontal_dorsal_surface_appearance smooth_adjacent_to_orbital bearing_discrete_knoblike_processes;

{106 Dorsal_half_of_prefrontal_pillar narrow expanded_anteroposteriorly;

{107 Medial_process_of_prefrontal_pillar expanded_dorsoventrally expanded_anteroposterirolly;

{108 Prefrontal_pillar_form solid with_large_pneumatic_recess;

{109 Medial_process_of_prefrontal_pillar_at_base wide constricted;

{110 Maxilla_appearance_on_suborbital_fenestra linear_medial_margin broad_shelf,_lateral_margin_concave;

{111 Anterior_face_of_palatine_process_anterirolly rounded_or_pointed notched;

{112 Anterior_ectopetrygoid_process tapered_to_a_point forked;

{113 Palatine_process_extension_beyond_anterior_end_of_suborbital_fenestra not_beyond_anterior_end_of_suborbital_fenestra;

{114 Palatine_process_form broad_anterirolly form_of_a_thin_wedge;

{115 Lateral_edges_of_palatines_appearance smooth_anterirolly lateral_process_projecting_into_suborbital_fenestra;

{116 Palatine-ptyergoid_suture at_posterior_angle_of_suborbital_fenestra far_from_posterior_angle_of_suborbital_fenestra;

{117 Pterygoid_ramus_of_ectopterygoid_form straight,_posterolateral_fenestra_margin_linear bowed,_posterolateral_fenestra_margin_concave;

{118 Lateral_edges_of_palatines_form parallel_posterior flare_posteriorly,_producing_shelf;

{119 Anterior_border_of_choana comprised_of_palatines entirely_surrounded_by_ptyergoids;

{120 Choana_projecting_at_maturity posteroventrally anteroventrally;

{121 Pterygoid_surface_around_choana flush_with_choanal_margin pushed_inward_anterolateral_to_choana_aperture pushed_inward_around_choana_to_form_neck_surrounding_aperture everted_from_flat_surface_to_form_neck_surrounding_aperture;

{122 Posterior_rim_of_internal_choana not_deeply_notched deeply_notched;

{123 Internal_choana_appearance not_septated with_septum_that_remains_recessed_within_choana with_septum_that_projects_out_of_choana;

{124 Ectopterygoid-ptyergoid_flexure_appearance flexure_disappeares_during_ontogeny flexure_remains_throughout_ontogeny;

{125 Ectopterygoid_extention_at_maturity_to_posterior_tip_of_lateral_pterygoid_flange
 __not_to_posterior_tip_of_lateral_pterygoid_flange;

{126 Maxilla_connection_with_lacrimal lacrimal_makes_broad_contact_with_nasal,_no_process
 maxilla_with_posterior_process_within_lacrimal
 maxilla_with_posterior_process_between_lacrimal_and_prefrontal;

{127 Prefrontal_form
 separated_by_frontals_and_nasals,_anterior_process_of_frontal_extending_far_anterior_to_the_an-
 terior_margin_of_the_orbit
 prefrontals_separated_by_the_frontal_and_nasals,_anterior_process_of_frontal_around_the_same
 _level_or_posterior_to_the_anterior_margin_of_the_orbit
 prefrontals_meet_medially,_anterior_process_of_frontal_around_the_same_level_or_posterior_to_
 the_anterior_margin_of_the_orbit;

{128 Lacrimal_and_prefrontal_size lacrimal_longer_than_prefrontal prefrontal_longer_than_lacrimal
 lacrimal_and_prefrontal_same_size_and_elongated;

{129 Anterior_tip_of_frontal_form simple_acute_point
 broad,_complex_sutural_contact_with_nasals;

{130 Ectopterygoid_extension_at_postorbital_bar extends_along_medial_face_of_postorbital_bar
 stops_abruptly_ventral_to_postorbital_bar;

{131 Postorbital_bar_form massive_slender;

{132 Postorbital_process prominent,_dorsoventrally_broad,_two_spines
 short_and_generally_not_prominent;

{133 Ventral_margin_of_postorbital_bar flush_with_lateral_jugal_surface
 inset_from_lateral_jugal_surface;

{134 Postorbital_bar_connection_with_skull_table
 continous_with_anterolateral_edge_of_skull_table inset_from_skull_table;

{135 Margin_of_orbit flush_with_skull_surface dorsal_edges_of_orbit_upturned
 orbital_margin_telescoped anterior_margins_of_orbit_telescoped;

{136 Ventral_margin_of_orbit_form not_upturned,_ventral_margin_gently_circular
 anterior_margin_upturned,_ventral_margin_gently_circular
 anterior_margin_upturned,_ventral_margin_with_a_prominent_notch;

{137 Palpebral_form single_ossification multiple_ossifications;

{138 Quadratojugal_spine_appearance prominent_at_maturity
 greatly_reduced_or_absent_at_maturity;

{139 Quadratojugal_spine_position_into_infratemporal_fenestra
 low,_near_posterior_angle_of_fenestra
 high,_between_posterior_and_superior_angles_of__fenestra;

{140 Posterior_angle_of_infratemporal_fenestra quadratojugal_forms_posterior_angle_of_fenestra
 jugal_forms_posterior_angle_of_fenestra quadratojugal-
 jugal_suture_lies_at_posterior_angle_of_fenestra;

{141 Postorbital_contacts_neither_quadrate_nor_quadratojugal_medially
 quadratojugal_but_not_quadrate_medially

quadrate_and_quadratejugal_at_dorsal_angle_of_infrat._fenestra
quadratejugal_with_significant_descending_process;

{142 Quadratojugal_process long_anterior_process_along_lower_temporal_bar
_modest_process,_or_none_at_all,_along_lower_temporal_bar;

{143 Quadratojugal_extention extends_to_superior_angle_of_infratemporal_fenestra
does_not_extend_to_superior_angle_of_infratemporal_fenestra;

{144 Postorbital-squamosal_suture_orientation_to_skull_table passes_ventrally passes_medially;

{145 Dorsal_and_ventral_rims_of_squamosal_groove parallel flaring_anteriorly;

{146 Quadrate_and_squamosal_on_external_auditory_meatus not_in_contact_posteriorly
suture_extends_dorsally_along_caudal_margin_of_meatus
extends_only_to_caudovernal_boarder_of_meatus;

{147 Caudal_margin_of_otic_aperture not_defined_and_merging_into_exoccipital
smooth_and_continous_with_paroccipital_process inset;

{148 Frontoparietal_suture_position deeply_within_supratemporal_fenestra
making_modest_entry_into_supratemporal_fenestra_at_maturity on_skull_table_entirely;

{149 Frontoparietal_suture_between_supratemporal_fenestrae concavoconvex linear;

{150 Supratemporal_fenestra_appearance dermal_bones_do_not_overhang_rim_of_fenestra
parietal_overhangs_the_rim_at_maturity
postorbital,_squamosal_and_parietal_overhang_rim_at_maturity fenestra_closes_during_ontogeny;

{151 Anteromedial_corner_of_supratemporal_fenestra shallow_fossa_or_no_fossa smooth;

{152 Medial_parietal_wall_of_supratemporal_fenestra imperforate bearing_foramina;

{153 Parietal_and_squamosal_on_supratemporal_fenestra
widely_separated_by_quadrate_on_posterior_fenestra_wall
approaching_each_other_on_fenestra_without_making_contact
meeting_along_posterior_wall_of_fenestra;

{154 Skull_table_surface_at_maturity sloping_ventrally_from_sagittal_axis planar
slopes_ventrally_toward_sagittal_axis_at_maturity,_lateral_elements_planar;

{155 Squamosal_on_skull_table horizontal_or_nearly_so
upturned_to_form_a_discrete_posterolateral_horn
producing_a_high_transversely_oriented_eminence_at_the_posterior_margin_late_in_ontogeny;

{156 Posterolateral_squamosal_rami rami_along_paroccipital_process_short
rami_along_paroccipital_process_significant;

{157 Squamosal_form does_not_extend_to_lateral_extent_of_paroccipital_process
extends_to_lateral_extent_of_paroccipital_process;

{158 Supraoccipital_exposure_on_dorsal_skull_table absent small large
large_such_that_parietal_is_excluded_from_posterior_edge_of_table;

{159 Anterior_foramen_of_cranial_nerve_VII ventrolateral_to_basisphenoid_rostrum
ventral_to_basisphenoid_rostrum;

{160 Braincase_wall_lateral_to_basisphenoid_rostrum sulcus_on_anterior_braincase_wall
braincase_wall_smooth,_no_sulcus;

{161 Basisphenoid_anterior_to_trigeminal_foramen not_exposed_extensively exposed_extensively;

{162 Prootic_on_external_braincase_wall extensively_exposed largely_obsured_by_quadrate_and_laterosphenoid_externally;

{163 Laterosphenoid_bridge comprised_entirely_of_laterosphenoid with_ascending_process_or_palatine;

{164 Capitate_process_of_laterosphenoid oriented_laterally_toward_midline oriented_anteroposteriorly_toward_midline;

{165 Parietal_pneumatic_system parietal_with_recess_communicating_with_pneumatic_system parietal_solid,_without_recess;

{166 Lateral_braincase_wall significant_ventral_quadrate_process_on_braincase_wall q-pt_suture_linear_from_basisphenoid_exposure_to_trigeminal_fo;

{167 Lateral_carotid_foramen opens_lateral_to_basisphenoid_at_maturity dorsal_to_to_basisphenoid_at_maturity;

{168 External_surface_of_basioccipital_ventral_to_occipital_condyle oriented_posteroventrally_at_maturity oriented_posteriorly_at_maturity;

{169 Posterior_pterygoid_process tall_and_prominent small_and_project_posteroventrally small_and_project_posteriorly;

{170 Basisphenoid_appearance_ventral_to_basioccipital thin_anteroposteriorly_wide;

{171 Basisphenoid_exposure not_broadly_exposed_ventral_to_basioccipital exposed_as_broad_sheet_ventral_to_basioccipital;

{172 Exoccipital_on_paroccipital_process with_very_prominent_boss with_small_or_no_boss_on_paroccipital_process;

{173 Lateral_eustachian_canal_openings dorsal_to_medial_eustachian_canal lateral_to_medial_eustachian_canal;

{174 Exoccipital_termination dorsal_to_basioccipital_tubera sending_robust_process_ventrally,_participating_in_bo_tubera sending_slender_process_ventrally_to_basioccipital_tubera;

{175 Quadrate_foramen_aerum_position on_mediodorsal_angle_of_quadrate on_dorsal_surface_of_quadrate;

{176 Quadrate_foramen_aerum_size_at_maturity small comparatively_large absent;

{177 Quadrate_appearance_on_dorsal_surface_of_ramus lacking_prominent,_mediolaterally_thin_crest bearing_prominent,_mediolaterally_thin_crest;

{178 Attachment_scar_for_posterior_mandibular_abductor_muscle forming_modest_crest_on_ventral_surface_of_quadrate_ramus forming_prominent_knob_on_ventral_surface_of_quadrate_ramus;

{179 Quadrate_hemicondyle small,_ventrally-reflected_medial_hemicondyle small_medial_hemicondyle_dorsal_notch_for_foramen_aerum with_prominent_dorsal_projection_between_hemicondyles with_expanded_medial_hemicondyle;

{180 Iris_colour greenish/yellowish brown;

{181 Postoccipital_osteoderms two_or_more one;

{182 Paired_midline_scale_rows fewer_than_eight eight_to_14 more_than_14;

{183 Ectopterygoid_maxillary_ramus_form less_than_two-thirds_of_lateral_margin_of_suborbital_fenestra more_than_two-thirds_of_lateral_margin_of_suborbital_fenestra;

{184 Ectopterygoid_maxillary_ramus_termination at_lateral_margin_of_suborbital_fenestra lateral_to_it,_maxilla_separating_the_ectopterygoid_from_fenestra;

{185 Palatine-maxillary_suture_intersection_at_suborbital_fenestra at_its_anteromedial_margin nearly_at_its_antermost_limit;

{186 Frontal_with_midsagittal_crest_between_orbits lacks bears;

{187 Cervical_neural_spines_form anteroposteriorly_broad posterior_neural_spines_thin_and_rod-like;

{188 Largest_premaxilla_tooth second third fourth third_and_fourth_similar_largest all_similar_in_size fourth_and_fifth_similarly_largest first_for_similar_in_size;

{189 Dorsal_surface_of_surangular smooth large_sulcus_next_to_the_anterior_half_of_the_glenoid_fossa;

{190 U-shaped_depression_of_the_frontal_at_the_point_of_maximum absent present;

{191 Head_shape relatively_flat formed_like_a_wedge_and_trapezoid_in_cross-section;

{192 Anterior_jugal_process extends_anterior_to_the_anterior_process_of_frontal_at_the_same_level_as_the_anterior_process_of_frontal_well_posterior_to_the_anterior_process_of_frontal_;

{193 Notch_between_the_premaxilla_and_maxilla_in_adults present not_present;

{194 Anterior_maxilla_and_dentary_teeth without_or_weak_dorsoventral_ridges_on_the_lateral_surface with_dominant_dorsoventral_ridges_on_the_lateral_surface;

{195 If_largest_dentary_alveolus_is_between_11th_and_14th_and_a_series_behind_it 11th 12th 13th_or_14th;

{196 Surangular-angular_suture_lingually_originates_near_the_ventral_border_of_the_external_mandibular_fenestra_near_the_dorsal_border_of_the_external_mandibular_fenestra_and_straight near_the_dorsal_border_of_theexternal_mandibular_fenestra_and_bowed;

{197 If_supraoccipital_exposure_on_skull_table_is_large_or_very_large,_is__ trapezoid triangular block-shaped;

{198 Edge_of_the_maxillary_alveoli lower_or_at_the_same_level_than_the_space_between_toothrow_edge_of_maxillary_tooth_alveoli_higher_than_the_space;

{199 Ventral_border_of_exoccipital_ventrally_projected,_hiding_the_posterior_opening_of_the_cranioquadrate_passage_from_the_occipital_view_straight,_sharpen_or_smoothly_convex_and_does_not_hide_the_posterior_opening_of_the_cranioquadrate_passage_from_the_occipital_view_;

{200 Occipital_surface_at_maturity sloped,_visible_in_dorsal_view_
vertical_or_not_visible_in_dorsal_view;

{201 Ventral_premaxilla-maxilla_suture_
short_and_ends_posteriorly_before_the_3rd_maxillary_alveoli
elongated_and_extends_or_exceeds_the_3rd_maxillary_alveoli_;

{202 Number_of_teeth_on_maxilla less_than_18_teeth 18_to_22_teeth more_than_22_teeth;

{203 Lateral_edge_of_the_skull_table_at_the_level_of_the_postorbital-squamosal_suture_
situated_laterally_or_at_the_same_level_as_the_quadrate_condyle_in_dorsal_view_at_maturity
situated_medially_to_the_quadrate_condyle_in_dorsal_view_at_maturity;

{204 Frontal_ending_at_the_same_level_or_posterior_to_the_anterior_extension_of_the_prefrontal
extends_well_anterior_to_the_anterior_extension_of_the_prefrontal;

{205 Maxilla_posterior_process_without_tooth_in_ventral_view short_or_absent
long_longer_than_the_distance_between_the_three_last_teeth_;

{206 Interorbital_bridge narrower_to_equivalent_than_the_width_of_the_orbit
broader_than_the_width_of_the_orbit;

{207 Supratemporal_fenestra_at_maturity
longer_than_wide_or_rounded,_posterior_bar_of_supratemporal_fenestra_thick_
wider_than_long,_posterior_bar_of_supratemporal_fenestra_thick_
wider_than_long,_posterior_bar_thin_;

{208 Medial_crest_on_the_basioccipital present absent;

{209 Posterior_dentary_process_between_splénial_and___angular_on_the_ventral_side absent
present;

{210 Dorsal_margin_of_the_articular_on_the_retroarticular_process_
largely_visible_in_lateral_view slightly_or_not_visible_in_lateral_view_;

{211 Posterior_margin_of_the_orbit_measured_at_the_level_of_the_postorbital-
frontal_suture_in_the_orbital_margin_
_anterior_to_the_posterior_margin_of_the_suborbital_fenestra
posterior_or_at_the_same_level_than_the_posterior_margin_of_the_suborbital_fenestra;

{212 Basioccipital-
exoccipital_process_ventral_to_occipital_condyle_(basioccipital_plate)_in_posterior_view
with_parallel_or_ventrally_convergent_sides_ventrally_divergent_sides_;

{213
Smooth_medial_depression_ventral_to_the_basioccipital_and_posterior_to_the_medial_Eustachian
_foramen absent present;

{214 Dentary_teeth_series_behind_to_alveoli_12-13_pointed_to_slightly_blunt
globular,_different_in_size_among_them_globular,_at_least_four_subequal_in_size_
molariform_multicusped absent;

{215 First_four_alveoli_in_the_dentary same_size_or_smaller_than_other_dentary_alveoli_
the_largest_within_the_dentary_;

{216 Obits_late_in_ontogeny longer_than_wide_wider_than_long_to_rounded_;

{217 The_series_composed_by_the_last_three_premaxillary_teeth_diverge_posteriorly_to_paraxial
tend_to_converge_posteriorly,_straight_among_them_;

```
{218 Dentary,_level_of_the_first_and_fourth_alveoli  
lower_than_the_level_of_the_eleventh_and_twelfth_alveoli_  
equal_to_higher_than_the_level_of_the_eleventh_and_twelfth_alveoli;  
;
```

```
ccode + 38 47 61 80 123 148 150 153 158 192 202 *;
```

```
proc /;  
comments 0  
;
```

4. Dataset: Walter et al., supplementary dataset (modified Chabrol et al. (2024); continuous and discrete characters; .tnt)

nstates cont;

nstates 32 ;

xread 'Data saved from TNT'

330 156

&[cont]

Bernissartia_fagesii 0.494 1.272 ? ? ? 0.173 ? 0.870 7.000 0.375 0.717 ? ? ? ?
 ? 16.000 ? ? ? 60.000 ? ? ? ? ?

Isisfordia_duncani 0.646 1.482 0.657 0.180 0.093 0.232 0.362 0.823 0.000 0.525 0.663 0.346
 0.421 1.016 3.650 1.918 ? ? ? ? 30.000 ? ? 0.754 1.112 ?

Acynodon_iberoccitanus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 13.000 ? ? ? ? ? ? ? ? ?

Agaresuchus_fontisensis 0.534 1.366 1.375 0.420 0.287 0.308 0.576 0.595 ? 0.591 0.921
 0.191 0.430 1.379 3.259 ? 15.000 ? ? ? ? ? ? ? ? ?

Allodaposuchus_precedens 0.563 1.778 1.700 0.254 0.388 0.388 ? 0.794 11.000 0.529 0.913
 0.129 0.366 ? 2.900 ? 14.000 ? ? ? ? ? ? ? ? ?

Glen_Rose_form ? ? ? ? ? 0.147 ? 0.699 9.000 0.525 0.598 ? 0.533 0.308
 2.858 2.421 11.000-12.000 ? ? ? ? ? ? ? ? ?

Hylaeochampsia_vectiana ? 1.517 ? ? ? 0.328 ? 1.052 0.000 0.410 0.560 ? 0.250
 0.846 ? 2.333 ? ? ? ? ? ? ? ? ?

Iharkutosuchus_makadii 0.428 1.292 1.500 0.344 ? 0.257 ? 0.667 18.000 ? ? ?
 0.295 1.219 ? 1.664 13.000 ? ? ? ? ? ? ? ? ?

Lohuecosuchus_megadontos 0.482 1.579 1.667 0.296 ? 0.428 ? 0.693 5.000 0.420 0.824
 0.171 0.516 0.684 3.364 ? 10.000-11.000 ? ? 1.122 ? ? ? ? ?

Portugalosuchus_azenhae ? 1.074 ? ? ? 0.224 ? 0.595 0.000 0.705 0.903 ? 0.354
 1.222 ? ? ? 2.333 36.000 ? ? ? ? ? ? ?

Shamosuchus_djadochtaensis ? 0.824 ? ? 0.425 0.241 0.503 0.597 0.000 0.535 0.800 ?
 ? ? 3.878 2.607 ? ? ? ? ? ? ? ? ?

Wannchampsus_kirpachi ? ? ? ? ? ? ? ? 0.733 0.000 0.651 0.537 ? ? ?
 2.769 1.375 11.000 ? ? ? ? ? ? ? ? ?

Acresuchus_pachytemporalis 0.535 2.529 1.134 0.264 0.189 0.337 0.687 0.798 15.000 0.518
 0.488 0.147 ? ? ? 1.389 11.000 1.373 38.000 1.088 ? ? ? ? ?

Aktiogavialis_caribesi ? 0.787 ? ? ? 0.283 ? 0.657 12.000 0.640 0.794 ? 0.386
 1.130 ? 1.767 19.000 ? ? ? ? ? ? ? ? ?

Alligator_mcgrewi 0.444-0.478 1.495-1.518 1.291-1.429 0.242 ? 0.220-0.230 0.399-0.489
 0.679-0.788 8.000 0.425-0.496 0.738-0.829 0.203-0.217 0.530 1.667 2.147 ? 13.000 1.912-
 3.169 20.000 1.163 54.000 ? ? ? ? ?

Alligator_mefferdi 0.524 1.803 1.324 0.328 ? 0.355 0.491 0.750 4.000 0.368 1.074 ? ?
 1.438 2.622 1.750 14.000 1.914 38.000 1.158 ? ? ? ? ? ?

Alligator_mississippiensis 0.579-0.586 2.000-2.021 1.421-1.475 0.466 0.288 0.322-0.341 0.479-
 0.578 0.711-0.835 11.000 0.408-0.453 0.793-0.862 0.154-0.157 0.380 0.947-1.000 3.330
 1.607-2.048 15.000 2.200-2.618 11.000 1.174-1.391 24.000 0.832 0.592 0.687-0.783 1.070-
 1.159 0.492

Alligator_olseni 0.481 1.865 1.257 ? ? 0.320 ? 0.763 8.000 0.586 0.931 ? ? ?
 3.330 1.342 15.000 2.925 19.000 1.193 37.000 ? ? ? ? ?

Alligator_prenasalis 0.554-0.555 1.656-1.781 1.230-1.515 ? ? 0.278-0.308 0.532-0.617
 0.669-0.755 7.000 0.516-0.604 0.711-0.737 0.213 ? ? ? ? 14.000 2.017-2.533 22.000
 1.229-1.252 24.000 0.914 0.507 0.739 1.220 ?

Alligator_sinensis 0.575 1.960 1.563 0.383 0.275 0.320 0.429 0.747 10.000 0.464 0.808 0.163
 0.471 1.267 2.326 1.950 13.000 2.059 21.000 1.154 17.000 0.869 0.581 0.689-0.744 1.107-
 1.206 0.517

Hassiacosuchus_haupti 0.417-0.538 1.778 1.333 ? ? 0.311 0.706 0.756 ? 0.500 0.643-
 0.706 ? ? ? ? ? 14.000 1.412-1.500 46.000 1.250 65.000 ? ? 0.941 1.490 ?

Navajosuchus_mooki 0.480-0.506 ? 0.867 ? ? ? ? ? ? ? 0.625 ? ? ? ?
 ? 14.000 1.550 21.000 ? ? 0.730 0.671 0.764 ? ?

Allognathosuchus_polyodon ? ? 1.273 ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? 1.605 ? ? ? ? ? ?

Allognathosuchus_wartheni 0.472 ? 1.129 ? ? ? 0.718 ? ? 0.540 ? 0.161 ? ?
 ? 1.625 12.000 1.088 38.000 ? ? ? ? ? ? ?

Arambourgia_gaudryi 0.376 1.270 1.400 ? ? 0.216 0.370 0.730 0.000 0.481 0.846 ? ?
 1.333 ? 1.833 ? ? 31.000 ? ? ? ? ? ? ?

Argochampsa_krebsi ? 1.143 ? 1.237 0.409 0.304 ? 0.804 6.000 0.533 0.875 ? ?
 0.933 ? 1.813 26.000 ? ? ? ? ? ? ? ?

Asiatosuchus_germanicus 0.547 1.727 1.444 ? ? 0.410 0.436 0.791 16.000 0.327 0.806 ?
 ? ? ? ? 14.000 2.167 23.000 ? 23.000 0.775 0.606 0.761 1.391 ?

Asiatosuchus_nanlingensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? 0.911 ? ? ? ? ? ?

Australosuchus_clarkae 0.526-0.552 1.906-2.033 0.988 ? 0.167 0.200-0.258 0.650 0.851-
 0.875 7.000 0.340-0.482 0.593-0.971 0.196 0.263 ? ? ? 14.000-15.000 ? ? ? ?
 ? ? ? ? ?

Baru_darrowi ? ? 1.154 ? 0.517 ? ? ? ? ? ? 0.210 0.382 ? ? ?
 13.000 ? ? ? ? ? ? ? ? ?

Baru_huberi ? ? 1.010 ? 0.242 ? ? ? ? ? ? 0.202 ? ? ? ? ? ?
 ? ? ? ? ? ? ? ?

Baru_wickeni ? ? 0.839 ? 0.409 ? ? ? 15.000 ? ? 0.167 0.437 ? ? ?
 12.000 1.736-1.790 ? 1.553-1.690 ? ? ? ? ? ?

Borealosuchus_acutidentatus 0.603 1.237 1.200 ? ? 0.203 ? 0.619 0.000 0.545 0.949 ?
 ? ? ? ? 20.000 ? ? ? ? ? ? ? ? ? ?

Borealosuchus_formidabilis 0.646 1.171 1.224 ? ? 0.200 ? 0.514 0.000 0.550 1.020
 0.241 0.335 0.702 2.667 1.308 20.000 1.728 36.000 ? 55.000 1.033 0.527 ? 1.080 0.556

Borealosuchus_sternbergii 0.574-0.600 1.257-1.552 1.152-1.471 0.110 0.276-0.296 0.261-
 0.308 0.341-0.529 0.637-0.759 0.000-5.000 0.443-0.651 0.700-0.968 0.209-0.432 0.302-0.376
 0.750-0.833 2.595 1.641-1.650 19.000 2.789-3.611 21.000-24.000 1.059 ? ? ? 0.705 ?
 ?

Borealosuchus_threensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 ? ? ? ? ? ? ? ? ? ?

Borealosuchus_wilsoni 0.604 ? 0.867 0.321 ? 0.455 0.904 0.548 ? 0.592 1.302 ? ?
 ? ? ? 18.000 ? ? 1.846 60.000 ? ? 0.710 1.231 0.377

Bottosaurus_harlani ? ? ? ? ? 0.290 1.008 0.533 8.000 0.482 0.896 ? ? ? ?
 ? ? 1.284 27.000 ? ? ? ? ? ? ?

Boverisuchus_magnifrons ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
 17.000 ? ? ? ? ? ? ? ? ? ?

Boverisuchus_vorax 0.584 1.453 0.891 0.157 ? 0.471 0.633 0.754 9.000 0.520 0.565 0.259
 0.418 1.106 ? ? 17.000 ? ? ? 13.000 ? 0.679 0.870 1.408 0.458

Brachychampsia_montana 0.583 2.522 0.885-1.000 0.088 0.163 0.402 0.721 0.935 14.000 0.512
 0.773 0.331 0.476 1.257 2.956 2.240 14.000 2.024 12.000 1.177 30.000 ? ? ? 1.160 ?

Brochuchus_pigotti 0.658 1.765 0.931 0.397 0.282 0.382 0.492 0.897 6.000 0.377 0.783 0.184
 0.351 1.250 2.133 1.348 14.000 ? 21.000 ? ? ? ? ? ? ?

Caiman_brevirostris ? ? ? ? 0.308 ? ? ? ? ? ? ? ? ? ? ? ? 1.867 ?
 ? ? ? ? ? ? ? ? ?

Caiman_crocodilus 0.512-0.623 1.257-1.528 1.000-1.698 0.309-0.457 ? 0.214-0.303 0.554-
 0.671 0.584-0.760 5.000-15.000 0.273-0.432 0.775-0.862 0.159-0.219 0.339-0.481 1.339-
 1.693 2.126 1.409-1.433 14.000-17.000 1.773-1.905 21.000-33.000 1.162-1.661 18.000 ?
 0.530 0.771-0.803 1.100-1.282 0.636

Caiman_gasparinae ? ? 1.220 0.763 0.470 0.447 ? 0.772 14.000 0.261 0.739 ? ? ?
 ? ? ? ? ? ? ? ? ? ? ?

Caiman_latirostris 0.539 2.195 1.343 0.355-0.653 0.304 0.341 0.685 0.659 8.000-9.000 0.259
 0.786 0.178 0.508 2.000 2.581 1.571 13.000 1.513 30.000 1.317 ? 0.814 0.608 0.754-0.757
 ? 0.538

Caiman_lutescens_MACN ? ? ? ? ? 0.462 ? 0.598 13.000 0.304 0.417 ? ? ?
 ? ? ? ? ? ? ? ? ? ? ?

UCMP_39978 ? ? 1.064 0.202 0.280 ? ? ? ? ? ? ? 0.187 0.450 2.077 2.294
 ? 13.000 ? ? ? ? ? ? ? ? ?

Caiman_wannlangstoni 0.479 1.333 ? ? ? 0.314 ? 0.726 7.000 0.346 0.769 ? ? ?
 ? ? 12.000 ? ? ? ? ? ? ? ? ?

Caiman_yacare 0.567-0.579 1.575-1.595 1.115-1.208 0.269-0.318 0.333-0.366 0.325-0.329
 0.686 0.646-0.663 2.000-11.000 0.349-0.353 0.667-0.692 0.177 0.385-0.406 1.941-2.063
 2.316 1.348 14.000 1.618 23.000-37.000 1.342 0.000 ? ? 0.733-0.791 1.058-1.311 ?

Ceratosuchus_burdoshi 0.529 1.733 0.938 ? ? 0.343 ? 0.717 ? 0.614 1.034 0.339 ?
 ? ? 1.436 14.000 ? ? ? ? ? ? ? ? ? ? ?

Crocodylus_acutus 0.639 1.678 0.718 0.704 0.422 0.533 0.347 0.833 15.000 0.440 0.818 0.186
 0.394 1.333 2.535 1.464 14.000 1.741 33.000 1.511 17.000 ? ? 0.712-0.741 1.041-1.121 ?

Crocodylus_affinis 0.575-0.606 1.612-1.726 0.833-1.098 0.310-0.314 0.390 0.189-0.658 0.512-
 0.632 0.553-0.777 2.000-8.000 0.452-0.480 0.988-1.055 0.218 0.239-0.443 0.789-1.381 3.464
 1.460-1.546 13.000-14.000 1.930-2.150 41.000 1.371-1.491 33.000 ? 0.557 ? ? ?

Crocodylus_anthropophagus ? ? 0.843 ? ? ? ? ? ? ? ? 0.195 ? ? ?
 ? 14.000 1.166 23.000 ? 23.000 ? ? ? ? ?

Asiatusuchus_depressifrons 0.561 1.518 1.227 0.363 0.375 0.301 0.554 0.675 8.000-13.000
 0.518 0.862 ? ? ? ? 1.579 14.000 1.700 31.000 ? 17.000 ? ? 0.779 1.084 ?

Crocodylus_intermedius 0.644-0.653 1.393-1.432 0.656-0.889 0.747 0.417 0.423-0.493 0.417-
 0.544 0.757-0.832 3.000 0.357-0.465 0.931-1.067 0.203-0.286 0.282-0.320 1.304-1.550 2.525
 1.300-1.389 14.000 1.929-2.011 34.000 1.665 ? ? ? ? ? ?

Crocodylus_johnstoni 0.686 1.138 0.815 0.498 0.421 0.294 0.524 0.688 4.000 0.547 0.841
 0.265 0.275 1.085 2.487 1.404 14.000 2.117 25.000 1.877 14.000 1.014 0.468 0.690-0.729
 1.116-1.192 0.432

Crocodylus_megarhinus 0.662 2.193 0.700-0.807 0.419-0.429 0.416 0.307 0.505 0.887 7.000-
 8.000 0.360 0.850 0.161-0.348 ? ? 2.393 1.548 13.000 1.947 ? ? ? ? ? ? ?
 ?

Crocodylus_mindorensis 0.548 1.495 0.703 0.511 ? 0.276 0.406 0.838 12.000-16.000 0.474
 1.054 0.185 0.377 0.706 2.535 1.562 13.000 2.013 33.000 1.847 ? ? ? ? ? ?

Crocodylus_moreletii 0.603 2.255 0.830 0.629 0.455 0.519 0.463 0.896 11.000 0.432 0.829
 0.125 0.415 0.640 2.067 1.719 14.000 1.366 30.000 1.367 ? ? ? 0.715-0.719 1.035-1.106
 ?

Crocodylus_niloticus 0.567-0.613 1.737 0.826 0.491 0.424 0.495 0.341 0.859 5.000 0.494
 0.619 0.169 0.342 1.143 2.285 1.563 13.000-14.000 1.257 33.000 1.310 20.000 0.822-0.949
 0.431-0.489 0.660-0.771 1.116-1.174 0.524-0.633

Crocodylus_novaeguineae 0.602 1.446 0.833 0.544 0.361 0.357 0.362 0.839 12.000 0.489
 0.870 0.171 0.355 1.000 2.105 1.211 13.000-14.000 1.467 33.000 1.111 ? ? ? 0.721
 1.227 ?

Crocodylus_palustris 0.533-0.601 2.087 0.850-0.873 0.579-0.863 0.365 0.470 0.410 0.904
 3.000 0.471 0.592 0.229 0.457 2.769 2.000 ? 14.000-15.000 1.205 40.000 1.097 19.000 0.942
 0.551 0.722-0.730 1.059-1.174 0.460

Crocodylus_porosus 0.602-0.634 1.967-2.008 0.768-1.051 0.648-0.667 0.403-0.412 0.348-
 0.519 0.420-0.437 0.820-0.908 9.000-14.000 0.410-0.413 0.653-0.902 0.108-0.114 0.403-
 0.449 1.783-2.000 2.159 1.217-1.265 14.000 1.469-1.649 36.000 1.095-1.121 17.000 0.921
 0.476 0.581-0.692 1.090-1.125 0.547

Crocodylus_rhombifer 0.558-0.625 1.646 0.769 0.151-0.333 ? 0.441 0.347 ? 7.000-15.000
 0.373 0.698-0.875 0.191 0.466 1.382 2.805 1.742 13.000-14.000 1.928 30.000 1.158 19.000
 0.825 0.470 0.726-0.784 1.221-1.314 0.573

Crocodylus_siamensis 0.581-0.614 1.723-1.853 0.837-0.953 0.549 0.287-0.291 0.475-0.547
0.324-0.375 0.733-0.758 12.000 0.432-0.500 0.806-0.906 0.189-0.190 0.409-0.434 1.389-1.571
1.962 1.433-1.500 14.000 1.467 38.000 1.302 12.000 0.885 0.495 0.736 1.120 ?

Crocodylus_thorbjarnarsoni 0.595 1.913 1.034 0.175 0.427 0.501 0.482 0.834 12.000 0.423
0.933 0.126 0.513 1.900 2.773 ? 13.000 1.433 37.000 1.248 ? ? ? ? ? ?

Crocodylus_palaeindicus 0.554-0.573 1.690-1.750 0.900-1.260 0.780-1.157 0.265-0.411 0.439-
0.473 0.333-0.397 0.771-0.793 10.000-14.000 0.299-0.415 0.759-1.043 0.151-0.221 0.422-
0.457 1.600 1.604 1.692-1.909 11.000 1.379 ? 1.486 ? ? 0.520 ? ? ?

Crocodylus_chechchiae 0.610 1.810 0.880 0.530 0.260 0.540 0.460 0.770 11.000-13.000 0.370
0.840 0.180 0.400 1.600 ? 1.570 12.000-14.000 1.100 27.000 ? ? ? ? ? ? ?

Crocodylus_falconensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

Prodiplocynodon_langi 0.556 1.804 0.881 0.304 ? 0.296 0.507 0.542 ? 0.478 0.896 0.289
0.451-0.460 0.821 2.327 1.354 ? ? ? ? ? ? ? ? ? ?

Albertosuchus_knudsenii ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

Orientalosuchus_naduongensis 0.549 ? 1.066 ? ? 0.207-0.241 0.261 1.335 ? 0.393
1.260-1.563 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Dongnanosuchus_hsui 0.455-0.507 1.575 1.027-1.333 0.319 ? 0.236 0.375 0.701 ? 0.360-
0.397 1.111-1.478 0.255 0.291-0.416 ? 2.586 1.620 ? ? ? ? ? ? ? ? ? ?

Kinyang_mabokoensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

Dadagavialis_gunai ? 0.938 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 22.000
? ? ? ? ? ? ? ? ?

Krabisuchus_siamogallicus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

Protoalligator_huiningensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

Eurycephalosuphus_gannanensis 0.589 ? 1.653 ? ? ? ? ? ? ? 0.563 1.045 ?
0.404 ? ? ? ? 0.690 ? ? ? ? ? ? ? ?

Diplocynodon_darwini 0.479-0.618 1.386-1.424 1.000 0.446-0.623 ? 0.203-0.228 0.481-
0.740 0.877-0.915 1.000-6.000 0.407-0.511 0.667-0.833 ? 0.364 1.000 2.378 ? 18.000
2.818 43.000 ? 53.000 ? 0.443 0.716-0.890 1.077-1.198 ?

Diplocynodon_deponiae 0.455-0.484 ? 0.917 ? ? ? ? ? ? 2.000 0.400-0.500 0.333-
0.545 ? ? ? 3.231 ? 16.000 ? ? ? ? ? ? ? 0.750-0.789 1.200-1.531 ?

Diplocynodon_hantoniensis 0.566-0.680 1.908-1.970 0.773-1.076 0.141-0.226 0.296-0.333
0.265-0.293 0.635-0.723 0.968-1.010 9.000-10.000 0.550-0.564 0.551-0.591 0.216-0.249
0.392-0.464 0.918-0.962 3.258 1.713-1.905 17.000 1.857-2.138 44.000-45.000 1.466 37.000-
47.000 ? ? ? ? ?

Diplocynodon_muelleri 0.507 1.721 ? ? ? 0.233 ? 0.965 0.000 0.518 0.558 ? ? ?
? ? 20.000 ? ? ? 48.000 ? ? ? ? ?

Diplocynodon_ratelii 0.586 1.485 1.037 0.130 ? 0.265 0.625 0.824 8.000-9.000 0.429 0.792
? 0.349 1.067 3.543 1.533 16.000 ? ? ? 47.000 ? 0.430 ? ? ?

Diplocynodon_remensis ? ? ? ? ? 0.244 ? ? ? ? 0.667 ? ? ? ? ?
17.000 2.211 30.000 1.316 ? ? ? ? ? ?

Dollosuchoides_densmorei 0.668 1.225 0.813 0.385 ? 0.285 0.650 0.795 0.000 0.646 1.071
0.378 0.350 1.063 3.174 ? 15.000 ? ? ? ? ? ? ? ?

Eocaiman_cavernensis ? ? ? ? ? ? ? ? ? ? ? ? ? 0.633 ? ? ?
14.000 1.833 28.000 ? ? ? ? ? ? ?

Eocaiman_palaeocenicus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
1.556 24.000 1.202 ? ? ? ? ? ?

Eogavialis_africanum 0.693-0.725 0.857-1.118 0.909-1.128 0.620-0.823 0.518 0.247-0.308
0.359-0.604 0.604-0.882 7.000-16.000 0.440-0.661 0.974-1.129 0.091 0.357-0.358 1.026-1.417
? 1.433-1.886 20.000 ? 21.000 ? ? ? 0.374 ? ? 0.485

Eosuchus_lerichi 0.653 ? 0.815 ? ? ? 0.576 ? 0.000 0.576 0.868 0.250 0.410 1.733
3.646 1.524 16.000-17.000 ? ? ? ? ? ? ? ? ?

Eosuchus_minor 0.657 ? ? ? ? ? ? ? ? 1.000-5.000 ? ? ? ? ? ? ?
17.000 ? 23.000 ? ? ? ? ? ? ?

Eothoracosaurus_mississippiensi 0.689 0.955 1.030 ? ? 0.318 0.433 0.577-0.656 5.000
0.547-0.571 0.938-1.079 ? ? ? ? 1.936 22.000 ? ? ? ? ? 0.288 ? ? ?

Euthecodon_arambourgi 0.748 1.608 0.966 0.590 ? 0.304 0.486 0.886 1.000 0.443 0.806
0.091 ? ? ? 15.000 ? ? ? ? ? ? ? ? ?

Gavialis_browni ? 0.853 ? ? ? 0.441 0.550 0.588 10.000 0.568 1.216 ? 0.481 ?
2.222 ? 18.000 ? ? ? ? ? ? ? ? ?

Gavialis_gangeticus 0.716-0.727 0.799-0.892 0.719-1.045 0.429 0.581-0.605 0.387-0.496
0.503-0.550 0.555-0.677 6.000 0.543-0.622 1.113-1.195 0.105-0.118 0.465-0.589 1.500-2.357
3.256 1.490-1.932 23.000-24.000 1.905-2.318 23.000 1.887-2.148 40.000 1.020 0.436-0.485
0.553-0.614 1.132-1.189 0.723-0.838

Gavialis_lewisi ? 0.974 ? ? ? 0.346 0.200 0.789 8.000 0.497 0.940 ? 0.427 5.496
2.523 2.510 ? ? 33.000 ? ? ? ? ? ? ?

Gavialosuchus_eggenburgensis 0.676 1.382 0.904 ? 0.577 0.274 0.579 0.682 11.000 0.579
1.032 ? ? ? ? 1.385 15.000 ? ? ? ? ? ? ? ?

Globidentosuchus_brachyrostris ? ? ? ? ? ? ? ? 0.759 14.000 0.245 0.815 ? ?
? ? ? ? ? ? ? ? ? ? ? ? ?

Gnatusuchus_pebasensis 0.450 2.115 ? ? ? 0.165 ? 0.921 5.000 0.319 0.700 ? ?
? 3.520 ? 9.000 ? ? ? ? ? ? ? ?

Gryposuchus_colombianus ? 0.850 ? ? ? 0.313-0.375 ? 0.563-0.631 8.000 ? ?
? 0.466 ? ? ? 21.000 1.389-2.125 ? 1.469 ? ? ? ? ?

Gryposuchus_croizati ? ? 1.258 0.548 ? ? ? ? 27.000 ? ? ? ? ? ?
2.133 19.000 ? ? ? ? ? ? ? ?

Gryposuchus_neogaeus 0.787 ? 1.143 0.665 0.527 0.289 ? 0.483 8.000 0.675 1.266 0.080
? ? ? 1.667 ? 2.581 18.000 ? ? ? ? ? ?

Gryposuchus_pachakamue ? 0.840 0.959 0.413 0.636 0.291-0.344 ? 0.664-0.782 19.000-29.000 0.564-0.693 1.065-1.144 ? 0.434-0.502 1.448 ? ? 22.000 1.859 29.000 ? ? ? ? ? ? ? ?

Ikanogavialis_gameroi ? 1.140 ? ? ? 0.240 0.923 0.520 15.000 0.654 1.294 ? 0.400 ? ? 1.471 30.000 ? ? ? ? ? ? ? ? ? ?

Jiangxisuchus_nankangensis 0.551 1.434 ? ? ? 0.217 0.531 0.603 7.000 0.617 0.852 0.324 ? ? 2.733 ? 14.000 ? ? ? ? ? ? ? ? ? ?

Kambara_implexidens ? 1.256-1.466 0.820 0.427 ? 0.195-0.239 0.332-0.399 0.839-0.894 2.000 0.399-0.415 0.773-0.791 0.274 ? 0.966 ? 1.484 15.000 2.592 15.000 ? ? ? ? ? ? ? ?

Kambara_murgonensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 16.000 ? ? ? ? ? ? ? ? ? ?

Kambara_taraina ? ? ? ? ? ? ? 0.878 7.000-11.000 0.419 0.722 ? ? ? 2.793 ? 14.000 ? ? ? ? ? ? ? ? ? ?

Kentisuchus_spenceri ? 1.022-1.395 0.875 ? ? 0.271-0.322 ? 0.722-0.752 3.000-16.000 0.509-0.583 0.889-1.080 ? 0.341 0.969 ? 1.421-1.706 13.000 1.462 ? ? ? ? ? ? ? ?

Kuttanacaiman_iquitosensis ? 1.840 0.662 0.344 ? 0.203 ? 0.640 9.000 0.409 ? ? ? 1.667 1.634 ? 13.000 ? ? ? ? ? ? ? ? ? ?

Leidyosuchus_canadensis 0.596-0.615 1.710 1.079 0.121 ? 0.215 0.556 0.581 ? 0.648 0.629 0.323 0.487-0.494 0.941-1.176 3.333 1.696 18.000 ? 30.000 ? ? ? ? ? ? ? ?

Mecistops_cataphractus 0.670 1.458 0.938 0.500 0.515 0.361 0.553 0.916 8.000 0.447 0.794 0.282 0.314 1.625 1.785 1.333 13.000 1.964 32.000 1.705 23.000 1.057 0.410 0.717-0.740 1.144-1.203 0.510

Mekosuchus_inexpectatus ? ? 1.000 0.119 ? ? ? ? ? ? ? ? ? ? ? 1.486 ? 2.250 55.000 1.040 ? ? ? ? ? ? ?

Mekosuchus_sanderi ? ? ? ? ? 0.409 ? 0.536 ? 0.487 0.548 ? ? ? ? 1.900 ? ? ? ? ? ? ? ? ? ?

Mekosuchus_whitehunterensis ? 2.000 35.000 ? ? ? ? ? ? ? ?

Melanosuchus_niger 0.495 2.090 0.953 0.641 0.281 0.320 0.550 0.820 17.000 0.180 0.722 0.156 0.534 2.762 2.366 1.326 13.000-14.000 1.485 47.000 1.253 7.000 0.767 0.481 0.711-0.761 1.241-1.297 0.603

Maroccosuchus_zennaroi ? ? 1.140 0.531 0.427 0.312 ? 0.594 0.000-11.000 0.614 1.194 ? ? ? ? ? 14.000 2.043 22.000 1.295 ? ? ? ? ? ? ?

Mourasuchus_amazonensis 0.745 3.178 2.057 0.340 ? 0.434 1.046 0.704 0.000 0.211 0.579 0.332 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Mourasuchus_arendsi ? 3.140 ? ? ? 0.420-0.482 ? 0.570-0.691 ? 0.215-0.276 0.810-0.857 ? ? ? 1.922 1.528-2.000 ? ? ? ? ? ? ? ? ? ?

Mourasuchus_atopus ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 5.750 3.152 ? ? 2.500 ? 1.250 10.000 ? ? ? ? ?

Necrosuchus_ionensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? 0.502 0.763 1.141 0.363

Osteolaemus_tetraspis 0.523-0.558 1.531-1.673 1.277-1.364 0.397 0.325 0.250-0.282 0.256-0.317 0.634-0.745 0.000 0.222-0.259 0.717-1.000 0.047-0.149 0.350-0.381 1.617-2.000 1.675 1.714-1.733 12.000 1.487-1.615 39.000 1.350-1.667 2.000 0.761-0.770 0.504-0.569 0.739-0.786 1.133-1.228 0.406-0.444

Paleosuchus_palpebrosus 0.544 1.210 0.674 0.306 ? 0.275 0.397 0.824 0.000 0.000 ? 0.156 0.419 2.400 2.121 1.261 14.000-15.000 2.272 31.000-39.000 1.250 20.000 0.758-0.791 0.507-0.651 0.750-0.821 1.260-1.300 0.590-0.599

Paleosuchus_trigonatus 0.549-0.592 1.238-1.328 1.030-1.143 0.274-0.366 0.400 0.236-0.279 0.390-0.500 0.754-0.837 0.000-3.000 0.000 ? 0.203-0.205 0.433-0.460 1.308-2.105 2.121 1.267-1.400 15.000-16.000 2.478 29.000-31.000 1.438 32.000 0.715 0.636 0.770-0.776 1.246-1.273 0.553

Paratomistoma_courti ? ? ? ? ? 0.263 ? 0.688 6.000 0.511 0.982 ? ? ? ? 1.264 ? ? ? ? ? ? ? ? ? ?

Penghusuchus_pani 0.683 1.392 ? ? 0.313 0.289 ? 0.597 15.000 0.543 1.083 ? 0.350 1.175 2.925 1.727 16.000 ? ? ? ? 0.788 0.488 0.610 1.206 0.602

Piscogavialis_jugaliperforatus 0.766 1.086 1.371 0.775 ? 0.223 0.486 0.800 12.000 0.479 1.030 0.038 0.300 1.119 3.476 1.538 28.000 ? 13.000-24.000 ? ? ? 0.356 ? ? ?

Planocrania_datangensis 0.596 1.016 1.050 ? ? 0.444 ? 0.683 ? 0.628 0.741 ? ? ? ? ? 18.000 ? ? ? ? ? ? ? ? ?

Planocrania_hengdongensis 0.519 ? ? ? ? 0.233 0.400 0.713 ? 0.457 0.653 ? ? ? ? 2.125 ? ? ? 1.083 ? ? ? ? ? ?

Procaimanoidea_utahensis 0.485 ? 0.900 0.184 ? 0.218 ? 0.909 ? 0.663 0.482 0.174 ? 0.890 ? ? 13.000 ? 18.000 ? ? ? ? ? ?

Protocaiman_peligrensis ? ? ? ? ? 0.259 ? 0.634 12.000 0.538 0.749 ? ? ? ? ? ? ? ? ? ? ? ?

Purussaurus_brasiliensis 0.630 2.381 0.696 0.262 0.367 0.540 1.121 0.524 1.000 0.576 0.663 0.268 0.631 4.800 ? 1.684 14.000 2.167 ? 1.000 13.000 ? ? ? ? ?

Purussaurus_mirandai ? ? ? ? ? ? ? ? ? ? ? ? 0.400 ? ? ? 14.000 ? ? ? ? ? ? ? ?

Purussaurus_neivensis 0.549 2.136 0.654 0.368 0.279 0.403 0.929 0.757 0.000 0.410 0.563 0.153 0.427-0.500 3.600-5.000 2.239 1.702 14.000 ? 20.000 1.154 13.000 ? ? ? ? ?

Quinkana ? ? 1.167 0.500 0.486-0.500 ? ? ? ? ? ? ? ? ? ? 12.000-14.000 ? ? ? ? ? ? ? ?

Siquisiquesuchus_venezuelensis 0.730 1.045 ? ? ? ? ? 0.606 ? 0.650 1.038 ? ? ? ? ? ? ? ? ? ? ?

Stangerochampsia_mccabei 0.463 1.750 0.883 0.100 ? 0.243 0.687 0.718 5.000 0.682 0.708 0.298 0.477 1.953 3.367 ? 14.000 1.450 30.000 ? 37.000 ? ? 0.750 ? ?

Thecachampsia_antiquus ? 1.315 ? 0.617-0.676 ? 0.256 ? 0.717 11.000-12.000 0.402 1.242 ? ? ? ? ? 14.000 ? ? ? ? ? ? ? ?

Thecachampsa_sericondon 0.694 1.209 0.940 ? ? 0.233 0.506 0.761 15.000 0.518 1.000
0.238 0.433 0.960 3.538 ? 14.000 ? ? ? ? ? ? ? ? ? ?

Thoracosaurus_isorhynchus 0.734 0.970 0.735 0.282 ? 0.364 0.500 0.707 0.000-2.000 0.543
1.053 ? 0.293 1.455 ? 2.182 20.000 ? ? ? ? ? ? ? ? ? ?

Thoracosaurus_neocesariensis ? ? 1.091 0.844 ? 0.301-0.399 ? 0.609-0.634 8.000-
15.000 0.593-0.623 1.123-1.300 ? ? ? ? 1.313-1.604 ? ? ? ? ? ? ? ?
? ?

Tomistoma_cairense ? 1.205 ? ? ? 0.260 0.468 0.849 0.000 0.419 1.038 ? 0.363
0.909 3.692 1.350 ? ? ? ? ? ? ? ? ? ? ? ?

Tomistoma_dowsoni ? 1.347 0.758 ? 0.583 0.429 ? 0.857 0.000 0.536 0.844 ? ? ?
? 1.483 15.000 ? ? ? ? ? ? ? ? ? ?

Tomistoma_lusitanica 0.682 1.572 0.717 0.967 ? 0.250 0.511 0.761 0.000 0.511 0.900 ?
? ? ? ? 14.000 ? ? ? ? ? ? ? ? ? ?

Maomingosuchus_petrolica 0.697-0.723 0.872-1.111 0.750-0.805 0.196 ? 0.308-0.333
0.667-0.714 0.667-0.808 3.000-9.000 0.476-0.567 0.833-0.882 ? ? 0.820 ? ? 15.000
? 21.000 ? 31.000 ? ? ? ? ? ?

Tomistoma_schlegelii 0.666-0.670 1.217-1.655 0.704-0.907 0.800-0.835 0.636-0.720 0.293-
0.345 0.436-0.489 0.848-0.942 12.000-20.000 0.458-0.500 0.846-0.983 0.157-0.212 0.312-
0.456 0.632-1.207 2.472 1.464-1.756 17.000 2.308-2.500 20.000 1.568-1.878 44.000 0.931
0.394 0.640-0.710 1.071-1.224 0.659

Toyotamaphimeia_machikanensis 0.711 1.511 1.115 0.354 0.459 0.223 0.548 0.638 2.000
0.260 0.758 ? 0.302 1.181 3.815 1.452 16.000 2.077 24.000 1.500 40.000 0.852 0.569 0.531
? ?

Trilophosuchus_rackhami ? ? ? ? ? ? 0.282 ? 0.000 0.518 0.349 ? 0.329 ?
1.929 1.643 ? ? ? ? ? ? ? ? ? ? ? ?

Tsoabichi_greenriverensis 0.466-0.546 1.360-1.447 0.940-1.359 ? ? 0.252-0.257 0.350
0.929-1.040 ? 0.370 0.391 ? ? ? ? ? ? ? ? ? ? ? ? 0.745-0.851
1.312-1.542 0.593

Ultrastenos_willisi ? ? ? ? ? 0.215 ? 0.783 13.000-16.000 0.473 0.664 ? ? ?
2.615 1.642 ? ? ? ? ? ? ? ? ? ? ?

Voay_robustus 0.535 1.473 1.083 0.412 0.372 0.402 0.539 0.679 23.000 0.303 1.000 0.250
0.463 1.000 3.273 1.560 13.000 1.933 25.000 1.128 32.000 ? 0.617 ? ? 0.582

Wannaganosuchus_brachymanus 0.236 1.521 0.995 ? ? 0.271 ? 0.750 11.000 0.556
0.800 ? ? ? ? ? 13.000 ? ? ? 46.000 ? ? 0.812 1.293 0.538

Theriosuchus_pusillus ? 1.008 ? ? ? 0.220 ? 0.686 ? 0.600 0.875 ? ? 0.557
3.091 ? 13.000 ? ? ? ? ? ? 0.800 ? ?

Qianshanosuchus_youngi 0.463 1.096 0.500 0.250 0.571 0.290 0.464 0.735 2.000 0.480 0.583
0.277 0.423 ? ? ? ? ? 6.000 ? ? ? ? ? ? ? ?

Borealosuchus_griffithi ?
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Deinosuchus_riograndensis ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
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Bernissartia_fagesii

00000?00010?0?0000?000?100??120000?00??0011101??0000?0??00?101000?0100
0??0??1??0?0013000100????????0000?000030000000100?0??0000001?0100000000?0?0
001000010000?000????????0002100??0?00?000?01??011000000?0?????????????
??01?1?01001?00??1?100????0?00000000?0????????0?1100100

Acresuchus_pachytemporalis

000010100021101?00001010?01??0110010001??001?12012001001??11100020000011
01?110011100?101211100100?00110001001000100102000010000000??????1?????0??010000
?????????????0?0??1110??1?0?11021021?0001?00120200110?00001110000?11??0?????
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Acynodon_iberoccitanus

?00010100010??0000001010?1100?000010100??[0
1]010101??00000??011001?2??0?0??01??10021??????3?0?0?0?0??0??0??0??0000350001600001
00020000010?1110?0001000001?00?0?12?0??0?00000??1?????0?110?1000??0?10?000?
??0??0??0??
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Agaresuchus_fontisensis

000010000000??1000001000?001?0100010100??001110110100000??00?0111000?0??1
00?10001010??010?01001000000100110000?0100?320001000000001011010000?011010000??0?
011200000?00000000??1??????11021020?10?10?000??0?100?0?110110??000001?????
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Aktiogavialis_caribesi

00000?00010??1?000??0?0100??????1?0??001101110010001??0?0011?1?00?????
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2?0000?000?0011??0??????????3??????0????????????????????????????????????
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Albertosuchus_knudsenii

????????????1????01?11??????01101?0??????011110??0?0??1?0?0??00?000?
????1?0?0??0?00?0??0??0??02?000?20??11000200??????0??????????????11120??
?0??????0????????????11??00???
?1??1????????????????????????????????????

Alligator_mcgrewwi

00000?00010??0001000010?0101?1000000001?0000101200?[0
1]000010?21110101010001001?11002100011011010000000011000100000020003200[0
1]01000000001010011110011000001200001120111101100000?001110??1?001111220?1??1001
000111000011001001010000?011000100011100??1100000101?1????????200?1101??????
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Alligator_meffferdi

000010000010??1?01000010?0101?1200000001?1?00101200?1000010?211101010100010
01?11001100011012011000000001000100?000100032000010100000001010001??01100000120
0001120011??11000000?001110??1?1011001021??10001000120100010?11001011010?00000010?
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Alligator_mississippiensis

000010000010??100100001000101?120[0 1]000001110[0
1]0101200?100001[0 1]121110101000001001?110011000[0 1]101101100[0
1]00000110001001000100032000010100000010100010?101100001200001120011110000001
001110?11?1011001021??00011000120100010?11001111010?0010001000111001100[0
1]01000101111010110[0 1]0000010110111100011101100010102111100

Alligator_olseni

000010000010??1001000010?0110?12010000??0?00101200?0000010?2111010100000??
01?110011000??0110110?100000100??00?00010003200001000000001110?011?101?000001200
?01120011??10000000?????????????1111200?0??0001000120100010?01001111010?00?????????
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Alligator_prenasalis 00000??00010??0001000010?0101?1200000101?0?[0 1]010120101000[0
1]10?2111010100000??01?11001100011011011000000000100010[0
1]00002000320000100010000001100010?0[0
1]01000001200001120011101?000000???1?????????1111210?0??1001000120100010?0100101101
0?000?1??10?????????0000?1???1?????0??00??101101110010??????00??012111100

Alligator_sinensis 000010000010??1001000010?0101?120000000110000101200?10000101211101010000010
01?1100110001101101100000000010001001000100032000010000000000000110?100000000120
000112001111100000001001110?11?0011001121??00001000120100010?01001011010?00000010
1011100110100000011121??011011??00101101111210??1?1100011112111100

Allodaposuchus_precedens 000010000010??0000001000?001?0110000?001??001110110000000??201001100000010
000?10001010??0103010110000001001100000010000200011010?0000010000000?0110200000???
1011200111?00000001??1??????1??021?2????0??0?0?????????????????????????????????
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Allognathosuchus_polyodon 00000??00????0000001000?000?012010000????0?0?0????????????????????1000??0??
??00?000?200001??0?00?01?????0?????????????????????
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Allognathosuchus_wartheni 00000??00000?0?0000?01??0101?020100000????000??200?0000010??1?????10?????????
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Arambourgia_gaudryi 10000??00010??0?00001010?0110?1201000001000100?020100000110?211101010000???
01??0111000??011111000000000000010??0??0??200?01??1000?00?01?10????????????0?????
?1200?1??0?0?00?????????????01?021?????????0?11010001??010??11?0?????????????????????
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Argochampsa_krebsi 00000??00000??100001?101??00?01000000001??0011011100100010?210111?1111?0??0
00??10200000??00010000?1001111?010000120103701120000001010000?0000??000??01020?1
?11210000?0000?011??0??????????1??0?0????0?????1????00????101??1?1????????????????0??
??0100????1????????????????????0????????????????????001???

Asiatosuchus_depressifrons 00000??00010??10000010010000?01200000001??0000010110000010?01110100010100?
00111001100001000001000000000100000000011001310001001000010020000000?011010000020
010112001????1000?0?001111001?1111021110??10010?00110100001?00110011000?00?????????
?????1??1110000111?21??11110?0????000101110100?????????????????101???

Asiatosuchus_germanicus

00000?00010?0000001000?000?010000000?0?00001111?000010?0111010001000?0
???0011000010002010010000??1?0?0000000000100000010000100200?0000?0?1010000?????
??120??01?000????????????????1102110?1?0000?0011010000??10010?110??????????10????
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Asiatosuchus_nanlingensis

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??000????????????????????
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Australosuchus_clarkae

00000?00010?00000010010000?01000000001?0?000?101110000010?011?011100001??
1???0011100?110000?1000000000?00??0?0010013100011010?000001??0000??10000000200
1????????????????0?????1?????????11021020??100??001??100?01?0?0????????????????
1????????????????????????????????????101????????????????????101???

Baru_darrowi

00000?00????000001?0000000?0120000100????00101????????????1?100000?????
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1]00????011200????0?10??0????????????1??2112??10????001????00????????11????????
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Baru_huberi

00010?00????0?000010000?00?01?0000?0????????????????????????????????????
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Baru_wickeni

00010?00010?0000001000?001?0110000100????0010?1111000001?0?1??100010????
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01120011?00110000????????????11021120??1001?0?11010000110001001101100????????
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Borealosuchus_acutidentatus

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0?????10????0????1??0??0?????????001?001?300120000000?00110?0000????00??00??0????
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Borealosuchus_formidabilis

00000?00010?0?0001?000?000?01100000001001000?00110000001??0?1?010000000??
00??001100001011301000000000100010000011000330012001000001010000000?0110000000??
0011200101000000000????0????01002120?1?0000?00110100110?00101011000?00000?0?10
00001001100001011011??11110?00100100001000001????????????10002??

Borealosuchus_griffithi

00000?00010?000001?000?00000110100000????00000011??0001??1?1?01?000?01000
11?1?0?1????00?0?000??000010101?00001[0
1]0013300010010??0?0010?0000??101?0?1??11?1120?1??0?0?000????????????100210100
?00?00?001?010010?00001?11000????0????0???1??????0?010021?0?1?10?????1????????
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Borealosuchus_sternbergii

00000?00010?00000120000000?011000000010010000000100000010?01100100000000?
0001100110000101100100000000010001000001[0 1]001[0 3]3000100100000001[0 1]000000?[0
1]1100000012011011200100?00000000?001??0?00111002110?1??0000?00120100100?00100011
000?0??0?00??10101??0?0?0101?0?1????????00??000001000????????????????0002?0

Borealosuchus_threensis

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10021020?00????0?10120010?00?00011010?0????????0????????????????
1??1?????0????????????0????????????????????0002??

Borealosuchus_wilsoni

00000?00010?000001?001?????110000?????000?01010?0000??0?00?1?????0??0?
?????10?00?0??00?0?0?????????0?01?001?300020010000?????0?0?0?????????0??????1??
??010000??0????????????0?????????????????101100100?00?0?110?????0?0????????????
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Bottosaurus_harlani

????10000010????????????????????0000?0?1??001??211100100?????1?0002100????0??
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??????0??0??1??????????10210?????0????0011010011??01?0??1?00111????????????????
????1??1????????????0??10111110????????????????1?????

Boverisuchus_magnifrons

10?10?00010?000001000?00????00?0??0????0?1?0101??0000?????????1?0????0?00?
?????10??00000?1????????????????000000001030100001201000?1??0000??1111000?0?00??12
?0?0?0?1????0?????????????1102100????0????0?1????0?0????0????????????????????
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Boverisuchus_vorax

10010?00010?00000010000000?0100100000?0?1010020100000010?01110100000000?
0??10011000100010010010?0000100??000031000030100001201000010000000?0111100000200
001120010??000?000??1?????????1102110?0?0000?001??1?1??0?000010010?0????????0?
??1??110010??11?11????110?????001101110100????????????????101???

Brachychampsia_montana

00000?00010?0100010101?0101?1101000001?0?0000120111000011?1110101000000?
011110011000100111110000000010000020?013000310000100010000110100010?1001000001?0
00011200011010000000?0?1110?01?10110?1121??1?010?0?12010001?01001110000?0?????00
1110?101000?0011????????????000000010111?????????????????0241111??

Brochuchus_pigotti

00010?00010?0?00001000?000?1100000100????00101210?0000010?01110101000110?0
????00110010100020100000000100?00001001001210002001000001010000000?1010210000201
111120010??30100000??1110????0?110?102????0????0?1102000010????0?1??110????????????
?????1??????1??1????11?0?????001????11????????????????????111???

Caiman_brevirostris

010011100??0??1000001010?01?0?20001?0????001????????1????????????10????????
??0011????????1?????????00?000?????0?00?200?010?0100?000????????????????0?1000??12?
?1??????0?0?????????????????11001121??0001??001??????10??001????????????????????
?????1??1?????0??111???

Caiman_crocodilus 000011[0 1]00010??10000[0 1]10000001?0000000000110000100201[1
2]00100111211101020000110111100110001101211100000000010001001[0 1]0010013200[0
1]1101000000010100[0 1]10?0[0 1]10[0 1
2]000011000111201111110000001001110??1?0011021021??00011000120[1 2]00110?00[0
1]0111001111010011111001111001000101111010110100011101111000111011100100231
11211

Caiman_gasparinae
000???0?010??1?0001?000?01?0?????????????0??21120011?1??211?0?????????????
11001100?????????0?00?0?????????01?001?200?010????0?????????????????????????
?????????????1??10???
????????????????????????????????????0?????????????????????

Caiman_latirostris 010011100010??10000010100001?002[0 1]0000001100001012012[0
1]011011121110102000011101?1100110001101211100000000010001001100[1
2]001320000101000000110100010?0[0
1]1000000110001112011111100000010011110?1?0011021121??00011000121200110?000011100
0111110[0 1]00111101001111001000101?1??0110110100?1110111?????1011[0
1]0010023111211

Caiman_lutescens_MACN
????110?0020????????????????????1001?????001??2112001101?????????????????????
?0011???
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Caiman_wannlangstoni
010111100010??0?00001010?001??1110010001??001002012001001????1?010?0??01???
????001100?110121?100000?00?1?????????1??3200001000100?????????111001000000??0011
120?0?????00?00???
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Caiman_yacare 000010100010??10000[0
1]10000001?00210010001000001002012001001112111010[1
2]00001110111100110001101211100000000010001001100100132000[0
1]101000000010100010?0010000001100011120111111000001001110?01?0011021021??00011[
0 1]00120[1
2]00110?0000111100111100001??1110011110000010111??1110110100011101111100??1011[
0 1]001?0?3111211

Ceratosuchus_burdoshi
00000?00011100?00001010?001?0001101000???00000???000001??1??101?00?????
???00?1?00?????110000?000?1000?????0320003200001010?0000?0?10101??0?0100000??0???
12?????????00?????????????????1101210?0?0??0?1????????0???1?????????????????
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Crocodylus_acutus
00100??00010??10000010001001?010000000011011011020100000010001110100000010?
[1 2]0000001100001000201000000000100101001001001310002000000000010010000?11112[0
1]000020110112000010001000000101111001?0111021020??00010?0011020000101001001101100
001011010000010011001001110?1????1110001010001101110200??01100000111111000

Crocodylus_affinis 000010000010??1000001000?000?0120000000??0?0001[0
1]20100000010?011101000000?0?10?010011000000002?100000000010010001001[0 1]000[0
1]10001000000010020000000?01101100002000011200101000000000???11110?1?0111021110??0

0010?00110100001010[0
1]10011000?00000110?0??1????????????????????001101?0100????????????????111???

Crocodylus_anthropophagus
00000?00?111100000010001?0???00000?0?11010?1??201????0?????1??10?0??0??2?
???00?1000010002??000000?0?1101010?00?10?13100020010000000100??????11?2?0??011??
1?????????0?00??????????????11021020?10?10?0?11010000??10110?110110??00?1??0??1?
?????10??1????????????????0?101????????????????????11????

Crocodylus_checchiai
00100??00010??1000001000?000?01000000001101001012010000001000?11010000?00??
0???00011000000002010000?000010???1000001001110002001000000001000000?00102[0
1]00000?100?120000??000000010?11?????????1?0?1?????????????1?????????????1?????????
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Crocodylus_falconensis
00100??00010??100001?000?000?0100010000????00012?10?00010???1101000????????
???0?11?0????????100?0??0????????00????00?0?0?0????0?0?00??1????????????????
????????????????????????1?0?1????????????11????????????????????????????????????
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Crocodylus_intermedius 00100??00010??10000010001000?0120000[0
1]0011010011020100000010001110100000010?20000001100000000201000000000100101000001
001310002001000000010010000?11112[0
1]0000201101120000100000000011111001?1111021120?00010?0011010000101001001101100
0010110?000010011001001110?1??1110?01010?????????????011100001112111?00

Crocodylus_johnstoni 00000?00010??10000110001000?01000[0 1]0[0
1]0011010011020110000010001110100000110?[1
2]00000011000110000010000000001001010110110012101020000000010[0 1]0000[0
1]00?11111[0 1][0
1]000201101120000100000000011111101?1111021120?00010?00110200001010010011011000
00011010000010000101001110?1??1110?01000001101112000?011100001112111100

Crocodylus_megarhinus
00000?00010??10000010000000?0100010100??0010120110000010?01110100010010?
200000011000010002010000000010000101100100111000200100000002000000?111110000020
11011200001000100000?1?111??1??111021120?00010?00110100000?0?110011011000?????
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Crocodylus_mindorensis
00010??00010??10000010001001?010000000011010011020100000010001110100000010?
20000001100001000201000010000100101001002001210002001000000010000100?111121000020
1101120000100000000011111001?0111021020?00010?00110100001110010011011000000110
?????????????????1?0?1????????0?????????????????011000001112111000

Crocodylus_moreletii
00100??00010??10000010001001?010000000011010010120100000010001110100000010?
100000011000010002010000000010010100100300111000200000000001000000?111121000020
110112000010001000000101111001?0111021020?00010?00110100001110010011011000000110
?????1?????????1?0?1????????0?????????????????011000001112111000

Crocodylus_niloticus 00000?00010??100[0 1]0010001001?01000000001101[0
1]011120100000010001110100000010?2000000110000100020100000000010010100100[1
2]0013100020010000000100[0 1]0000?01112[0 1]00002011011200001000[0

1)000000101111101?0111021020??00010?0011020000111001001101100000011010000010011101
001110111011110?0101000110111120010011100001113111000

Crocodylus_novaeguineae

00010??00010??10000010001000?010000000011010010020100000010001110100000010?
10000001100001000201000000000100101001002001310002001000001010000100?111121000020
110112000010000000000111110?1?0111021020??00010?00110100001110010011011000000110
?????????????????1?0?1?????????0?????????????????????011100001113111000

Crocodylus_palaeindicus

00000??00010??1000001010?00?????0?????00?????0[0
1]101??100000010??11010000001??2000?0111000?000?0100000000100101000?01001110002
001000000010000000?011021000?2?1?01120000?001?00?????????????????11021020??00010?0?1
10100001?10?1001100110?????????????????????????1??1??1??1?10?????????1101?????????????????
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Crocodylus_palustris

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1]10120100000010001110100000010?[1
2]00000011000010002010000000010010100000001010002001000000010000000?01]1102[0
1]00002011011200001000100000010111101?0111021020??00010?0011010000111001001101100
000011011000010000101001110?1??1110?01010001101111200??011100001112111000

Crocodylus_porosus

00010??00010??10000010[01]0100[01]?010000000011010[01]10[0
1]20100000010001110100010010?[12]000000110000100020100000000010010100100[1
2]001310002001000000010000000?11112[01]00002011011200001000[0
1]00000110111101?0111021020??00010?00110200001010010011011000[01]00110100000100[0
1]00010011102110?1110001010000101111200??011000001112111000

Crocodylus_rhombifer

00100??00010??10000010001000?010000010011010010120100000010001110100000010?
[1
2]000000110000100020100000000100101001001001010002001000000010010000?11112100002
0110112000010000000000101111001?0111021020??00010?0011010000101001001101100000011
011000010011101001110111011110001010001101111110??011100001112111000

Crocodylus_siamensis

00010??000111110000010001000?0100000100110111012010000001000111010001000?
2000000110000100020100000000010010100100100131000200100000001100000?111021000020
110112000010001000000101111101?0111021020??00010?00110200001010010011011000000010
?000010001001000110?1??1110?01010001101111210??011000001112111000

Crocodylus_thorbjarnarsoni

00000??00010??0000001000?00?01100000001???1010120??110001?????1?01?00??000?1
?????00110000100?20?00?0000??10?10?000002001310002001000000010000000?1111200000????
011200000?001?0000??1?????????11021020??0?10?0?11020000??10?10?111110?0100110????
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Dadagavialis_gunai

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?????0?????????????????????????????????0?????????2711120000001010000?0?00??0?0?001????0?????
?????????0?????0?????????????3?????????????????????????10????????????????????????????????
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Deinosuchus_riograndensis

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??111011100?????????00?00?00?1?????0000130000300000010?00?001??0000?????0?????????1??1

??????????00?????????????1002102??000??00100210?10?10001?111???0?010?????????
????????0?1???1?????0?????????1????????????????????10????

Diplocynodon_darwini 00000-?00010??0000012000?000?01[0
1]0000000??0000101100000010?11110101000000?011010011000010110010000000010001000
0010001030001101000000011000010?11?????0?0?1111201101020000?00?????????????100210
20??10010?00110100110?01001111010?10000?0100010010?01000000111?1???1?1001000000110
1110000??????00??112100201

Diplocynodon_deponiae 00000-
?00010??101001200??000?0110?00000????000?10110001001??[0 1]111010100000??01 -
?00021?0?????0000??0??????0????????300?11010000?00110??????1?????0????111120
1?00-
2??00????????????????1002102????0010?001??000??0??1?1?0????????????????????????
1???1?????0?????0??101111000??????????0?2101211

Diplocynodon_hantoniensis 000110000010??0001012000?000?0100000000????00111011[0
1]0000010??1110101000000?01101001100001011001000000001000100000100000300011010000
00011000010?0110000001100111201101020000000??1110??1?0?10021020??100100001101001
01201001110010?10?????00????1??0100000011?21???0?0?????001101111000????????????
1002??

Diplocynodon_muelleri
00?010000010????1101201??000?0100?00100????001?101100000010?2?1????100??0??0
11?????1?0?01011??10?0000??10?0?0?0?0?00??300??10?0000?00110?00??1100?000????101
12011010??00?00????????????10?2?021??0????0?1????????????0??100????????????????
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Diplocynodon_ratelii
000110000010??00000010000000?01000010010010011000100000010?11110101000000?
0110?002100000011001000000000100000000010001030001101000000011000000?111010000110
010112011010200000001001110?11?1110021020??00010?001101000010010010110?0??0?????
?0??1?0100000?11??1?????0?????001101111100????????????????1002??

Diplocynodon_remensis
000110000010??0000012000?000?01000101001??000?101110000010?2111010000000??
0??0100110000?01101100000000100010000010001030001?01000000110?000?01??0??00?000
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1]01120110102000000????1??0????011002100?0??0010?00110100100?00001110010??0??????
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Dollosuchoides_densmorei
00000?00010??1?0001?001?001?0100000000????001002010100?0??????1?????????0?
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20000??00000????????????????1103?20?10?0?0?00110200001100?100110????0????????????
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Dongnanosuchus_hsui
01010??00010??1000001001?000?0010000100????0010121110000000?0?1101?000?010?1
1?10001100000001101000000001000000000001010001001010001010000000?12111?000?????
0112001?10??100010????????????11????1????????????0????????????????????????????
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Eocaiman_cavernensis
0000111000?0????????????00????????00????????02010000?0?????1??102?00????????

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Eocaiman_palaeocenicus

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Eogavialis_africanum

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0??111110000000020100001101110000100001[2
3]01127111200000010100000000?011120000000001121000100000011??00?0??0?1103030
?30?0000?00110100001110000110?0?0????????????????????????????????0?????1
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Eosuchus_lerichei

00000?00000?1?00012001?000?01001000101?0?00010001?0000010?0100?100100010?0
00?00011000011002010000000?1000000000200037011200000000110000100?010000000100
001120000100000000??0????????11030?0?21?00?0?00????????????????????????????
?1????11101?1????????????????????????11????????????????????011???

Eosuchus_minor

00000?00010??100001?001?000?010000010??0?00010100?1000010?0?00?100100?0??
??0?10110000?100201000001000100000000010003701120000001001100?0000?011000000000
0?112?000??000?001??0?1??0?01111103120?21?00?0?0011010000?00000110010?00????
??1?00001?11?1??1?????0?????0?0100110????????????????1010???

Eothoracosaurus_mississippiensi

00000?00000?1?0001?001?000?01?00?01?0????00010011?100001????0??1?1????????
??1?0100?0000??10000?0?01000000001200027?102000001010000?000??0?000000?0????1
12?0?00?000?000??0??????1003030?2??0??0?1001?001??10?0??1?010????????????
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Eurycephalosuphus_gannanensis

00000?00?10??000001?001?010?1000??0110??0000100120001010?011101?000?010?1
111001210000000?00000000001010100?01?000?100011010100?1??00000??10??????????
112000?100?00000??????????110?202?010010??11011001?01?0??110?0?10????????
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Euthecodon_arambourgi

00010?00010?0?00012101?000?0100000001101001?021110000010??1110100000010?
1??0000110010100020100000?0????????00001?0012700020000?000?11??0?0??0?2000?02011
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Gavialis_browni

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??111100?0000?01??0?????????010????????701120000001010000?1100?01010?001?0??011
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Gavialis_gangeticus

00000?00000?11000122010101?110001010000000021011101100010002001013110100?

00001111000000000100001111101001000014111270112000000101100001100?010100001000
00011210000?000010110000110?01?201103040?31?0100?01110210001201000011000?00000100
1000001000011111110110100010000110000010110010010100000010210?0000

Gavialis_lewisi

??00??00000????????????10???100010?00?0?0021???101000010???0010?3110100?00
001111100?00000?100001101111001??????????7??12??000101?00000?00?011100001?00?001
1212000?30101011????????????1?????0??1?01?0?01110?1000120100001?0???0?????????????
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Gavialosuchus_eggenburgensis

00000??00010??1?0001?001??00?10000100?0???001?02110000001????1?01110001????
1???101100????0??1000000001000??0??03101?2411120000?00?10100?000?????0??0??0200???
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Glen_Rose_form

000010000000??0000000000?0111?1200000001?0?1010000100000100?0?11010000?????
???100??0?0?????????0?010000000100?0000001?00000010000000010000000?01000000010?00
10000000?00000?1?0?0?1?0?0??0?0102120?20?0000?000?????0?0????????????00????????????
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Globidentosuchus_brachyrostris

0000??00010??10000?01??001?0??10010?0???000112112001001??????1?200?00????
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Gnatusuchus_pebasensis

0?000??100?0??1?0??01010?0???1?0001000????0000120120010011??????1??0??????0?
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20100101100?10?????????????0100?20?1?0?0??00120?00110?0001?1100?0????????????????
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Gryposuchus_colombianus

00000??00000??1100012001?000?0100010000????0021011101100?10?0200100311110??0
??011?0200000000001000011101111001000?2211?2701120000??101000000100?011100000?0?0?
0?12?????????0?0??0?00?0??01001103030?20?001??0011?1?000100?0000111?0?0000100????
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Gryposuchus_croizati

00000??000?0??100001??01????????????????0?????02100?0?1?00?1????00?113??0??????
?1???1??????0??1?0?0?11??111??010?1?01??7?1120000?1????????????????????1??00?11??
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Gryposuchus_neogaeus

00000??00000??1?00012101?????????0??0????????002?0??1?1?0001???2????????????0????
??1102?00????00?1?0001111111001000?2211?27?1?20000001????????????????????????
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Gryposuchus_pachakamue

00000??00000??1?00012001?000?0100010100????001101010110001????0011?1??110??0
00??1?01000?0000?010?0?01101111??011?2111?2711120000001010000?0100?0???0??100?000

112???0?000?101???0?????????1103030?20?0?00?001111000012010100111???0?????????????
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Hassiacosuchus_haupti

10000??00010??000??01010?001?01201010001?0?000?010??0000010?21110101000000?0
1?1100110?0??1???0?000?0?0?????????????????0??2000010?0100?00??10????0?????????????
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Hylaeochampsia_vectiana

00000??00000?????????????1100?120101000????0011?01101001000?0?00??10?00?0????
??10110010????0?0110110000100010?????????????60?0?0??0?000100011?0?01?12?0100?0?0?1
2?0000?0000010????10?0???
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Iharkutosuchus_makadii

00000??00010??1000001011?1100?12010010?????0?010?11100200?????0?????00000?01
???00?0010?0103001101?100?000?00??03300016001010?020000011001000?01112001000?0?0
1120001?00000101???1??????0?104110?1?0?00?000????0010?00?00000000??????0?????
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Ikanogavialis_gameroi

00000??00000??1?0001?101?000?01000?0100????00110111?1?0001?0?0010?31?????0?
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2???00?000?0?11?????????????1?3040?30??????1?????0?????????1?????????????????????
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Isisfordia_duncani

00000??00010??1?00001010?001?0100100000????0000010100000110?01000101100000?0
00??0011?00??00000000000000000001002?0032000070010100200000001000000??1000000?????
010000001000000?00?????????????????3??????0?0??0?1101000??01????00?????????????1?0??
???1100??1011??1??0?00?????000??10010?0?????????????102111100

Jiangxisuchus_nankangensis

0000100000?0????00001000?000?0100000000????000?10111000001??0111?1?00??010?0
00?00011?000?00?2?1000000?00?000??0?00110000100?10010000?002?000000?11?000000????1?
01120010110000000?????????????11021020?10?10?001?01??01?????????????????????????
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Kambara_implexidens

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00000011000000010?100000000010000?0000010013100020010000?????0?0?00?01101010000001
0?120000102?11000????1?0??1?01?1021020?000??00110100?01?0?000?1?0110000??1?????
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Kambara_murgonensis

00000??001?0??1?0000100??00?01000000?0????001??2011000?0?0??1??1?00?0?0??10
0??0011?0?????10?0?????????????????0?0?????????0????????????????????????????????12??
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Kambara_taraina

00?00??00110??1000001001?000?01000?0000????000?12111000001??????1?000?0??1?
??0021?00?0010010000?000100?0?0000?00121000200?0000?00100?0000?01110??00?????01

120??0??2?1100?0????????????1102102????00??001?01?00?11001???110?????????????????
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Kentisuchus_spenceri 00000??00000??1?00001001?001?01[1
2]0000100????0011020101001010????1001?0000?00?????11100??????????0?000001000??0000
?1011210012000000001?100?0000?011020000?2???0?12??0????100?0?????????????????????
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Kinyang_mabokoensis
00000??00010??10000?1??01????????????0??1?0010121???100000??1101?00??0??2??
??001100??0001200000000000100?1?0000010011100010010000?0000000000?0111?10000??01
1200000?00100000????????????11021120???0?10?001101000011?001001111??0000110?????
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Krabisuchus_siamogallicus
00000??00010??000000100??000?0?00010100????000012011?00001??????1?00??????1?
??????1?????00??0000?0??????????00?01?00??2???00??0100?0?10??????11?0??????????0112
000????????????????????11?02010??0?1????11110????????00?????????????????????
?????1????????????????0????????????????????????????????1?????

Kuttanacaiman_iquitosensis
00?0110000?0??1?00001010?0?????0001000??0000121???1?011?2???1????????0??
?????1????10121?000000000?000????00?000?200001000100?00??10????00??0??01??000112
0111??1100??0??????????????1?2?121??00?????1??1????????????1?0?????????????????
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Leidyosuchus_canadensis
000010000010??00000110000000?01000000010000010101101000010?011101000?0000?
00101001100001011000001000000100010[0 1]000100003300000000000000[0 1]0[0
1]0010?01100000000000011200101020000000??11010?001?1002100?0??0000?00110100111101
?01?10000?00?000????0????????????????????????????????????001?????0????????????1111??

Lohuecosuchus_megadontos 000010100010??0000001000?000?111??0?100????0011111??000[0
1]00??011001000000010100?10011010??010301010000?00?00?100000010011200000000000002
0000000?0111200000??10011200?00?00000000??1??????11021020??10?10?000??0001000
?1??11010?00????0????????????????????????????????????00????????????????

Maomingosuchus_petrolica
00000??00010??1000011001?000?0100000001??001102?100000010?01110100000100?
000??0011000??00??01000000001000010010?001?310112000000000110000[0
1]00?0110000000201001120000??30000000??1??0????0?110?020?2??00?0?0?1202000011?1?10
0110????000000??????00111000001???1????????????0?001??1????????????1011??

Maroccosuchus_zennaroi
00000??00010??1000001001?001?0100000001??001?0210?0001010?011001000??010?0
0010101100011000??1000000000100??100?00?011?1000200?0000?01100?0000?01??????02?1?0
11200000?001000????0????????1102120?1??000??00110200001?100???10000?0????????????
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Mecistops_cataphractus
00000??00010??10000110010000?010000000011010000020110000010001110100000010?
10010001100001000201000000000100101001011011310002000000001010000100?1[0
1]11110102011011200001000000000110111001?0111021120??10010?001102000010100000110
1100100011010010010001101101111000101000110?111200??0111000001121110?0

Mekosuchus_inexpectatus

????0??00010?0?0001?00??0??120101?021??101??11??00????1??00000????1??
??0021????0010?0?0?0?00?000????00?000????1??0?0?0????????????2??????0100?????
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0010??11??1?????0??

Mekosuchus_sanderi

?0??0????010????????????????01??1?2????101??20110000110?0?1??100000????1??
??012?00?0?0010010?0????????????????????100?1?010?001??????00????????1??0100?????
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Mekosuchus_whitehunterensis

?0?0??0????????????????010?02????001??0????????????????????????????????
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Melanosuchus_niger

010011100010??10000010100001?00[1
2]000100011000010120120010011?21110101000011201?11001100011012111000000011000100
10001001020000100000000000100010?000000001100011120111110100000100111[0
1]?0?0011021021?00011000120100110?00001110001111011011011001111001?001?111??0
110210100011101111000??1011000100231112?1

Mourasuchus_amazonensis

000010101011001?0?01?011?0100?121101000????002?12012001111????1?010300?00??0
1????011001110100110010?01110??0010?00??0001??0?00?0?0110??10?00?00?0?0000?0
112??????0?00?0?1??110?????11?3?02??10????0?1202?0??????0?????011????????????
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Mourasuchus_arendsi

000011101011001?0101?011?01?1?121101000????002?12112001[0
1]11??211?01?30??001101?110011000110100110010000111010??0000?30003??0001??0?0?000?
1??010?1?100?000??0?01120????????00??0011?211?01?030?????0????0?1????0????????
??0????010?1????11??110????100?1??1????????????01??????????1????????????

Mourasuchus_atopus

00?011101????1?010????1??0????1?1101000????002????????????????1?0103000??????
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2111?11100?0????????????1103002??100?10001??10011120100111100111????????????
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Navajosuchus_mooki

000010000010??0?00001000?000?0120110000????000?[0 1][1
2]0100000010?2?110101000????0??110011????012111000?0000?1000?01??00200032000010001
0000010?00010??110000012000??12?0?11?10????0????1????????1111210?1??1011000111000
11100100??1??0?010001????????????????????????????????????10111????????????1
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Necrosuchus_ionensis

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Orientalosuchus_naduongensis

01010??00010??1001001001?000?0010000000??0000121120000010??1101?000?000?0

1?010??1????00??110000?0??0?00?000000010100011010?000010000000?12??0?00????0
112000?1?0?100011?????????11022020??001??0?11110?10????0?100?????1??10???1????
??01??0?0?1???1??

Osteolaemus_tetraspis

00010??00010??1001000000000?0100001001101001002010001001?001110101000010?
20000002100101000200000000001000100011010002100020010000000211[0
1]00110111020000120110112000010301000000101110?11?0111021020??10010?00110101101000
0100110110000001101000001000010000011011101111000102000?101111110100111[0
1]1000102111100

Paleosuchus_palpebrosus 10000??00010??10000010000000?0100[0

1]000001100001002111002001?1??110102000011101?11002000011012111000000001000100111
1[0
1]00?320000101100000111100010?011000000110001112001110110000001001110?01?001102102
1??10012100120101110?00001110000?11101001001110110000100110121??011001012101110
1111110??101111110022111211

Paleosuchus_trigonatus

00000??00010??1001001000000?10001000001000001002111002001?1??1101020000111
01?110020000[0
1]101211100000000010001001111000?320000101100000111100010?01100000011000111201111
0110000001001110?01?0011021021??10012100120101110?0000111000?1110100100111101100
00100110121??0110?10121011101111100??101111111022111211

Paratomistoma_courti

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1?1?1?0?0?????????0?0000001000?????????????????2??0?????????????????????????????
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Penghusuchus_pani

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???1111000?1??020100000?001?0001?????????501120000000010100?0000?0100000000????00
1213000?00100000??011??????1100130?20?00?0?0012?000?01????0?????10?0??????1000??1
1?0?1111011??211??0110??????0??011110010????????????????000???

Piscogavialis_jugaliperforatus

00000??00000??1?00012101?00?????0?101001??0001020101100010?01001111101010?0
000011020000000030100001111111?010?0?1501?271112000000101000000100?0111100010000
0011210?10?2?0000?1??000?0????0?1103040?21?00?0?0011010001110??????1??0?????0?????
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Planocrania_datangensis

10000??00010??0?00001001?0?????0000000????001?00010000001??011101?00000?????
???0???0???0??????0?00?0??1?0?????02?00??3000100?2000?0?100?0000??????????????12
?0????????0????????????????110??0??00???
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Planocrania_hengdongensis

??00??00010????????????0?????0000000????000??010000001??011??1??000???????
??0??0??00010?1?00??0?0????0??????1??300?000?2000??10000?0????????????????112?
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Portugalosuchus_azenhae

????0??0010????????????1????1?0??01001???0001?0110000001??00001101000100????
010?????????????0?0?0?0?1????0????????????0????000?0??1000000?01000000?00??0?12?
0000?00000?1?001?0?0??11????????????0?0?0010?00?010????????????1??00????????????
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Procaimanoidea_utahensis

10000??00010?0?00001010?0100?120100000????0000120100000010??11101010000??0?
??1?00110001001211100000000?0001000000100002000010110000????0?1?10?010000000?0?0?
011200011?10000000????????????1110200?0??000?0?11110000??1001010000??10000?????
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Prodiplocynodon_langi

000010000010??100000100??0?????0????00??00111??100000010??11010000?000??0
00?0111010?0000010000?00001010110000010001100000000?0010020000100?01102000012??01
112000??00000000??
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Protoalligator_huiningensis

000????0?????1000?0000?0????????????????????????????????????01?0????????????
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4]?00?1??0?00??111210?????0?????
110?0?1??
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Protocaiman_peligrensensis

????????010????????????????????????????????????0?1??00100010011??11?0????????????1
100110001?01111100000?0??
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Purussaurus_brasiliensis

01000??10020??1000001110?0110?1210010001??0010121120010010?211101020000?11
011110011100?001211100000000110001000001200022000010?0?00?0?1??0010?00?0??0??00
0??1????????????0????????????????11001021??0000100012010011??010?1110000?1????????
????????????1??1????????????1?1101????????????????????111???

Purussaurus_mirandai

01000??10020??1000001110??101?1110010?0????001012011??1001????1??1?0000??0?
??1??1?0????????????????????0?00000200?2??0001?0000????1?0010?00?0??0??0??0?1112
02?11????0????????????11?2?02??0?0?001202?0??11?01?100????????????????
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Purussaurus_neivensis

000010000020??1000001010?0110?1210010001??001012011001001??2111010200001??
01111001110010012111000000001000100?00?10000200001000?0000010100010?001000000100
00111202011111000001001110?1?0????????????100?120100110?1?001?10000?11?01?01??
10100110000000?101?1????????????0?11????????????????????

Qianshanosuchus_youngi

000110100010??1000001000?0000011000010?11000011111100010101011101000100???
0??1000?100001????01?000?0?0?????0?0?11001?1000?0??10001??0?00100?1?101000?1[1
2]000????????????0????????????????????????????????1[1
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Quinkana [0 1]0010??00????0000001001000[0
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Shamosuchus_djadochtaensis
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Siquisiquesuchus_venezuelensis
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Stangerochampsia_mccabei
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11?10011?0??1??11100000??00?000?02000020003200001000100000001?1110?00010000012?00
011200111011000000?????????0?1101110?0?1001000110100010??100??10?00?010100?????
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Thecachampsia_antiquus
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Thecachampsia_sericondon
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Theriosuchus_pusillus
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Thoracosaurus_isorhynchus
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Thoracosaurus_neocesariensis
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Voay_robustus 00010??000211100000010000000?0100000000110111101[1
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Wannaganosuchus_brachymanus
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Ccode

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- +[/72 15 +[/5 16 +[/40 17 +[/2 18 +[/81 19
- +[/2 20 +[/292 21 +[/255 22 +[/244 23 +[/197 24
- +[/211 25 -[/100 26 -[/100 27 -[/100 28 -[/100 29
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-[/100 325 -[/100 326 -[/100 327 -[/100 328 -[/100 329

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cnames

{0 Snout_length_to_total_skull_length;
{1 width_at_the_anterior_orbital_margin_to_cranial_table_wi;
{2 external_naris_proportion;
{3 anterior_margin_thickness_of_the_external_nares_to_leng;
{4 dorsoventral_height_to_medioventral_width_at_the_5th_a;
{5 minimum_width_between_orbits_to_maximum_width_of_cr;
{6 infratemp_fenestra_length_to_cranial_table_length;
{7 cranial_table_length_to_its_width;
{8 minimum_angle_subtended_by_posterolateral_margin_of_
{9 supratemp_fenestra_length_to_cranial_table_length;
{10 supratemp_fenestra_width_to_its_length;
{11 incisive_foramen_width_to_width_ofthe_rostrum_at_pm-msutu;
{12 suborbital_fenestra_width_to_its_length;
{13 choanal_width_to_its_length;
{14 pterygoids_width_to_its_length;
{15 basioccipital_tubera__width_to_occipital_condyle_width;
{16 number_of_maxillary_alveoli;

{17 EMF_length_to_its_height;
{18 minimum_angle_subtended_by_dorsal_margin_of_EMF_a;
{19 retroarticular_process_length_to_its_width;
{20 angle_subtended_by_anteroposterior_flare_of_the_scapul;
{21 coracoid_length_to_scapula_length;
{22 expansion_of_distal_coracoid_to_proximo-distal_coracoid_len;
{23 proximodistal_ulna_length_to_proximodistal_humeral_lengt;
{24 femur_length_to_humeral_length;
{25 expansion_of_distal_ischial_blade_to_length_of_ischium;
{26 canthi_rostralii;
{27 anterolaterally_ridges_on_lateral_surface_of_rostrum;
{28 Dorsal_boss_on_sagittal_axis;
{29 sup_preorbital_ridges absent present;
{30 sup_spectacle absent present;
{31 sub_spectacle_fossa lacking deep;
{32 sub_spectacle_to_level_to_anterior_margin_of_orbit posterior anterior;
{33 fossa_from_frontal_to_external_naris;
{34 prominence_at anteromedial_orbital_margin;
{35 fossa_at_intersection_of_postorbital_frontal_and_parietal;
{36 angle_subtended_by_posterolateral_skull_table_adges_to;
{37 sup_squamosal_horn absent present;
{38 sub_squamosal_horn_position posterior anterior;
{39 sub_squamosal_horn_direction dorsally dorsally_and_laterally;
{40 external_nares_orientation;
{41 ghara_in_external_nares;
{42 crest_circumscribing_narial_margin;
{43 premaxilla_notch_posterolateral_to_naris;
{44 fossa_on_naris_lateral_margin;
{45 nasal_into_naris absent present;
{46 nasal_into_naris_extension bisect protrude_partially excluded_internally;
{47 contact_between_nasal_and_premaxilla;
{48 anterior_limit_of_pm_and_m_suture_relative_to_naris_post;
{49 premaxilla_dorsal_process_extent;

{50 cecal_recesses_on_narial_canal;
{51 maxilla_posterior_extent_relative_to_postorbital_bar;
{52 sup_contact_between_lacrimal_and_nasal present absent;
{53 maxilla_posterior_process_in_lacrimal;
{55 sub_contact_between_lacrimal_and_nasal_maxilla absent present;
{76 sup_dorsal_supraoccipital_exposure absent present;
{77 sub_dorsal_supraoccipital_exposure_shape small moderate large;
{151 notch_for_4th_dentary_tooth absent present;
{192 sup_choanae_septum absent present;
{193 sub_choanae_septum_external_projection within project;
{206 sup_lateral_laterosphenoid_bridge absent present;
{207 sub_lateral_laterosphenoid_bridge_morphology short robust;
{208 sup_caudal_laterosphenoid_bridge absent present;
{209 sub_caudal_laterosphenoid_bridge_morphology short long hypertrophied;
{210 sub_lateral_laterosphenoid_bridge_ascending_process absent present;
{211 sup_eipterygoid present absent;
{212 sub_eipterygoid_retraction_from_the_cavum_epitericum overhanging isolated;
{229 sup_perforation_of_spl_for_ramus_of_CNV absent present;
{230 sub_perforation_of_spl_for_ramus_of_CNV_number one two;
{233 sup_EMF absent present;
{234 sub_EMF_size narrow moderate large;
{235 sub_EMF_intersection_with_surangular_dentary_suture anterior posterodorsal;
{236 sub_EMF_intersection_with_surangular_angular_suture posterodorsal posterior ventral;
{237 dentary_posterior_process_in_an_to_EMF present absent;
{241 sup_surangular_anterodorsal_process absent present;
{242 sub_surangular_anterodorsal_process_anterior_extent one onetwo three;
{253 sup_articular_ant_process_in_adductor_chamber absent present;
{254 sup_articular_ant_process_in_adductor_chamber_pos dorsal ventral;
{324 dorsal_osteoderms_keel absent present;
{325 dorsal_osteoderms_shape rectangular square;

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Ancstates

-0 -1 -2 -3 -4 -5 -6 -7 -8 -9
-10 -11 -12 -13 -14 -15 -16 -17 -18 -19
-20 -21 -22 -23 -24 -25 -26 -27 -28 +29
+30 -31 -32 -33 -34 -35 -36 +37 -38 -39
-40 -41 -42 -43 -44 -45 -46 -47 -48 -49
-50 -51 -52 -53 -54 -55 -56 -57 -58 -59
-60 -61 -62 -63 -64 -65 -66 -67 -68 -69
-70 -71 -72 -73 -74 -75 +76 -77 -78 -79
-80 -81 -82 -83 -84 -85 -86 -87 -88 -89
-90 -91 -92 -93 -94 -95 -96 -97 -98 -99
-100 -101 -102 -103 -104 -105 -106 -107 -108 -109
-110 -111 -112 -113 -114 -115 -116 -117 -118 -119
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-160 -161 -162 -163 -164 -165 -166 -167 -168 -169
-170 -171 -172 -173 -174 -175 -176 -177 -178 -179
-180 -181 -182 -183 -184 -185 -186 -187 -188 -189
-190 -191 +192 -193 -194 -195 -196 -197 -198 -199
-200 -201 -202 -203 -204 -205 +206 -207 +208 -209
-210 -211 -212 -213 -214 -215 -216 -217 -218 -219
-220 -221 -222 -223 -224 -225 -226 -227 -228 +229
-230 -231 -232 +233 -234 -235 -236 -237 -238 -239
-240 +241 -242 -243 -244 -245 -246 -247 -248 -249
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-270 -271 -272 -273 -274 -275 -276 -277 -278 -279
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-310 -311 -312 -313 -314 -315 -316 -317 -318 -319
-320 -321 -322 -323 -324 -325 -326 -327 -328 -329

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xgroup

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agroup

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taxcode

+0 +1 +2 +3 +4 +5 +6 +7
+8 +9 +10 +11 +12 +13 +14 +15
+16 +17 +18 +19 +20 +21 +22 +23
+24 +25 +26 +27 +28 +29 +30 +31
+32 +33 +34 +35 +36 +37 +38 +39
+40 +41 +42 +43 +44 +45 +46 +47
+48 +49 +50 +51 +52 +53 +54 +55
+56 +57 +58 +59 +60 +61 +62 +63
+64 +65 +66 +67 +68 +69 +70 +71
+72 +73 +74 +75 +76 +77 +78 +79
+80 +81 +82 +83 +84 +85 +86 +87
+88 +89 +90 +91 +92 +93 +94 +95
+96 +97 +98 +99 +100 +101 +102 +103
+104 +105 +106 +107 +108 +109 +110 +111
+112 +113 +114 +115 +116 +117 +118 +119
+120 +121 +122 +123 +124 +125 +126 +127
+128 +129 +130 +131 +132 +133 +134 +135
+136 +137 +138 +139 +140 +141 +142 +143
+144 +145 +146 +147 +148 +149 +150 +151
+152 +153 +154 +155

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proc/;

5. Dataset: Walter et al., supplementary dataset (modified Chabrol et al. (2024); discrete and rediscritised characters; .tnt)

xread

330 156

Bernissartia_fagesii

00???0?0000????0??0????00000?00010??0?0000?000?100??120000?00???0011101?
??0000?0???00?101000?01000??0??1?0?0013000100?????????0000??0000300000000100?0?
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Acresuchus_pachytemporalis

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Acynodon_iberoccitanus

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Agaresuchus_fontisensis

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Aktiogavialis_caribesi

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Albertosuchus_knudsenii

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Alligator_mcgrewi

0010?0[0 1]00000101?0[0
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Alligator_mefferdi

1010?00001?0100010?????000010000010??1?01000010?0101?1200000001?1?0010120
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Alligator_mississippiensis

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001110?11?1011001021??00011000120100010?11001111010?0010001000111001100[0
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Alligator_olseni

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Alligator_prenasalis

101??0[0 1]00100????0[0
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Alligator_sinensis

10100000100000100000101[0 1][0
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Allodaposuchus_precedens

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Allognathosuchus_polyodon

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Allognathosuchus_wartheni

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Arambourgia_gaudryi

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Argochampsia_krebsi

?0?100?0010??0?02?????????00000?00000??100001?101??00?01000000001??00110111
00100010?210111?1111?0?000??10200000??00010000?1001111?0100001201037011200000010
10000?0000??000?01020?1?11210000?0000?011??0??????????1??0?0????0??????1??00?????
101??1?1??????????????0?????0100???1????????????????????????0????????????????????001???

Asiatosuchus_depressifrons 1010000[0

1]10????0001?1?10?00000?00010??10000010010000?01200000001??0000010110000010?0111
0100010100?001110011000010000010000000001000000001100131000100100001002000000?0
11010000020010112001????1000?0?001111001?1111021110??10010?00110100001?0011001100
0?00????????????1?1110000111?21??11110?0????000101110100????????????????101???

Asiatosuchus_germanicus

101??000100????000?10111?00000??00010??0000001000?000?0100000000??0?0000111
11?000010?0111010001000?0?0??0011000010002010010000??1??0?0000000000100000010000
100200?0000?0?1010000?0?????120??01?000?0????????????????1102110?1??0000?0011010000?
?10010?110??????????10????????????????????1????100?????00?10111010??????????????111?
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Asiatosuchus_nanlingensis

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??000????????
??10?1120?000?0?00110?0001?1010?0110??
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Australosuchus_clarkae

100?000000000??0?????????00000?00010??0000010010000?01000000001?0?000?101
110000010?011?011100001??1??0011100?110000?1000000000?00??0??0010013100011010?00
0001??0000??100000002001????????????????0?????1?????????11021020??100??001??100?01?
0?0????????????????????1????????????????????????????????????101????????????????????101???

Baru_darrowi

?1?1?????00??0?????????00000?00?????000001?0000000?0120000100????00101????
??????????1?100000????????????????????????????????????000000001010000000000?1020
000010?011110[0
1]00?????011200????0??10??0????????????1??2112??10????001????00?????????11?????????
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Baru_huberi

?1?0?????0????????????????00010??00?????0?000010000?00?01?0000?0????????????
??0?000000101000100100001??0??
001?????1?2?1??11021020??10?1????????????????
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Baru_wickeni

?0?0??1?1?00??00?1?????00010??00010??0000001000?001?0110000100????0010?111
1000001?0?1??100010??0??0001100?????0?0?000000100100001?0000?010001001000010
0100?0010?011110100020?001120011?00110000????????????11021120??1001?0?1101000011
0001001101100??

Borealosuchus_acutidentatus

101?0?0010????1??????0000?00010?0?0001?00?000?011000000????000?0101
0?00001?????1000000??000????10??0?????1?0????0?????????001?001?30012000000?00
110?0000????00?00?0?0????????????00???
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Borealosuchus_formidabilis

101?0?001100010101?011?0100000?00010?0?0001?000?000?01100000001001000?001
10000001?0?1?01000000?000?001100001011301000000001000100000110003300120010000
0101000000?011000000?0001120010100000000?????0?????01002120?1?0000?001101001
10?00101011000?00000?0?1000001001100001011011?1110?00100100001000001?????????
10002??

Borealosuchus_griffithi

1000?0?00110?10110?????00000?00010?000001?000?00000110100000????0000001
1????0001??1?1?01?000?0100011?1?0?1????00?0?000?000010101?00001[0
1]0013300010010?0?0010?0000??101?0?1??11?1120?1??0?0?000????????????100210100
?00?00?001?010010?00001?11000????0????0???1?????0?010021?0?1?10?????1?????????
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Borealosuchus_sternbergii 101000[0 1]00[0

1]0000101100???1?00000?00010?00000120000000?01100000001001000000100000010?0110
010000000?000110011000010110010000000010001000001[0 1]001[0 3]3000100100000001[0
1]000000?[0
1]1100000012011011200100?00000000?001??0?00111002110?1??0000?00120100100?00100011
000?0??0?00?10101?0?0?0101?0?1????????00?000001000????????????????0002?0

Borealosuchus_threensis

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?0???
0?????????0????????????????1??1?????0?????????????0????????????????0002??

Borealosuchus_wilsoni

1?00?010?11????1?10??11000000?00010?000001?001?????110000??????000?0101
0?0000??0?00?1?????0?0?0?????10??00?????00?0?0?????????0?01?001?300020010000????
?0?0?00?????????0??????1???010000????0?????????????0????????????????101100100?00?0
?110?????0?0????????????????????1???1?????000????00?0?010001????????????000200

Bottosaurus_harlandi

?????010000?????01?????????10000010????????????????????0000?0?1????001??21110
0100?????1?0002100????0??????1?0?1101??10?1??0?????????????????0??????????100???????
?0?0?01?0?000?????1??12?????????0??0???1?????????10210?????0???0011010011??01?0??1
?00111????????????????????????1??1?????????????0??10111110????????????????1?????

Boverisuchus_magnifrons

????????????????0?????????10?10?00010??000001000?00???00?0??0????0?1?0101??
0000?????????1?0????0?00??????10??00000?1?????????????????000000001030100001201000?1??
?0000??1111000?0?00??12?0?0?0?1????0?????????????1102100????0????0?1???0?0????0??
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Boverisuchus_vorax

1000?000010000?0??1?11010010?00010?0000001000000?010010000?0?1010020
100000010?0111010000000?0??10011000100010010?0000100??0000310000301000012010
0001000000?0111100000200001120010?000?000??1?????????1102110?0?0000?001??1?11?

??0?000010010?0??????0??1??110010??11?11????110?????001101110100????????????10
1???

Brachychamps_a_montana

100000001101001100000??0?00000?00010??1000101011?0101?1101000001?0?000012
0111000011?1111010100000?01111001100010011110000000010000020?01300031000010001
0000110100010?1001000001?000011200011010000000?0?1110?01?10110?1121??1?010?0?12010
001?0?01001110000?0??????001110?101000??0011????????????000000010111??????????????0
241111??

Brochuchus_pigotti

10000000000000100?0??????00010??00010??0?00001000?000?1100000100????0010121
0?0000010?01110101000110?0????00110010100020100000000100?000010010012100020010000
01010000000?101021000020111120010??30100000??1110????0?110?102????0?0??0?11020000
10????0?1??110????????????????1??????1??1??11?0????001??11????????????????111?
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Caiman_brevirostris

????0?????????0?????????010011100??0??1000001010??01?0?20001?0????001?????
??1????????????10?????????0011????????1????????00?000?????0?00??200?010?0100?000??
?????????????0?1000??12??1?????0?0??????????????11001121??0001??001?????10??001??
????????????????????????????????1??1?????0????????????????????????????????????111???

Caiman_crocodilus

10[0 1]0?0[0 1]00000001000[0 1][0 1]1?11[0 1]1000011[0
1]00010??10000[0 1]10000001?0000000000110000100201[1
2]00100111211101020000110111100110001101211100000000010001001[0 1]0010013200[0
1]1101000000010100[0 1]10?0[0 1]10[0 1
2]000011000111201111110000001001110??1?0011021021??00011000120[1 2]00110?00[0
1]01111001111010011111001111001000101111010110100011101111000111011100100231
11211

Caiman_gasparinae

??1100?0100????????????????000????0?010??1?0001?000??01?0????????????????0??2112
0011?1??211?0????????????11001100?????????0?00?0?????????01?001?200?010????0?????
??1??10?????????????????????????????????????
??0????????????????????

Caiman_latirostris

101[0 1]0000000011100010?011?1010011100010??10000010100001?002[0
1]0000001100001012012[0
1]011011121110102000011101?1100110001101211100000000010001001100[1
2]001320000101000000110100010?0[0
1]100000011000111201111110000001001110?1?0011021121??0001100012 1200110?000011100
0111110[0 1]00111101001111001000101?1??0110110100?1110111?????1011[0
1]0010023111211

Caiman_lutescens_MACN

????0?0100????????????????110?0020????????????????1001?????001??21120
01101????????????????????0011??
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Caiman_wannlangstoni

00??0?0000????0?????????01011100010??0?00001010?001??1110010001??00100201
2001001????1?010?0?01????????001100?110121?10000?00?1?????????1??3200001000100???

?????111001000000??0011120?0????00?00??
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Caiman_yacare 10100000[0 1]0000[0 1]1000[0 1]01??1[0 1]?000010100010??10000[0
1]10000001?00210010001000001002012001001112111010[1
2]00001110111100110001101211100000000010001001100100132000[0
1]101000000010100010?00100000011000111201111110000001001110?01?0011021021??00011[
0 1]00120[1
2]00110?0000111100111100001??11100111100000010111??111011010001110111100??1011[
0 1]001?0?3111211

Ceratosuchus_burdoshi
100??0?0?111??00?????????00000?00011100?00001010?001?0001101000????00000???
?000001??1??101?00?????????00?1?00?????110000?000?1000?????0320003200001010?0000?
0?10101?0?0100000?0???12?????????00????????????????1101210?0??0??0?1?????????0???
1????????????????????????????????????1??1?????

Crocodylus_acutus
100101001000001000111??10?00100??00010??10000010001001?01000000001101101102
0100000010001110100000010?[1
2]0000001100001000201000000000100101001001001310002000000000010010000?11112[0
1]000020110112000010001000000101111001?0111021020??00010?0011020000101001001101100
001011010000010011001001110?1??1110001010001101110200??011000001111111000

Crocodylus_affinis 10[0 1]00[0 1][0 1]000[0
1]0000000100?1??000010000010??1000001000?000?0120000000??0?0001[0
1]20100000010?011101000000?0?10?010011000000002?100000000010010001001[0 1]000[0
1]100010000000100200000000?01101100002000011200101000000000??11110?1?0111021110?0
0010?00110100001010[0
1]10011000?00000110?0??1?????????????0????????????????001101??0100????????????111???

Crocodylus_anthropophagus
??0??????0????000?1????00000?00?111100000010001?0????00000?0?11010?1??201
????0??????1??10?0??0??2????00?1000010002??000000?0?1101010?00?10?1310002001000000
0100??????11?2?0????011?1?????????0?00????????????11021020??10?10?0?11010000??10
110?110110????00?1??0??1?????10??1?????????????????0??101????????????????11?????

Crocodylus_checchiai
1001010010000??0001??????00100??00010??1000001000?000?010000000011010010120
10000001000?11010000?00??0??00011000000002010000?000010??10000010011100020010000
00001000000?00102[0
1]00000?100?120000??000000010?11?????????1?0?1????????????11????????????11?????????
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Crocodylus_falconensis
????????????????????????????00100??00010??100001?000?000?0100010000????00012?10
??00010??1101000??????????0?11?0????????100?0?0????????????00??????00?0?0?0?????0
?0?00??1??1?0?1????????????11????????????
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Crocodylus_intermedius 100100[0 1]000[0
1]000100011?????00100??00010??1000001000?0120000[0
1]0011010011020100000010001110100000010?200000011000000020100000000100101000001
001310002001000000010010000?11112[0

1)0000201101120000100000000011111001?1111021120??00010?0011010000101001001101100
0010110??000010011001001110?1???1110?01010?????????????011100001112111?00

Crocodylus_johnstoni 10000000010000100011110[0
1)000000??00010??10000110001000?01000[0 1]0[0
1)0011010011020110000010001110100000110?1
2)00000011000110000010000000001001010110110012101020000000010[0 1]0000[0
1]00?11111[0 1][0
1)000201101120000100000000011111101?1111021120??00010?00110200001010010011011000
00011010000010000101001110?1???1110?01000001101112000?011100001112111100

Crocodylus_megarhinus
100000000000??1000????????00000?00010??10000010000000?0100010100??0?0010120
110000010?01110100010010?20000001100001000201000000000100001011001001110002001000
000020000000?11111000002011011200001000100000?1?111??1??1111021120??00010?00110100
000?0?110011011000????????????????????????????1??1????????????????????????????????
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Crocodylus_mindorensis
1001?000101000100011?????00010??00010??10000010001001?01000000001101001102
0100000010001110100000010?2000000110000100020100001000010010100100200121000200100
0000010000100?11112100002011011200001000000000111111001?0111021020??00010?001101
00001110010011011000000110?????????????????1?0?1?????????0?????????????????0110000011
12111000

Crocodylus_moreletii
10010100100000100010??10?00100??00010??10000010001001?01000000001101001012
0100000010001110100000010?1000000110000100020100000000010010100100300111000200000
000001000000?111121000020110112000010001000000101111001?0111021020??00010?001101
00001110010011011000000110?????1?????????1?0?1?????????0?????????????????0110000011
12111000

Crocodylus_niloticus 10000000000000100010100[0 1]0100000??00010??100[0
1)0010001001?01000000001101[0
1)011120100000010001110100000010?2000000110000100020100000000010010100100[1
2)0013100020010000000100[0 1]0000?01112[0 1]00002011011200001000[0
1)00000010111101?0111021020??00010?001102000011100100110110000011010000010011101
00111011101110?0101000110111120010011100001113111000

Crocodylus_novaeguineae
10010000100000100010??11?00010??00010??10000010001000?01000000001101001002
0100000010001110100000010?1000000110000100020100000000010010100100200131000200100
0001010000100?1111210000201101120000100000000001111110?1?0111021020??00010?001101
00001110010011011000000110?????????????????1?0?1?????????0?????????????????0111000011
13111000

Crocodylus_palaeindicus 1011000010[0
1)000?000?0??1???00000??00010??1000001010?00?????0????00?????0[0
1)101??100000010??11010000001??2000?0111000??000?0100000000100101000?01001110002
001000000010000000?011021000?2?1?01120000??001?00????????????????11021020??00010?0?1
10100001?10?1001100110????????????????????1???1???1?10????????1101????????????????
????1111???

Crocodylus_palustris
100100000000011?001010110000000??00010??10000010101001?010000010011010[0

1]10120100000010001110100000010?[1
2]00000011000010002010000000010010100000001010002001000000010000000?[0 1]1102[0
1]00002011011200001000100000010111101?0111021020??00010?0011010000111001001101100
000011011000010000101001110?1??1110?01010001101111200??011100001112111000

Crocodylus_porosus 10[0 1]10[0 1][0 1]0[0 1]0000[0
1]10001010000100010??00010??10000010[0 1]0100[0 1]?010000000011010[0 1]10[0
1]20100000010001110100010010?[1 2]000000110000100020100000000010010100100[1
2]001310002001000000010000000?11112[0 1]00002011011200001000[0
1]00000110111101?0111021020??00010?00110200001010010011011000[0 1]00110100000100[0
1]00010011102110?1110001010000101111200??011000001112111000

Crocodylus_rhombifer 1000?00?[0
1]0000010001010011100100??00010??10000010001000?0100000100110100101201000000100011
10100000010?[1
2]0000001100001000201000000000100101001001010002001000000010010000?11112100002
0110112000010000000000101111001?0111021020??00010?0011010000101001001101100000011
011000010011101001110111011110001010001101111110??011100001112111000

Crocodylus_siamensis 10010[0 1]001[0
1]000010001010010?00010??000111110000010001000?01000001001101111012010000001000111
0100010000?20000001100001000201000000000100101001001001310002001000000011000000?1
11021000020110112000010001000000010111101?0111021020??00010?001102000010100100110
11000000010??000010001001000110?1??1110?01010001101111210??011000001112111000

Crocodylus_thorbjarnarsoni
101001001000101?0010?????00000?000010??0000001000?000?01100000001???1010120
??110001?????1?01?00?000?1????00110000100?20?00?0000??10?10?00000200131000200100000
0010000000?1111200000????011200000?001?0000??1????????11021020??0?10?0?11020000?
?10?10?111110?0100110??
?

Dadagavialis_gunai
?0?????????????1?????????00000?0000?0????00?0?1?100?01000101?0????0021021??
?????1????????111?01?????????0?????????????????????????0?????????2711120000001010000
?0?00??0?001????0?????????????0?????0????????????3?????????????????????????10????????
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Deinosuchus_riograndensis
1001?1?02010??02010??1??????0??01??0??100000?000?00001100100000?1??00101001
1?001010?210?01?100?100?0??111011100?????????00?00?00?1?????0000130000300000010?00?0
01??0000?????0??????1??1?????????????00????????????????1002102??000??00100210?10?10
001?111??0?010?????????????????0?1??1?????0????????????1?????????????????????10????

Diplocynodon_darwini 0000?0[0 1]00[0 1]0?001?111?0?010?00000-
?00010??0000012000?000?01[0
1]0000000????0000101100000010?11110101000000?0110100110000101100100000000010001000
0010001030001101000000011000010?11?????0?0?1111201101020000?00?????????????100210
20??10010?00110100110?01001111010?10000?0100010010?01000000111?1??1?1001000000110
1110000??????00??112100201

Diplocynodon_deponiae 0?0?????0[0 1]0?????0?0?????11?00000-
?00010??101001200??000?0110?00000????000?10110001001??[0 1]111010100000??01 -
?00021?0??0?0??0000??0??????0??0?????300?11010000?00110????????1?????0????111120
1?00-

2??00????????????????1002102????0010?001????000??0??1?1?0?????????????????????????????
1???1??????0?????0??101111000?????????????0?2101211

Diplocynodon_hantoniensis 10[0 1]000[0 1]0[0
1]10000000010?????000110000010??0001012000?000?0100000000????00111011[0
1]0000010??1110101000000?01101001100001011001000000001000100000100000300011010000
00011000010?0110000001100111201101020000000??1110??1?0?10021020??100100001101001
01201001110010?10?????00?????1??0100000011?21????0??0?????001101111000?????????????
1002??

Diplocynodon_muelleri
10??0?0010?????1??0?????00?010000010?????1101201??000?0100?00100??001?1011
00000010?2?1????100??0??011?????1?0?01011??10?0000??10?0?0?0?00??300??10?0000?00
110??00??1100?000????10112011010??00?00?????????????10?2?021??0??0?1???????????
0??100????????????????????????????????????1?????????????0??101??00????????????????1012??

Diplocynodon_ratelii
1010?000000?00000??0?0??000110000010??00000010000000?01000001001001001100
0100000010?11110101000000?0110?00210000001100100000000010000000001000103000110100
0000011000000?111010000110010112011010200000001001110?1?1110021020??00010?001101
000010010010110?0?0??0??0??0??1??0100000?11??1?????0?????001101111100?????????????
??1002??

Diplocynodon_remensis
?????0??0??0??0010?????000110000010??0000012000?000?01000101001??000?1011
10000010?2111010000000?0?0?0100110000?011011000000000100010000010001030001?010000
000110?000??01??0??00?000[0
1]01120110102000000????1?0?0??011002100?0?0010?00110100100?00001110010??0?????????
????????????????1?????????0??1002??

Dollosuchoides_densmorei
1000?0000111000?0?????????00000??00010??1?0001?001?001?0100000000????0010020
10100?0??????1?????????0?????????1?0??00??1??0??0??1????000?1111?2100120000000011
100?0000?01102?000?????01120000??00000??????????????1103?20?10?0?0?00110200001100
?100110????0?????????????????0??

Dongnanosuchus_hsui
0010?000?0100?10?????????01010??00010??1000001001?000?0010000100????0010121
110000000?0?1101?000?010?11?1000110000000110100000000010000000000001010001001010
001010000000?12111?000?????0112001?10??100010??????????????11????1????????????0????????
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Eocaiman_cavernensis
?????????????1????001??????0000111000?0?????????????00?????????00?????????020100
00?0?????1??102?00?????????????1?????????????0?0?0?????????????1????20000?00000000?10??
00111001000000?00??0?12?????1?????????????????????1121021??00??00110100?10?????????
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Eocaiman_palaeocenicus
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100001?0??

Gavialosuchus_eggenburgensis

100?1000111????00?????????00000?000010??1?0001?001?000?10000100?0???001?0211
0000001????1?01110001????1???101100?????0??10000000001000??0??03101?2411120000?00?1
0100?000?????0?????0200?????????????0???
???1??

Glen_Rose_form

?????0?0010?10110?????????000010000000?000000000?0111?1200000001?0?1010000
100000100?0?110100000?????????100??0?0?????????0?0100000000100?0000001?0000001000000
0010000000?010000000010?0010000000?00000?1?0?0?1?0?0?????0102120?20?0000?000??????0
????????????????00?????????????????????????????????1?????????????????????????????????1???????????

Globidentosuchus_brachyrostris

???????0100?????????????????0000??00010??10000?01??001?0??10010?0????000112112
001001?????????1?200?00?????????????1?0?????????0?????????????????000??00002?00010?0100?????
?001110??0?????????????12?????????????????????????????????11021001??11??0?0?120100110??0?0??
10001?111??

Gnatusuchus_pebasensis

00???0?0000????0?0?????????0?000??100?0??1?0?0?01010?0?????1?0001000????00001201
20010011???????1?0?0?????0?0?????1?0?010120??00?001000100010??0?000?000001000100???
??1??????0?0?0?00??0001120100101100?10?????????????????0100?20?1??0???00120?00110??0
001?1100??0??

Gryposuchus_colombianus

?0???0?00????0??10?0?????00000?00000??1100012001?000?0100010000????00210111
01100?10?0200100311110?0?0?011?020000000000100001110111001000?2211?2701120000??10
1000000100?011100000?0?0?0?12?????????0?0??0?00?0?01001103030?20?001??0011?1?0001
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Gryposuchus_croizati

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Gryposuchus_neogaeus

1?1110?00110??0?10?????00000?00000??1?00012101?????????0??0????????002?0?1?
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Gryposuchus_pachakamue ?00010?0111?[0

1]0??101????????00000?00000??1?00012001?000?0100010100????001101010110001????0011?1
??110??000??1?01000?0000?010?0?01101111??011?2111?2711120000001010000?0100?0??0??
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Hassiacosuchus_haupti [0

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2)0000100???0011020101001010???1001?0000?00?????111100?????????0?000001000?0000
?1011210012000000001?100?0000?011020000?2???0?12???0????100?0????????????????????
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Kinyang_mabokoensis

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00000000?0111?10000???011200000?00100000????????????11021120???0?10?001101000011?
001001111??0000110??

Krabisuchus_siamogallicus

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?00001???????1?00?????1???????1?????00?0000?0????????????00?01?00??2???00?0100?0?10
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Kuttanacaiman_iquitosensis

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??10?????00?0??01?0001120111??1100?0????????????1??2?121???00?????1??1?????????
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Leidyosuchus_canadensis

1010?000?10100001?1?????000010000010?0000011000000?01000000010000010101
101000010?011101000?0000?00101001100001011000001000000100010[0
1]000100003300000000000000[0 1]0[0
1]0010?0110000000000011200101020000000??11010?001?1002100?0?0000?001101001111 01
?01?10000?00?000???0?0????????????????????????????????001?????0????????????1111??

Lohuecosuchus_megadontos

0010?0?00000100?0??0?????000010100010??0000001000?000?111??0?100????0011111
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Maomingosuchus_petrolica 1000?0[0 1]00[0

1]0??0?0?0?0????00000?00010??1000011001?000?01000000001??001102?100000010?01110
100000100?000?0011000?00?0?10000000001000010010?001?310112000000000110000[0
1]00?0110000000201001120000??30000000??1?0??0?110?020?2??00?0?0?1202000011?1?10
0110????000000????????00111000001???1?????????????0?001??1????????????1011??

Maroccosuchus_zennaroi ??1100?0[0

1]11????0000?????00000?00010??1000001001?001?0100000001??001?0210?0001010?0110
01000?010?00010101100011000??100000000100??100?00?011?1000200?0000?01100?0000?01
??????02?1?011200000?001000?????0?????????1102120?1??000?00110200001?100???10000?0
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Mecistops_cataphractus 100110000000001000111101[0

1]100000?00010??10000110010000?010000000011010000020110000010001110100000010?1001
0001100001000201000000000100101001011011310002000000001010000100?1[0
1]11110102011011200001000000000110111001?0111021120??10010?001102000010100000110
1100100011010010010001101000110111000101000110?111200??0111000001121110?0

Mekosuchus_inexpectatus

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Mekosuchus_sanderi

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Mekosuchus_whitehunterensis

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???01021120??001??10101011100?0?0??????1
0?000??110??

Melanosuchus_niger

00010000100011100010100111010011100010??10000010100001?00[1
2]000100011000010120120010011?21110101000011201?11001100011012111000000011000100
10001001020000100000000000100010?0000000001100011120111110100000100111[0
1]?0?0011021021?00011000120100110?00001110001111011011011001111001?001?111??0
110210100011101111000??1011000100231112?1

Mourasuchus_amazonensis

1110?0100??1????????????????000010101011001?0?01?011?0100?121101000????002?1201
2001111????1?010300?00?01????011001110100110010??01110??0010??00????0001?0?00?0
?0110??10?00?00?0?0000?0112?????????0?00?0?1??1110?????11?3?02??10????0?1202?0?????
?0????011??

Mourasuchus_arendsi

?1??0?0?00??1[0
1]2?????????000011101011001?0101?011?01?1?121101000????002?12112001[0
1]11??211?01?30?001101?110011000110100110010000111010??0000?30003??0001?0?0?000?
1??010?1?100?000??0?01120?????????00?0011?211?01??030?????0????0?1????0?????????
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Mourasuchus_atopus

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??10?01?00?0?0000011202111?11100?0?????????????????1103002??100?10001??100111201001
11100111???001101??1110????????????

Navajosuchus_mooki

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0000010?00010??110000012000??12?0?11?10??0?????1?????????1111210?1??1011000111000
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Necrosuchus_ionensis

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Orientalosuchus_naduongensis

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010000000?12??0??00?????0112000?1?0?100011?????????????11022020??001??0?11110?10??
??0?100?????1?10???1?????01?0?0?1???1??

Osteolaemus_tetraspis 101000000000[0 1]10001[0 1]1011[0
1]000010??00010??10010000000000?01000001001101001002010001001?001110101000010?2000
00021001010002000000000001000100011010002100020010000000211[0
1]0011011102000012011011200001030100000101110?11?0111021020??10010?00110101101000
0100110110000001101000001000010000011011101111000102000?101111110100111[0
1]1000102111100

Paleosuchus_palpebrosus
1000?00000?00110001010111110000??00010??10000010000000?0100[0
1]000001100001002111002001?1??110102000011101?110020000110121110000000001000100111
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1??10012100120101110?00001110000?11101001001110110000100110121??011001012101110
1111110??101111110022111211

Paleosuchus_trigonatus10[0 1]000[0 1]000?00[0
1]10001000111100000??00010??10010010000000?10001000001000001002111002001?1??110102
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1]101211100000000010001001111000?32000010110000011100010?01100000011000111201111
0110000001001110?01?0011021021??10012100120101110?0000111000?1110100100111101100
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Paratomistoma_courti
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Penghusuchus_pani
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Piscogavialis_jugaliperforatus
1011?000101000002?0??0??00000?00000??1?00012101?00?????0?101001??0001020
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101000000100?01111000100000011210?10?2?0000?1??000?0?????0?1103040?21?00?0?00110100
01110??????1??0?????0?????????????????????????????????0?0??????1????????????????????00
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Planocrania_datangensis
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Qianshanosuchus_youngi

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Shamosuchus_djadochtaensis

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Siquisiquesuchus_venezuelensis

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Stangerochampsia_mccabei

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000001?1110?00010000012?00011200111011000000?????????????0?1101110?0??10010001101000
10??100??10?00?010100?????????????010000001????1??0?0?????001??10111100?????????????0
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Thecachampsia_antiquus

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Thecachampsia_sericondon

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011000000100?010120000020010112130010000000010?00110?????1?110?20?20?0??????1?01?0
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Theriosuchus_pusillus

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Thoracosaurus_isorhynchus

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00000010?00000111110100?000??10110000?0003010000000011000000000130102701120100000
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Thoracosaurus_neocesariensis ??11?0?0[0

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Tomistoma_cairense

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Tomistoma_dowsoni

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Tomistoma_lusitanica

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Tomistoma_schlegelii 100110001[0 1]0000100[0 1]01000[0 1][0

1]100000??00010??10000120010001?01000000001[0
1]010011020101001010001110100000100?000110011000010002010000000001000010010120113
10012000000001010000000?11000000020110112100010000000000101101001?201103030?20?0
010?00110200001200010011000?00000000100000100001010011?0111010110000010001101111
0001011100000022101000

Toyotamaphimeia_machikanensis

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10000?011000?0??????1001001??11111111?0111001110?0010001101110010?0????????????00??
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Trilophosuchus_rackhami

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Tsoabichi_greenriverensis [0 1]0[0

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UCMP_39978

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Ultrastenos_willisi

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Voay_robustus

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00000010000000?111020000020110112000?10301000001101111001?0011021020??10010?00110
1010011100100110110100?0110?????????????????0?1??1??01?0?????00110111100?????????
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Wannaganosuchus_brachymanus

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Wannchampsus_kirpachi

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213 219.221 223 234 242 283 292 296 307 322 323 *;

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APPENDIX 4: Complete list of *Diplocynodon* specimens examined for the thesis

Institutional abbreviations:

GMH: Geiseltal Museum of Martin-Luther-University Halle-Wittenberg, Halle (Saale), Germany;

HLMD: Hessisches Landesmuseum Darmstadt, Darmstadt, Germany;

IPS: Institut de Paleontologia Miquel Crusafont of Sabadell, Sabadell, Spain (= **ICP**; Institut Català de Paleontologia Miquel Crusafont);

MNHM: Museum National d'Histoire Naturelle, Paris, France;

NHMB: Naturhistorisches Museum Basel, Basel, Switzerland;

NHMUK : Natural History Museum United-Kingdom, London, United-Kingdom;

SMNK: Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany;

SMF: Senckenberg Museum Frankfurt, Frankfurt, Germany.

Table 1

Institution	Specimens no	Species
NHMB	NHMB Rz. 33	"gervaisi"
NHMB	NHMB Ro. 106	"gervaisi"
IPS	IPS 36361	"tormis"
DGP	DGP 11407	cf. muelleri
DGP	DGP 26814	cf. muelleri
DGP	DGP 26815	cf. muelleri
DGP	DGP 26816	cf. muelleri
DGP	DGP 26837	cf. muelleri
DGP	DGP 26839	cf. muelleri
DGP	DGP 26843	cf. muelleri
DGP	DGP 26844	cf. muelleri
DGP	DGP 26846	cf. muelleri
DGP	DGP 26849	cf. muelleri
DGP	DGP 26850	cf. muelleri
DGP	DGP 26858	cf. muelleri
DGP	DGP 26862	cf. muelleri
DGP	DGP 28164	cf. muelleri
DGP	DGP 26854	cf. muelleri
NHMB	NHMB Nb. 6	cf. muelleri
GMH	GMH-3654-1932	darwini
GMH	GMH 6026	darwini
GMH	GMH 6039	darwini
GMH	GMH 6040	darwini
GMH	GMH 6041	darwini
GMH	GMH 6043	darwini
GMH	GMH 6072	darwini
GMH	GMH 6028	darwini
GMH	GMH 6049	darwini
GMH	GMH 6073	darwini
GMH	GMH 6074	darwini
GMH	GMH 6075	darwini
GMH	GMH 6077	darwini
GMH	GMH 6784	darwini
GMH	GMH LVIII-28-1981	darwini
GMH	GMH XIV-761	darwini
GMH	GMH XIV-4549-1956	darwini
GMH	GMH XLI-96-1966	darwini
GMH	GMH XLI-313-1968	darwini
GMH	GMH XLIII-2	darwini
GMH	GMH XLVI-3-1969	darwini
GMH	GMH XXII	darwini
GMH	GMH XXII-555	darwini

GMH	GMH XXII-563	darwini
GMH	GMH XXII-571-1965	darwini
GMH	GMH XXII-580-1965	darwini
GMH	GMH XXII-587-1965	darwini
GMH	GMH XXII-588-1965	darwini
GMH	GMH XXII-700-1965	darwini
GMH	GMH XXII-720-1965	darwini
GMH	GMH XXII-754a-1966	darwini
GMH	GMH XXVI-55-1961	darwini
GMH	GMH XXXV-223a-1963	darwini
GMH	GMH XXV-474	darwini
GMH	GMH XXV-491-1963	darwini
GMH	GMH XXXVI-524-1966	darwini
GMH	GMH XXXVI-526	darwini
GMH	GMH XXXVII-32-1964	darwini
GMH	GMH XXXVII-54-1964	darwini
GMH	GMH XXXVII-55-1961	darwini
GMH	GMH XXXVIII-9-1964	darwini
GMH	GMH XXXVIII-35-1964	darwini
GMH	GMH XXXVIII-36a-1964	darwini
GMH	GMH XXXVIII-37-1964	darwini
GMH	GMH XXXVIII-47-1964	darwini
GMH	GMH XXXVIII-55-1964	darwini
GMH	GMH XXXVIII-57-1964	darwini
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HLMD	HLMD-Me 14600a	darwini
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HLMD	HLMD-Me 16990	darwini
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HLMD	HLMD-Me 9747	darwini
SMF	SMF-Me 10876	darwini
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SMF	SMF-Me 1142	darwini
SMF	SMF-Me 11560A	darwini
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SMF	SMF-Me 1341	darwini
SMF	SMF-Me 1467	darwini
SMF	SMF-Me 1538	darwini
SMF	SMF-Me 213	darwini
SMF	SMF-Me 222	darwini
SMF	SMF-Me 2748	darwini
SMF	SMF-Me 3780	darwini
SMF	SMF-Me 896	darwini
SMF	SMF-Me 898	darwini
SMF	SMF-Me 900	darwini
SMNK	SMNK-PAL 6517	darwini
HLMD	HLMD-Be 147	deponiae
HLMD	HLMD-Me 7496	deponiae
HLMD	HLMD-Me 8080	deponiae
SMF	SMF-Me 899	deponiae
SMF	SMF-Me 1114	deponiae
SMF	SMF-Me 1348abcde	deponiae
SMF	SMF-Me 2609	deponiae
SMF	SMF-Me 11053	deponiae
NHMUK	NHMUK-OR 30393	hantoniensis
NHMUK	NHMUK-OR 30396	hantoniensis
NHMUK	NHMUK-OR 30397	hantoniensis
NHMUK	NHMUK-OR 25178	hantoniensis
NHMUK	NHMUK-OR 30394	hantoniensis
NHMUK	NHMUK-OR 25166	hantoniensis
NHMUK	NHMUK-OR 30392	hantoniensis
NHMUK	NHMUK-OR 29694	hantoniensis
NHMUK	NHMUK-OR 30243	hantoniensis
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NHMUK	NHMUK-OR 30239	hantoniensis
NHMUK	NHMUK-OR 30336	hantoniensis
NHMUK	NHMUK-OR 30234	hantoniensis
NHMUK	NHMUK-OR 30241	hantoniensis
NHMUK	NHMUK-OR 30227	hantoniensis
NHMUK	NHMUK-R 1042	hantoniensis
NHMUK	NHMUK-R 5267	hantoniensis
NHMUK	NHMUK-R 1045	hantoniensis
NHMUK	NHMUK-R 1068	hantoniensis
NHMUK	NHMUK-R 1043	hantoniensis

NHMUK	NHMUK-OR 25170	hantoniensis
NHMUK	NHMUK-OR 30402	hantoniensis
NHMUK	NHMUK-OR 30251	hantoniensis
NHMUK	NHMUK-OR 30389	hantoniensis
NHMUK	NHMUK-OR 25188	hantoniensis
NHMUK	NHMUK-OR 25164	hantoniensis
NHMUK	NHMUK-OR 25174	hantoniensis
NHMUK	NHMUK-OR 25140	hantoniensis
NHMUK	NHMUK-OR 25248	hantoniensis
NHMUK	NHMUK-OR 25252	hantoniensis
NHMUK	NHMUK-OR 25186	hantoniensis
NHMB	NHMB Bc. 6	monsvalensis
NHMB	NHMB Spa 73	muelleri
NHMB	NHMB Spa 4	muelleri
MNHN	MNHN SG-539	ratelii
MNHN	MNHN SG-541	ratelii
MNHN	MNHN SG-13728ab	ratelii
MNHN	MNHN SG 628	ratelii
MNHN	MNHN SG 636	ratelii
MNHN	MNHN SG 633	ratelii
MNHN	MNHN SG 634	ratelii
MNHN	MNHN SG 635	ratelii
MNHN	MNHN SG 497	ratelii
MNHN	MNHN SG 498	ratelii
MNHN	MNHN SG 499	ratelii
MNHN	MNHN SG 543	ratelii
MNHN	MNHN SG 500	ratelii
MNHN	MNHN SG 557	ratelii
MNHN	MNHN SG 12853	ratelii
MNHN	MNHN BR 13105	remensis
MNHN	MNHN BR 4020	remensis
MNHN	MNHN BR 1694	remensis
MNHN	MNHN BR 2619	remensis
MNHN	MNHN BR 3425	remensis
MNHN	MNHN BR 3504	remensis
MNHN	MNHN BR 3511	remensis
MNHN	MNHN BR 3513	remensis
MNHN	MNHN BR 3527	remensis
MNHN	MNHN BR 3591	remensis
MNHN	MNHN BR 3596	remensis
MNHN	MNHN BR 12456	remensis
MNHN	MNHN BR 13214	remensis
MNHN	MNHN BR 13215	remensis
MNHN	MNHN BR 15013	remensis
MNHN	MNHN BR 15200	remensis

MNHN	MNHN BR 15260	remensis
MNHN	MNHN unnumbered	remensis
MNHN	MNHN BR unnumbered	remensis
MNHN	MNHN BR 15079	remensis
MNHN	MNHN BR 3488	remensis
MNHN	MNHN BR 13200	remensis
MNHN	MNHN BR 4153	remensis
MNHN	MNHN BR 13203	remensis
MNHN	MNHN BR 9027	remensis
MNHN	MNHN unnumbered	remensis

APPENDIX 5: Publications of the candidate during the PhD period

1. *The impact of molecular data on the phylogenetic position of the oldest crown crocodylian and the age of the clade*

Published as:

Darlim, G., Lee, M. S., **Walter, J.**, & Rabi, M. (2022). The impact of molecular data on the phylogenetic position of the putative oldest crown crocodylian and the age of the clade. *Biology Letters*, 18(2), 20210603.

2. *A shark turns into an undetermined crocodylian: the case of *Acanthias bicarinatus* Sismonda, 1849*

Published as:

Walter, J. D., Marramà, G., Pavia, M., Carnevale, G., & Delfino, M. (2024). A shark turns into an undetermined crocodylian: the case of *Acanthias bicarinatus* Sismonda, 1849. *Bollettino della Società Paleontologica Italiana*, 63(1), 0083-87.

3. *First record of *Metriorhynchidae* (Crocodylomorpha, Thalattosuchia) from the Lower Cretaceous of northeastern Italy: high-resolution biostratigraphy, morphological description and comparative pelagic taphonomy*

Published as:

Mongiovì, F., **Walter, J. D.**, Bizzarini, F., Cobianchi, M., Giusberti, L., Martire, L., ... & Delfino, M. (2024). First record of *Metriorhynchidae* (Crocodylomorpha, Thalattosuchia) from the Lower Cretaceous of northeastern Italy: high-resolution biostratigraphy, morphological description and comparative pelagic taphonomy. *Historical Biology*, 1-11.

4. *Expanded phylogeny elucidates *Deinosuchus* relationships, crocodylian osmoregulation and body-size evolution*

Published as:

Walter, J. D., Massonne, T., Paiva, A. L. S., Martin, J. E., Delfino, M., & Rabi, M. (2025). Expanded phylogeny elucidates *Deinosuchus* relationships, crocodylian osmoregulation and body-size evolution. *Communications Biology*, 8(1), 611.