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A new eusuchian crocodylomorph from the Cenomanian (Late Cretaceous) of Portugal reveals novel implications on the origin of Crocodylia

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The fossil record of Eusuchia extends back to the Early Cretaceous (Barremian), with the English species *Hylaeochampsa vectiana* being the oldest known representative of the clade so far. However, the eusuchian record from the Barremian to the Santonian is scarce and fragmentary worldwide. Here we described a new eusuchian crocodylomorph based on a partial skull and lower jaw from the Early Upper Cenomanian of the Tentugal Formation, in the Baixo Mondego region, west-central Portugal. The specimen exhibits a series of characters not seen in other taxa, allowing its assignment to a new genus and species named ***Portugalosuchus azenhae*** **gen. et sp. nov.** The results of a cladistic analysis place this specimen within Crocodylia, as the sister taxon to all other non-gavialoid crocodylians. Therefore, this Portuguese specimen represents the only well-documented and valid eusuchian species in the Cenomanian in Europe, and may be the oldest representative of Crocodylia known so far, helping to fill a gap in the fossil record of Eusuchia from the Barremian to the Campanian. In addition, the discovery of this new taxon sheds light on the radiation of Eusuchia and the origin of Crocodylia, which probably took place in Europe.

ADDITIONAL KEYWORDS: Crocodylomorpha – Eusuchia – phylogeny – systematics.

INTRODUCTION

Over the past ten years, a revolution in the study of the evolution of Crocodylomorpha has been carried out. Research efforts on this group of archosaurs has recently increased in Europe, thanks to the discovery of new and fairly complete fossil specimens, with important keys for understanding the evolution of this group. As a result, the evolutionary histories of many crocodylomorph clades (such as Thalattosuchia, Atoposauridae, Goniopholididae and Eusuchia) are being rediscovered and reinterpreted (Schwarz & Salisbury, 2005; Andrade *et al.*, 2011; Puértolas *et al.*, 2011; Salisbury & Naish, 2011; Buscalioni *et al.*, 2013; Puértolas-Pascual *et al.*, 2014; Tennant & Mannion, 2014; Narváez *et al.*, 2015, 2016; Turner, 2015; Turner & Pritchard, 2015; Tennant *et al.*, 2016; Young *et al.*, 2016). Nevertheless, the crocodylomorph remains from Portugal remain under-studied, and new research efforts on this topic are crucial to understanding the global evolutionary framework of several clades, such as Eusuchia and the crown group Crocodylia.

Of all Mesozoic crocodylomorphs, only Eusuchia remains until today. Eusuchia is a clade of neosuchian crocodylomorphs that possibly originated in the Early Cretaceous, with *Hylaeochampsa vectiana* Owen, 1874 from the Barremian on the Isle of Wight (Clark & Norell, 1992), being its oldest representative. The term 'Eusuchia', 'true crocodiles' in Greek, was first proposed by Huxley (1875), and is phylogenetically defined as the clade that includes the last common ancestor of

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Crocodylia, and *Hylaeochampsa vectiana* and all their descendants (Brochu, 2003). The transition from other neosuchians to Eusuchia involves subtle but far-reaching changes throughout the body and skull (Salisbury *et al.*, 2006), and many authors (e.g. Clark, 1986; Benton & Clark, 1988; Norell & Clark, 1990; Clark & Norell, 1992; Brochu, 1999; Salisbury *et al.*, 2006) agree that most members of Eusuchia exhibit the following combination of characters: a fully developed bony palate, in which the secondary choana is included within the pterygoids; procoelous vertebrae; and the presence of a sagittally segmented paravertebral shield (osteoderms).

Although Eusuchia is known to have existed since the Barremian, there is no other unequivocal record of the group until the Santonian, for which the hylaeochampsid *Iharkutosuchus* Ösi *et al.*, 2007 is known. Some fragmentary remains, and a few taxa from the Barremian to the Santonian, were assigned to Eusuchia (Salisbury *et al.*, 2006; Buscalioni *et al.*, 2011; Holliday & Gardner, 2012; Turner, 2015; Kubo *et al.*, 2018) or to Crocodylia (Efimov, 1982), but the association of these to Eusuchia is still unclear and under debate (Martin & Delfino, 2010; Holliday & Gardner, 2012; Turner, 2015; Turner & Pritchard, 2015). Regarding the crown group, the earliest confirmed records of recognized crocodylians are of alligatoroids and gavialoids from the Campanian in North America and Europe (Brochu, 2003; Buscalioni *et al.*, 2003; Martin & Delfino, 2010; Bronzati *et al.*, 2015; Mannion *et al.*, 2015; Puértolas-Pascual *et al.*, 2016). The record of well-known species of Cenomanian crocodylomorphs from Laurasia is lacking, and includes forms such as *Dakotasuchus kingi* Mehl, 1941, *Coelosuchus reedii* Williston, 1906, *Woodbinesuchus byersmauricei* Lee, 1997 and *Terminonaris robusta* Osborn, 1904 from the USA (Wu *et al.*, 2001; Adams *et al.*, 2011; Frederickson *et al.*, 2017), *Paralligator gradilifrons* Konzhukova, 1954 and *Paralligator major* Efimov, 1981 from Mongolia (Turner, 2015) and *Oceanosuchus boecensis* Hua *et al.*, 2007 in France. Although new Late Cretaceous basal eusuchians (e.g. Hylaeochampsidae and Allodaposuchidae) have been discovered recently, the few eusuchian occurrences in the middle of the Cretaceous remain fragmentary and uninformative (Stromer, 1925, 1933; Persson, 1959; Brochu, 2003). Therefore, the Cenomanian taxon from Tentúgal Fm. described here (Fig. 1) may represent the oldest record of Crocodylia and one of the oldest eusuchians, shedding light on the phylogenetic relationships of the main lineages of Eusuchia and Crocodylia.

THE EARLIEST RECORDS OF EUSUCHIA AND CROCODYLIA

As demonstrated above, the eusuchian fossil record during the Early Late Cretaceous is scarce and fragmentary. The phylogenetic position of the taxa *Pietraroiasuchus* (Early Albian, Italy), *Pachycheilosuchus* (Albian, United States) and *Isisfordia* (Late Albian–Early Cenomanian, Australia) is still controversial and the subject of debate (Narváez *et al.*, 2015; Turner & Pritchard, 2015). However, if finally considered as eusuchians (Salisbury *et al.*, 2006; Buscalioni *et al.*, 2011; Turner, 2015; Narváez *et al.*, 2016), they would represent the only members of the group (together with *Hylaeochampsa*) in the Lower Cretaceous.

Furthermore, the European fossil record of crocodylomorphs is very scarce during the early Late Cretaceous, with marine taxa, such as Pholidosauridae (e.g. *Oceanosuchus* Hua *et al.*, 2007), being the best-known forms during this time interval, particularly during the Cenomanian (Puértolas-Pascual *et al.*, 2016). In relation to Neosuchia, fragmentary remains of faunas are more typically found in the Early Cretaceous. For example, Bernissartiidae, Atoposauridae or Goniopholididae, have been recorded in the Cenomanian in France (Buffetaut & Pouit, 1994; Vullo & Neraudeau, 2008), and incomplete material assigned as undetermined neosuchians or eusuchians were recovered from the latest Middle Cenomanian to earliest Late Cenomanian of Spain (Buscalioni & Vullo, 2008; Vullo *et al.*, 2009; Torices *et al.*, 2012). It is worth mentioning, however, the possible presence of basal eusuchians in the Cenomanian of Gondwana, as Holliday & Gardner (2012) proposed that *Aegyptosuchus* (from the Cenomanian of Egypt) and *Aegisuchus* (from the Cenomanian of Maroco) would form the clade Aegyptosuchidae, which would be the the sister group of Crocodylia within Eusuchia.

Crocodylomorpha, especially the continental taxa, are practically non-existent during the Turonian and Coniacian in Europe. This is probably due to the transgressive episodes produced during this time interval in Europe (Fara & Benton, 2000; Martin & Delfino, 2010; Csiki-Sava *et al.*, 2015). The presence of the putative crocodylian *Tadzhikosuchus macrodentis* Efimov, 1982 in Asia (Tajikistan) during the Turonian–Santonian has been questioned and its affiliation cannot be considered valid due to its fragmentary nature (Martin & Delfino, 2010).

This scenario changes from the Santonian to the Maastrichtian. During this time interval, eusuchian diversity increased substantially, while other neosuchian clades become extinct (Buscalioni *et al.*, 2003). The first eusuchian radiation occurred in Europe during the Santonian–Early Campanian, with the appearance of taxa such as *Iharkutosuchus* (Hungary) and *Massaliasuchus* (France). Some marine taxa similar to *Thoracosaurus* have been recorded in this time interval, but unequivocal members of Gavialoidea are not described until the

Maastrichtian (Puértolas-Pascual *et al.*, 2016). The diversity of Eusuchia increased notably during the Campanian–Maastrichtian, including *Acynodon* (in Spain, Italy and France), *Musturzabalsuchus* (in Spain and France) and several members of Allodaposuchidae, i.e. *Allodaposuchus*, *Arenysuchus*, *Lohuecosuchus* and *Agaresuchus* (in Romania, France and Spain). The North American history is similar, where the oldest record of Crocodylia also dates from the Campanian–Maastrichtian, including taxa such as *Borealosuchus*, alligatoroids such as *Brachychampsa*, *Stangerochampsa*, *Albertochampsa*, *Leidyosuchus* and *Deinosuchus*, gavialoids such as *Thoracosaurus* and *Eothoracosaurus*, and crocodyloids such as *Prodiplocynodon* and *Albertosuchus* (Brochu, 1997; Buscalioni *et al.*, 2003; Martin & Delfino, 2010; Puértolas *et al.*, 2011; Wu & Brinkman, 2015; Puértolas-Pascual *et al.*, 2016).

Finally, recent studies suggested that paralligatorids could be eusuchians (Turner, 2015; Turner & Pritchard, 2015; Narváez *et al.*, 2016). Although still a subject under debate, this could extend the record of eusuchians back to the Late Jurassic (Pol *et al.*, 2009; Montefeltro *et al.*, 2013; Adams, 2014; Narváez *et al.*, 2015).

Crocodylomorphs in Portugal

Portugal is very rich in vertebrate fossils, mainly for the Late Jurassic, including mammals, crocodylomorphs and dinosaurs (Antunes & Mateus, 2003; Mateus, 2006). Comparatively, the Late Cretaceous, although apparently rich in vertebrates, requires much more research.

The oldest known crocodylomorph in Portugal is the Lower Jurassic *Mystriosaurus* (=*Steneosaurus*) *bollensis* (Antunes, 1967). The Late Jurassic outcrops provided an apparent peak in crocodylomorph diversity, with seven known taxa: *Machimosaurus hugii* von Meyer, 1837, *Lisboasaurus estesi* Seiffert, 1970, 1973, *Lusitanisuchus mitracostatus* Seiffert, 1970 (Schwarz & Fechner, 2004) *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005), cf. *Alligatorium*, *Goniopholis baryglyphaeus* Schwarz, 2002, and *Bernissartia* sp. (Buscalioni *et al.*, 1996; Krebs & Schwarz, 2000; Schwarz, 2002; Fechner, 2003; Schwarz & Fechner, 2004, 2008; Schwarz & Salisbury, 2005; Mateus, 2008; Ribeiro & Mateus, 2012; Mateus, 2013; Russo *et al.*, 2014, Young *et al.*, 2016), and two crocodylomorph eggs, to which were assigned distinct ootaxa (Russo *et al.*, 2014, 2017).

The Late Cretaceous provided fragmentary material that requires revision, such as '*Crocodylus*' *blavieri*? Gray, 1831 from the Upper Campanian–Maastrichtian of Viso, near Aveiro (Sauvage 1897–98). The Cenomanian of Portugal has a rich record that also requires revision: *Oweniasuchus pulchelus* Jonet, 1981 from the Upper Cenomanian, *Thoracosaurus* from the Middle Cenomanian of Cacém (Jonet, 1981), the *nomen dubium Oweniasuchus lusitanicus* (interpreted as a goniopholid) based on a fragmentary mandible from the Campanian–Maastrichtian and several remains from the Cenomanian of Portugal, and unidentified eusuchians from Nazaré (Buffetaut & Lauverjat, 1978; Callapez *et al.*, 2014). Cenozoic crocodylians from Portugal include *Iberosuchus macrodon* Antunes, 1975 (Lower to Middle Eocene), *Tomistoma calaritanus* Capellini, 1890 (Aquitanian–Helvetian), *Tomistoma lusitanica* Vianna & Moraes, 1945 (Burdigalian–Helvetian) and *Diplocynodon* sp. (Antunes, 1961, 1987, 1994).

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The crocodylian remains described here were collected from mixed siliciclastic-carbonate sediments in the Cenomanian West Portuguese Carbonate Platform, near the small village of Casais dos Carecos, Coimbra, Baixo Mondego Region, west-central Portugal (Fig. 1). This rural area of woodlands and small farms lies close to the Mondego River alluvial plain and shows large extensions with exposed surfaces of fossiliferous carbonate beds that contain easily accessed fossil vertebrates. The Cenomanian of Portugal is quite rich in vertebrate remains, representing the second most diverse assemblage in the Mesozoic, after the Late Jurassic (Mateus, 2006).

The sampling point was the northern exploitation front of the Beiraterra Quarry, one of several low-scale extractive industries active recently in the region (40°15’7.98” N; 8°34’8.09” W). The local section was previously studied and sampled to determine biostratigraphic units and fossil associations based on invertebrate fauna, mainly molluscs and echinoids (Azenha, 2003). The outcrop has also been used for educational studies (Azenha et al., 2006, 2008), including the fieldwork activities that led to the discovery of these remains.

The local stratigraphic succession consists of nearly 80 m of braided alluvial to coastal marine coarse sandstones (Figueira da Foz Fm – Middle Aptian to Middle Cenomanian) (Dinis *et al.*, 2008) overlaid by an onlapping sedimentary succession of inner-shelf sandy limestones, limestones and marls (Tentúgal Fm – uppermost Middle to Upper Cenomanian) (Fig. 1C). This highly fossiliferous marine unit has been widely studied in stratigraphy, micropalaeontology and invertebrate palaeontology, notably by Choffat (1898, 1900), Soares (1966, 1972, 1980), Soares & Marques (1973), Lauverjat (1982), Berthou (1984), Callapez (1998,

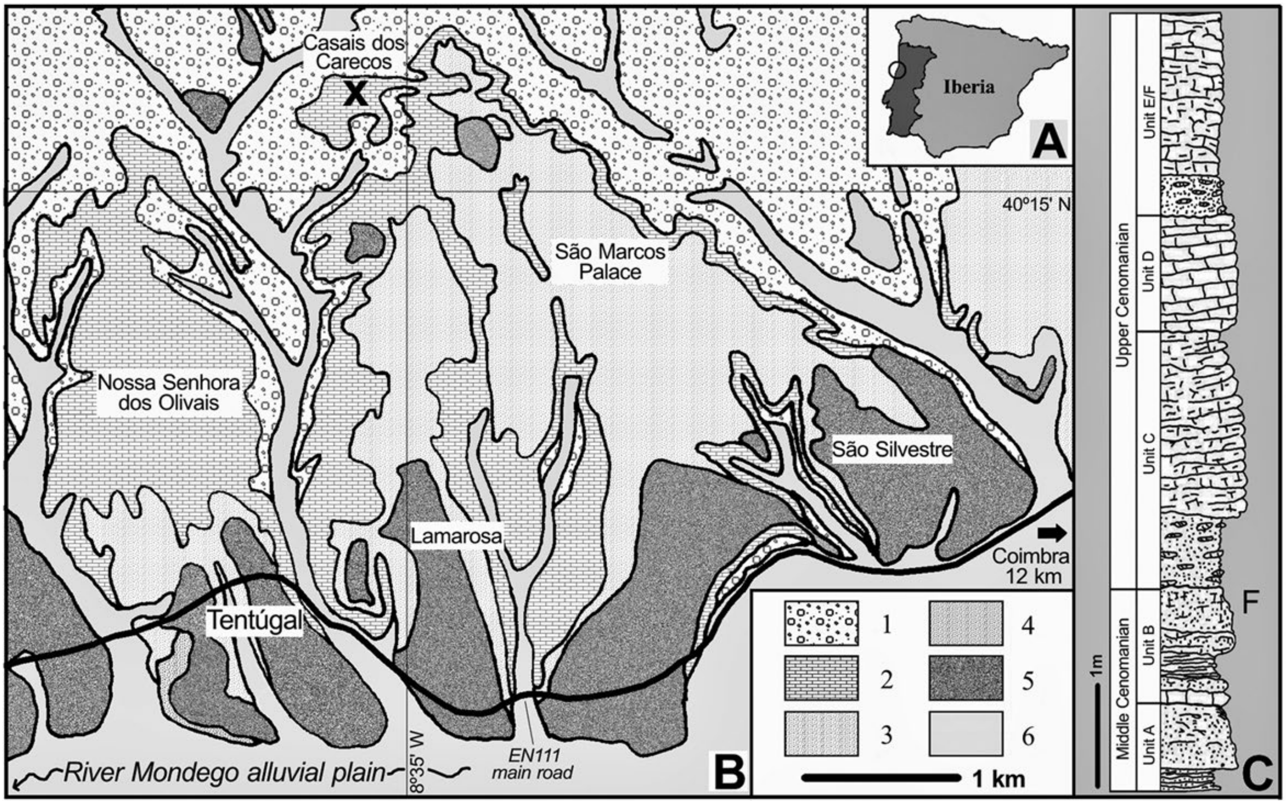

Figure 1. Geographic and stratigraphic settings of the studied area. A, location in the Iberian Peninsula. B, simplified geologic map and location of Casais dos Carecos fossil site in the Region of Baixo Mondego (Coimbra, West Central Portugal). Legend: 1, Figueira da Foz Fm. (Aptian to Middle Cenomanian alluvial coarse sandstones); 2, Tentúgal Fm. (uppermost Middle Cenomanian to Lower Turonian platform carbonates); 3, Furadouro Fm. (Lower to Upper Turonian marine and alluvial micaceous sandstones); 4, Oiã Fm. (Coniacian and Santonian alluvial coarse sandstones); 5, Pleistocene alluvial terraces; 6, alluvial surface deposits. C, stratigraphic section of the Beiraterra quarry outcrop [units after Choffat (1900) and Callapez (1998)]. Unit C correlates to the basal Upper Cenomanian *Calycoceras guerangeri* ammonite standard zone. Abbreviations: F, location of the crocodylomorph remains described here.

1999, 2003, 2004, 2008), Barroso-Barcenilla *et al.* (2011) and Callapez *et al.* (in press).

The carbonate sequence starts with a lower member of littoral plain mixed sandstones, mudstones, marls and sandy limestones, with small biostromes of *Gyrostrea*, *Exogyra*, *Anisocardia* and *Septifer* (Unit B – uppermost Middle to basal Upper Cenomanian – 1.10 m thick). The vertebrate remains studied here were sampled on the top of these strata.

This first succession is overlaid by a transgressive surface with an introduction of fully marine nodular carbonates (Units C and D – Upper Cenomanian – 4.0 m thick) with a rich and diverse fauna of euryhaline bivalves (*Neithea*, *Plicatula*, *Plagiostomma*, *Granocardium*, *Exogyra*, *Ceratostreon*), gastropods (*Harpagodes*, *Cimolithium*, *Plesioplocus*) and echinoids (*Heterodiadema*, *Diplopodia*, *Tetragramma*, *Anorthopygus*, *Hemiaster*). Ammonites and nautiloids indicate a typical Tethyan association with *Neolobites vibrayeanus* d'Orbigny, 1841, *Calycoceras naviculare* Mantell, 1822 and *Lessoniceras mermeti* Coquand, 1862, which correlates to the basal upper Cenomanian standard Biozone of *Calycoceras guerangeri* Spath, 1926 (e.g. Callapez, 2003; Barroso-Barcenilla *et al.*, 2011).

The upper part of the carbonate sequence (Units F to I – Upper Cenomanian – 6.5 m thick) consists of inner shelf nodular marly limestones and marls with *Vascoceras* ammonites and a benthic palaeofauna with *Rhynchostreon*, *Ceratostreon* and abundant moulds of *Tylostoma* (Callapez, 1998, 2003). The ammonite associations correlate to the Upper Cenomanian standard Biozones of *Metoicoceras geslinianum* d'Orbigny, 1850 and *Neocardioceras juddii* Barrois & Guerne, 1878 (Kennedy, 1984), but also with *Rubroceras*, *Pseudaspidoceras* and other common Tethyan genera.

Palaeogeographically, the faunal associations and the spatial articulation of facies record depositional and biotic episodes related with the West Portuguese Carbonate Platform, including the development of marginal marine and inner-shelf palaeoenvironments with abundant Tethyan non-reefal species. However, the lower part of the sequence exposed in Casais dos Carecos reveals a dominance of mixed sandy-carbonate oyster beds (*Gyrostrea*) and a low diversity, associated with epifaunal taxa. This suggests that *Portugalosuchus* gen. nov. inhabited a shallow and slightly restricted environment, possibly a littoral plain with drainage channels connected to inner sectors of the nearby carbonate platform.

INSTITUTIONAL ABBREVIATIONS

ML, Museu da Lourinhã, Portugal; MAFI, Magyar Állami Földtani Intézet, Hungary; MTM, Magyar Természettudományi Múzeum, Hungary; PSMUBB, Paleontology-Stratigraphy Museum, University BabesBolyai, Romania; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain.

SYSTEMATIC PALAEONTOLOGY

ARCHOSAURIA COPE, 1870

CROCODYLOMORPHA HAY, 1930 (*SENSU* WALKER, 1970)

NEOSUCHIA GERVAIS, 1871 (*SENSU* BENTON & CLARK, 1988)

EUSUCHIA HUXLEY, 1875

CROCODYLIA? OWEN, 1842 (*SENSU* BENTON & CLARK, 1988)

***PORTUGALOSUCHUS* GEN. NOV.**

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Etymology: Portugalo refers to Portugal, country where the fossil was found; *suchus* is the latinized form of souchos (Gr.), after a creature of Egyptian zoomorphism.

Type species: Portugalosuchus azenhae gen. et sp. nov.

***PORTUGALOSUCHUS AZENHAE* GEN. ET SP. NOV.**

urn:lsid:zoobank.org:act:1C6E6EB7-4F58-46D2-BCA7-AFA13D647493

Etymology: '*azenhae*' after Matilde Azenha, the geologist that discovered the specimen.

Holotype: ML1818, partial skull and mandible (Figs 2–10) recovered in anatomical association and belonging to the same individual (Supporting Information, Fig. S26). The specimen is housed in the Museu da Lourinhã (ML), Lourinhã, Portugal. ML1818 is comprised of the posterior part of left maxilla, posterior parts of prefrontals and lacrimal, posterior fragments of the nasals, left jugal, frontal, parietal, incomplete postorbitals, squamosal, supraoccipital, exoccipital, basioccipital, pterygoid, palatines and ectopterygoid. Furthermore, ML1818 also comprises a section of the left mandible, composed by the posterior portion of the dentary, with the last four tooth alveoli (two of which with teeth), coronoid, part of the splenial, angular and surangular.

Diagnosis: Autapomorphic traits are marked with an asterisk: *external mandibular fenestra located at the dentary–angular suture, with a posterior process of the dentary forming its anterior and dorsal margins, the angular forming its posterior and ventral margins, and without the participation of the surangular in the fenestra; absence of splenial process between the angular and coronoid; maxilla broadly separates the ectopterygoid from the maxillary tooth row; massive postorbital bar transversely flattened; ventral margin of postorbital bar flush with lateral jugal surface; *dorsal margin of the infratemporal fenestra very elongated, with the quadratojugal contacting the base of the skull table posteriorly, giving a trapezoidal contour to the fenestra (rather than triangular); and braincase wall lateral to the basisphenoid rostrum smooth, without sulci.

Age and horizon: Lower member of Tentúgal Formation (Unit B with *Gyrostrea ouremensis*), Upper Cenomanian, Late Cretaceous (standard Biozone of *Calycoceras naviculare*, about 95 Myr).

Type locality: Limestone quarry of Casal dos Carecos, near Tentúgal, Portugal (40°15'7.98" N; 8°34'8.09" W).

Description

Skull: The skull is well-preserved, although incomplete (Figs 2–3), lacking the rostrum, part of right maxilla and the surface of some posterior-most bones. Its maximum proximodistal length is 166 mm, the maximum width is 146 mm, and maximum dorsoventral height is 93 mm. The dorsal surface is sculpted with pits and grooves (consistent with most crocodylomorphs). Based on regression equations applied to extant species (Hall & Portier, 1994; Wu *et al.*, 2006; Platt *et al.*, 2009), the total cranial length of the specimen ML1818 is estimated at 30–35 cm and the total body length at 2.5–3 m.

The posterior part of the left maxilla preserves the last five or six alveoli, which are circular and without teeth. The lateral surface of the maxilla is damaged. The last maxillary alveolus is at the same level as the

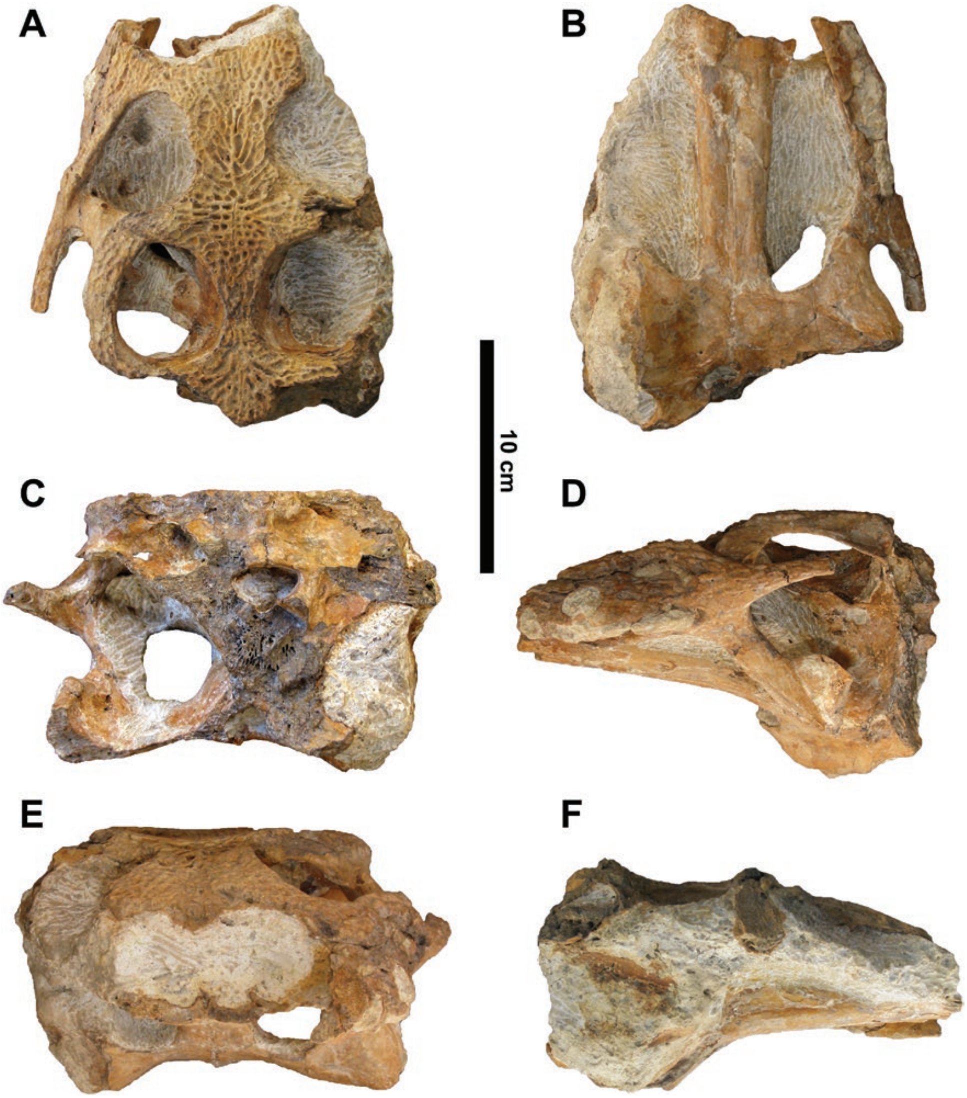

Figure 2. Photographs of the skull of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818, holotype) from the Cenomanian of Tentúgal, Portugal in: dorsal (A), palatal (B), posterior (C), left lateral (D), anterior (E) and right lateral (F) views.

posterior rim of the orbit. In the lateral view, the ventral rim of the maxilla has a gentle curvature as it converges with the jugal posteriorly. Ventrally, the maxilla is posteriorly pinched between the jugal laterally and the ectopterygoid medially. The maxilla does not participate in the infratemporal bar.

Both prefrontals are preserved and their posterior part form most of the anteromedial margin of the orbit. The prefrontals contact the nasal anteriorly and are separated by the frontal medially. The contact with the maxilla is not preserved. The orbital margin of the prefrontals is flush with the skull surface, without any kind of structure or elevation. On the surface of the lateral wall, within the orbit, the prefrontal bears two small foramina. Although most of the prefrontal pillar is surrounded by matrix, it is possible to determine that its dorsal region is anteroposteriorly expanded. Its medial process is not visible.

The left lacrimal is preserved but, as its anterior part is missing, the contact with the nasal is unknown. The posterior part of the lacrimal forms most of the anterolateral margin of the orbit. It has an extensive contact with the prefrontal medially, with the maxilla lateroventrally, and with the jugal posteroventrally. The preserved dorsal surface lacks any kind of elevation or preorbital structure.

The left jugal is present but damaged anterolaterally and the infratemporal bar is incomplete posteriorly. In the lateral view, the dorsal margin of the jugal has a dorsal ridge at the posterolateral margin of the orbit. This ridge is anterior to the postorbital bar, which is flush with the lateral surface of the jugal.

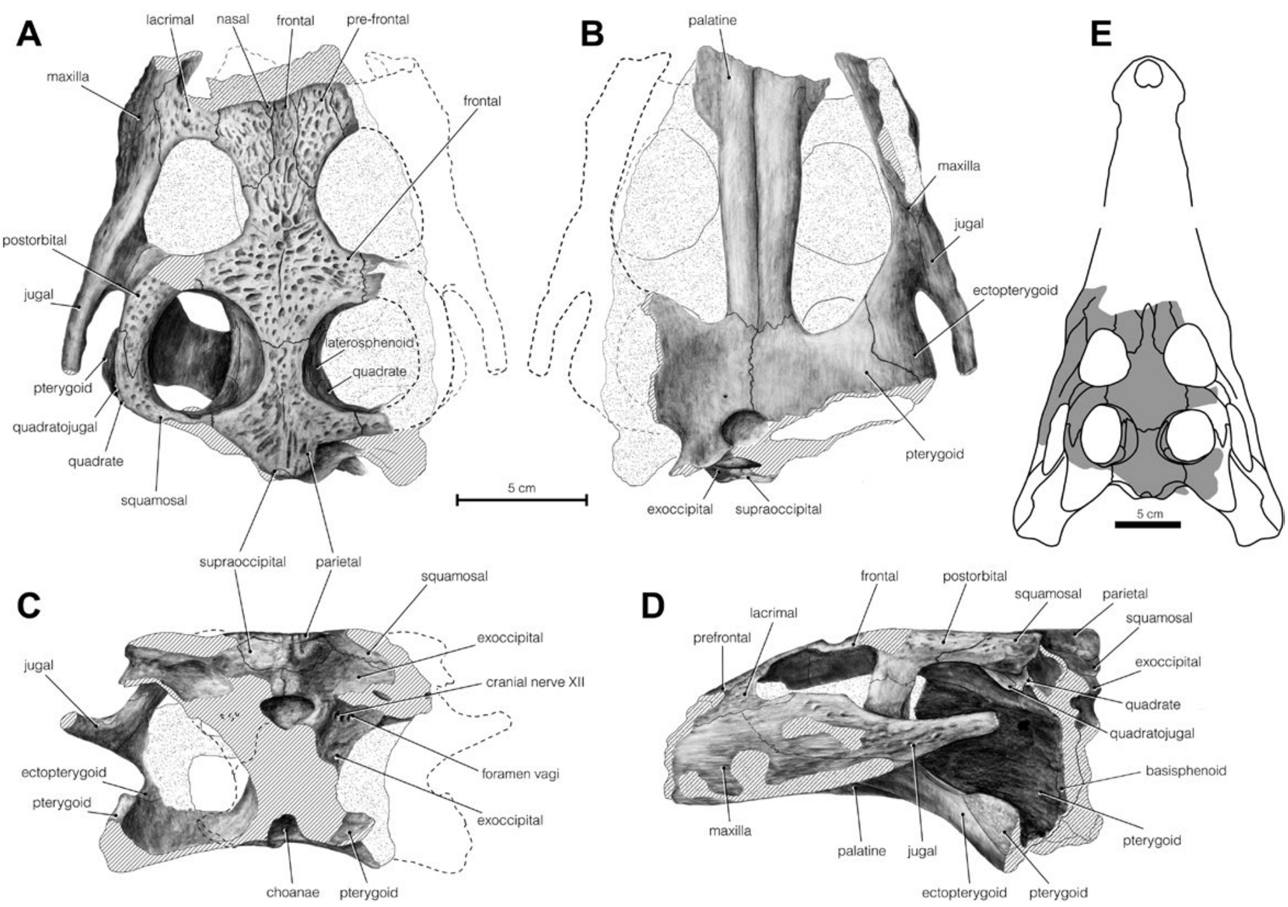

Figure 3. Drawings of the skull of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818, holotype) in: dorsal (A), palatal (B), posterior (C), and left lateral (D) views; Illustration by Joana Bruno. E, interpretative reconstruction of the skull in dorsal view, preserved bones in grey.

The dorsal process participates in the postorbital bar and projects itself dorsally until the midpoint of the posterolateral side of the postorbital bar. The base of the jugal part of the postorbital bar bears a large posterior foramen (Fig. 6). The presence and size of a medial jugal foramen, anterior to the postorbital bar, is unknown due to the matrix in this area. The infratemporal bar is slender and lateromedially flattened with a lens-shaped cross section.

The left postorbital is nearly complete, while only a small and poorly informative portion of the right postorbital is preserved. The dorsal surface at the skull table is sculpted. The contact with the squamosal occurs posteriorly, lateral to the supratemporal fenestra. In the dorsal view, the postorbital–squamosal suture is V-shaped. The postorbital bar is massive, anteroposteriorly longer than transversely wide, and the jugal extends until half of the extension of the bar (Fig. 6). Although the anterolateral corner of the skull table is partially eroded, the postorbital bar seems to be dorsally inset below the postorbital (Fig. 6C–D). The postorbital bar bears a dorsoventrally broad process on its anterior face with a spine at the dorsal portion (Fig. 6C–D). The presence of a second spine in the postorbital bar is unknown due to slight erosion. In the lateral view, the postorbital contacts the squamosal through a ventrally oriented suture. Although the sutures in this region are not very well marked in the ventromedial view (Fig. 6), the postorbital seems to contact both the squamosal and a long anterior process of the quadratojugal. The quadrate is posteriorly placed as an acute process between the squamosal and quadratojugal, without any contact with the postorbital.

The frontal is a single bone that forms the posteromedial margin of the orbits. It bears a long lanceolate anterior process, between the prefrontals and the posterior region of the nasals that extends beyond the anterior margin of the orbits. This process contacts the prefrontals laterally and the nasals anterolaterally. Although the anterior-most tip of this process was not preserved, it seems it would not surpass the anterior

Figure 4. Photographs of the left hemi-mandibule of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818, holotype) from the Cenomanian of Tentúgal, Portugal in: lateral (A), medial (B) ventral (C), dorsal (D), posterior (E) and anterior (F) views.

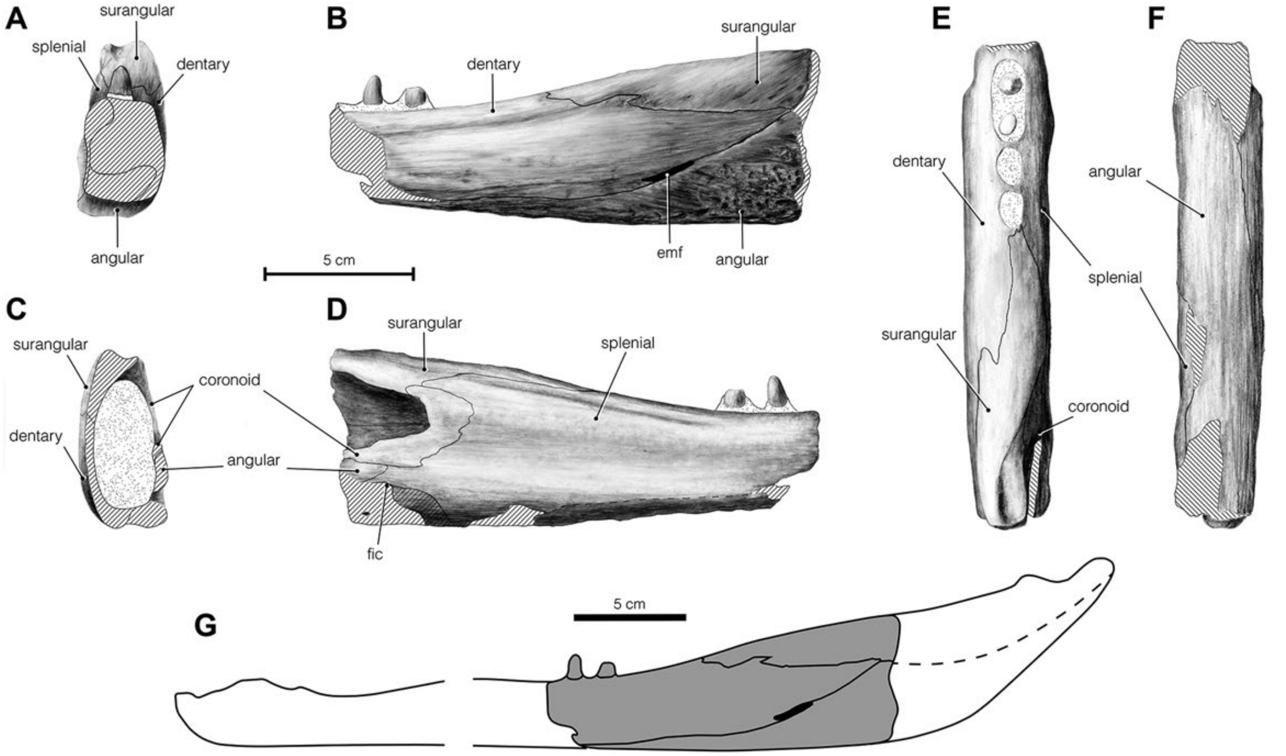

Figure 5. Drawings of the left hemi-mandibule of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818, holotype) from the Cenomanian of Tentúgal, Portugal in: anterior (A), lateral (B), posterior (C) medial (D), dorsal (E), and ventral (F) views. Illustration by Joana Bruno. G. interpretative reconstruction of the mandible in lateral view, preserved bones in grey.

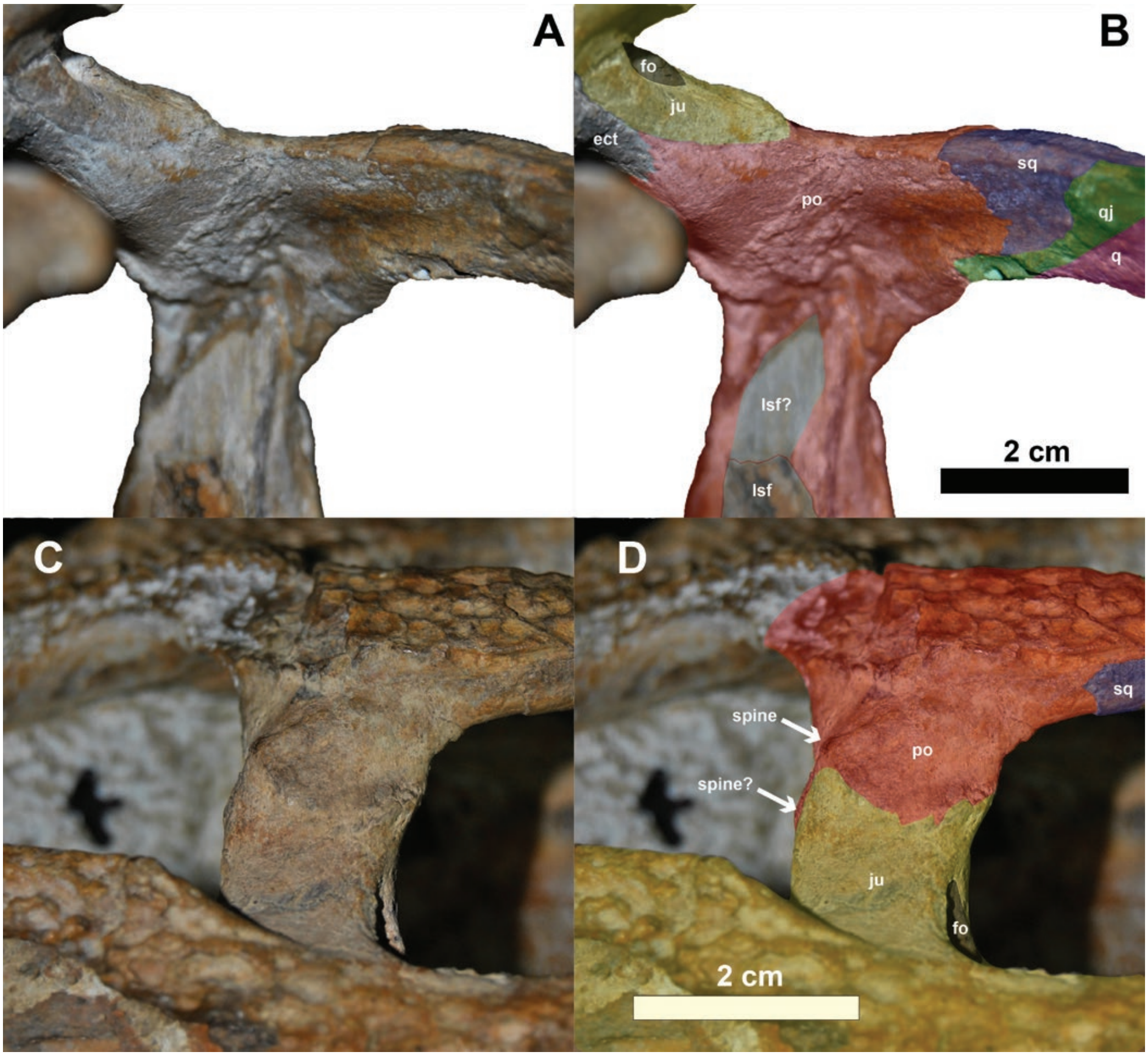

Figure 6. A, close-up and ventromedial view of the left postorbital area of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). B, as in (A), with coloured bones illustrating the proposed sutural contacts in this region. C, close-up and lateral view of the left postorbital area of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). D, same photograph as in (C) but with coloured bones illustrating the proposed sutural relationship of this region. Abbreviations: ect, ectopterygoid; fo, foramen; ju, jugal; lsf, laterosphenoid; p, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

height of the prefrontals and the lacrimals. The dorsal surface of the frontal is well-sculpted. Posterior to the orbits, the frontal contacts the postorbital laterally and the parietal posteriorly. The contact with the latter occurs with a simple transversely linear suture, placed between the supratemporal fenestrae (Figs 3A, 7). The frontal has an important contribution (about one-third) in the anteromedial margin of the supratemporal fenestra (Fig. 7). This margin bears two small longitudinal grooves, horizontally parallel to one another (Fig. 7). However, these grooves seem to be different from the shallow fossa present at the anteromedial margin of the supratemporal fenestra of some eusuchians, such as Allodaposuchidae.

The parietal is cross-shaped in dorsal view, contacting the frontal anteriorly, the squamosal laterally, and extending through a broad posterior projection above the supraoccipital. The parietal comprises the posteromedial margin of the supratemporal fenestra. The intertemporal bar is noticeably narrow, half the width of the interorbital space. The dorsal surface of the squamosal at the skull table is totally flat. Part of its length bears a midline longitudinal line, which is probably a result of taphonomical damage. The

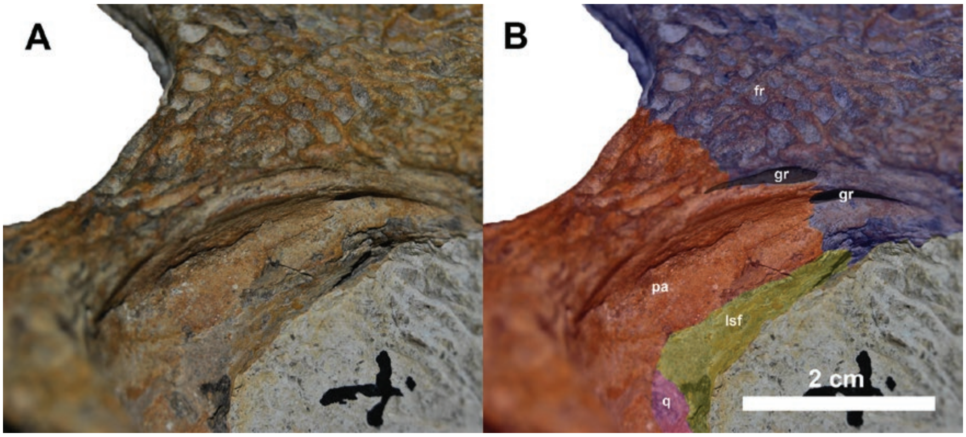

Figure 7. A, close-up of the medial margin of the right supratemporal fenestra of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). B, as in (A), with coloured bones illustrating the proposed sutural contacts in this region. Abbreviations: fr, frontal; gr, groove; lsf, laterosphenoid; q, quadrate; pa, parietal. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

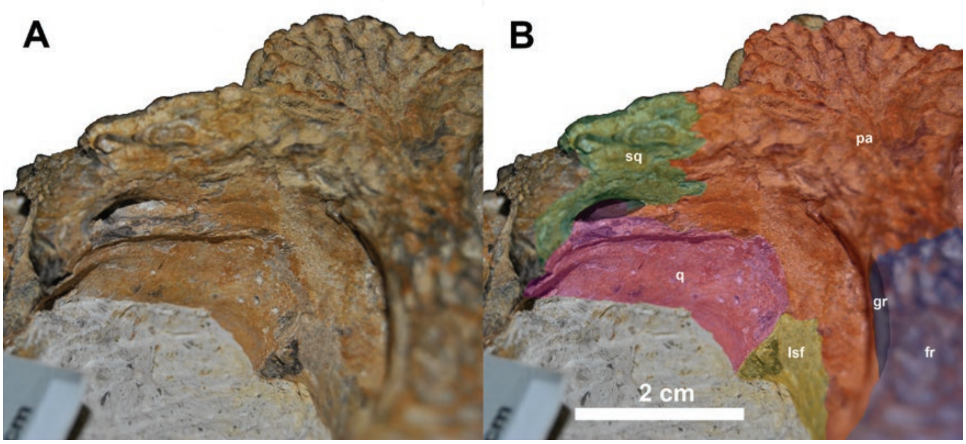

Figure 8. A, close-up of the posteromedial margin of the right supratemporal fenestra of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). B, as in (A), with coloured bones illustrating the proposed sutural contacts in this region. Abbreviations: fr, frontal; gr, groove; lsf, laterosphenoid; q, quadrate; pa, parietal; sq, squamosal. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

parietal wall of the supratemporal fossa is imperforate (Figs 7, 8).

The left squamosal is partially preserved, as well as a very small part of the right bone, near the contact with the parietal. The squamosal comprises the lateral margin of the supratemporal fenestra, which is transversely thin. In the dorsal view, the squamosal contacts the quadrate posteromedially and the postorbital anteriorly. In the posterior view, it contacts the exoccipital ventrally and the supraoccipital medioventrally. The lateral margins are smooth and the posterior- and lateral-most regions of the squamosal are not preserved, making unknow the morphology of the groove for the ear valve musculature. On the posterior wall of the supratemporal fossa, there is a large aperture for the temporal canal (Fig. 8). Around this canal, the parietal and squamosal are widely separated by the quadrate, which enters into the temporal canal (Fig. 8).

The left quadrate is very incomplete, comprising just a small portion around the inner ear. The right quadrate is more complete, but the posterior part that articulates with the mandible was not preserved. As such, the suture patterning of the squamosal and exoccipital around the otic aperture is not distinguishable. The quadrate projects a ventral process between the pterygoid and basisphenoid in the lateral braincase wall (Fig. 9).

Only a small portion of the left quadratojugal is present, lateral to the supratemporal fenestra and contacting the squamosal at the dorsal roof of the infratemporal fenestra. This contact is very posteriorly

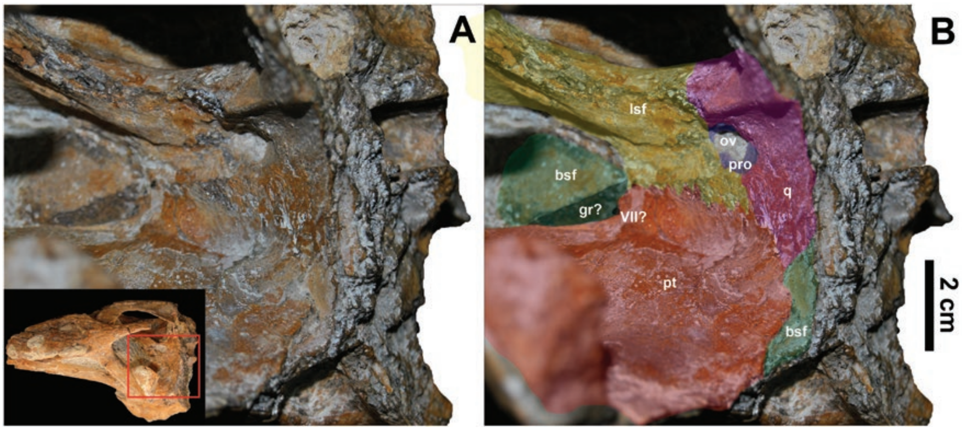

Figure 9. A, close-up of the left lateral braincase wall and foramen ovale region of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). B, as in (A), with coloured bones illustrating the proposed sutural contacts in this region. Abbreviations: bsf, basisphenoid; gr, groove (caused by erosion); lsf, laterosphenoid; q, quadrate; ov, foramen ovale; pro, prootic; pt, pterygoid; VII, foramen for the palatine ramus of the cranial nerve VII. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

placed in relation to the postorbital bar, so the dorsal roof of the infratemporal fenestra is horizontal, giving the fenestra a trapezoidal, rather than triangular, contour (Fig. 3D).

The supraoccipital is hexagonal in the posterior view due to the broad horizontal ventral contact with the exoccipitals. In the occipital view, the supraoccipital is posteriorly projected, forming a sagittal vertical ridge associated with two lateral concavities. Although the sutures in this region are not clearly visible, there is minimal participation of the supraoccipital on the dorsal surface of the skull table.

The right exoccipital, lacking the paroccipital process and its ventral-most part, is preserved. In the posterior view, lateral to the foramen magnum, there are three foramina. The medial-most corresponds to the foramen for the cranial nerve XII, and the other two correspond to the foramen vagi. The exoccipital is damaged ventrally, so its participation in the basioccipital tuberosity cannot be confirmed.

The basioccipital is very damaged, so the occipital condyle and the eustachian canals are not preserved. Only a small region of the basioccipital in the right ventral area was preserved, demonstrating that the external surface of the basioccipital, ventral to the occipital condyle, is vertical and posteriorly oriented.

The basisphenoid rostrum is a vertical thin sheet, dorsoventrally elongated, occupying the midline portion of the posterior cavity, below the laterosphenoid (Fig. 9). In the lateroventral region of the basisphenoid rostrum there is a groove (Fig. 9), which seems to be the result of erosion rather than a real sulcus, and the rostrum and the pterygoids are not recessed inward. Lateral to the basisphenoid rostrum, there are two perforations that also seem to be breakages rather than

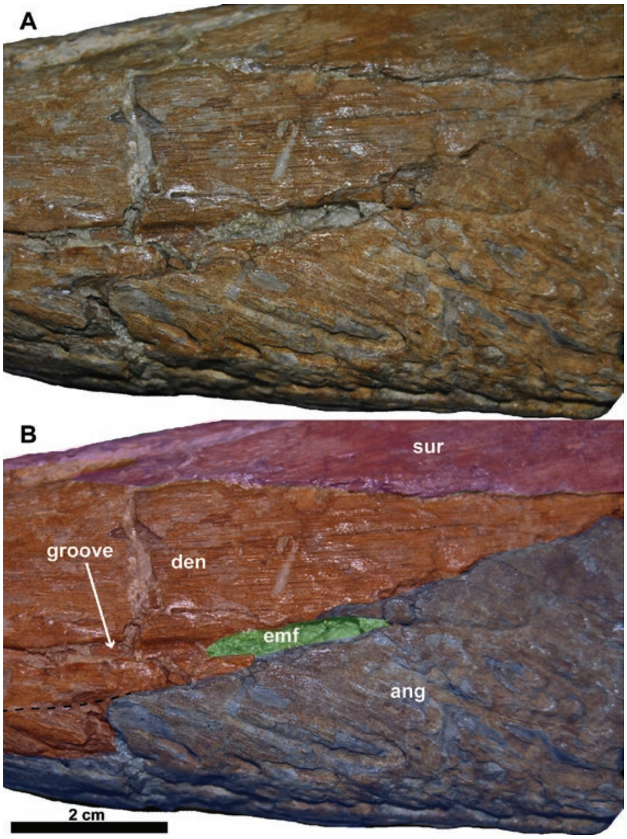

Figure 10. A, close-up of the mandible and external mandibular fenestra of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818). B, as in (A), with coloured bones illustrating the proposed sutural contacts in this region. Abbreviations: ang, angular; emf, external mandibular fenestra; den, dentary; sur, surangular. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

true foramina. Ventrolaterally, there is a foramen that may correspond to the palatine ramus of the cranial nerve VII (Fig. 9). In the lateral braincase wall, the basisphenoid is a thin lamina bordered by the quadrate dorsolaterally, the pterygoid ventrolaterally, the exoccipital dorsomedially and the basioccipital ventromedially (Fig. 9). The position of this lamina relative to the lateral carotid foramen cannot be determined. Although the occipital region of the basisphenoid is not well preserved, a broad exposure of the basisphenoid ventral to the basioccipital can be inferred, due to the shape and position of the posterior pterygoid process and the preserved parts of the basioccipital.

Only the left laterosphenoid remains. It is very elongated anteroposteriorly, and is x-shaped. It is located below the anteromedial margin of the supratemporal fossa. The anterior-most region and the lateral branch of the capitate process are not completely preserved, so its orientation can not be determined. Ventrally, it has a longitudinal ridge along its entire body. The foramen ovale is placed in the lateral braincase wall (Fig. 9). This foramen is surrounded by the laterosphenoid anteriorly and the quadrate posteriorly. There is an extensive exposure of the prootic around the trigeminal foramen (Fig. 9).

Both pterygoids are preserved, but the right one is incomplete laterally and the left one is incomplete posteriorly. This bone contacts the palatine anteriorly, the ectopterygoid laterally, the quadrate dorsally, and comprises the secondary choanae. The ventral surface of the pterygoid is nearly horizontal, except for a gentle transverse concavity towards the midline. The pterygoidal surface, lateral and anterior to the secondary choanae, is flush with the choanal margin. The choana is located very close to the posterior pterygoidal margin. The pterygoid posterior process is tall and prominent.

Both palatines are present, but incomplete anteriorly. The sutures with the maxillae are not distinguishable and, therefore, the morphology and extension of the anterior process of the palatine cannot be determined. The bones form a long bar bordered by the suborbital fenestrae. They contact the pterygoids posteriorly, at the end of the bar, anterior to the posterior margin of the fenestra. The lateral borders are almost parallel along their length and only gently narrower posteriorly. The vomers are only visible in section and are placed in the midline, dorsal to the palatines, totally obscured in the palatal view.

Only the left ectopterygoid is preserved. In ventral view, it contacts the pterygoid posteromedially, the maxilla anterolaterally and the jugal laterally. The anterior ectopterygoid process tapers to a point and the lateral border of the ectopterygoid is separated by the maxilla, avoiding contact with the last tooth alveolus. It gently curves medially, creating a small, subtle projection into the suborbital fenestra, and a bowed lateral margin of the fenestra. The posterior-most end of the ectopterygoid is not preserved. However, only the tip is missing and thus the ectopterygoid does not reach the posterior tip of the lateral pterygoid flange. Dorsally, the ectopterygoid extends along the medial face of the lower half of the postorbital bar.

The supratemporal fenestra is circular and nearly the same size as the orbit. The margins do not upturn, nor form any distinctive lip, and do not overhang the supratemporal fossa. The orbits have a sub-triangular outline, with a broader posterior half. The margins of the orbits are flush with the skull surface, not upturned or forming any different structure. The suborbital fenestra is three times longer than wide, being straight medially and curved laterally. The posterior part of the fenestra is broader than the anterior one, which ends in an acute shape. The fenestra's rim curvature is gentle and does not bear a posterior notch. The otic region is badly damaged and, therefore, it is impossible to see its sutural patterning. The secondary choana is a small, round, undivided fenestra slightly asymmetrically placed at the posterior margin of the pterygoids. The choana is damaged at its posterior section, but it is clear that the aperture is ventroposteriorly directed.

Mandible: The left mandible (Figs 4, 5) is partially preserved and is comprised of the posterior region of the dentary, the last four alveoli (two of them with teeth), the posterior part of the splenial, the anterior parts of both angular and surangular, and the coronoid.

The splenial is broad and occupies almost all of the medial surface of the preserved mandible. The splenial contacts the foramen *intermandibularis caudalis* and the angular posteroventrally, the coronoid posteriorly, the surangular posterodorsally and the dentary anteriorly. The medial surface is not perforated. However, as the region of the splenial anterior to the last four teeth is damaged, the presence of the exit for the cranial nerve V can not be determined. There is no posterior process of the splenial separating the angular and the coronoid.

The coronoid is badly preserved. It has a 'boomerang' shape and is placed in the anterior rim of the mandibular adductor fossa or Meckelian fossa. The anterior edge is damaged, so it is not clear where the foramen *intermandibularis medius* is located. The superior edge of the coronoid slopes strongly anteriorly, at an angle of about 45° from the horizontal plane. As the posterior region of the inferior process of the coronoid is broken, it can be seen in cross-section, showing the overlaps with the angular and the Meckelian fossa. The inferior process of the coronoid overlaps strongly into the inner surface of the Meckelian fossa. As the medial surface of the coronoid is partially damaged, it is impossible to know if it is perforated.

The dentary bears the last four alveoli, two of them with teeth. Posteriorly, the dentary is wedged between the angular and surangular, in the lateral view. The lateroventral area of the dentary is crossed by a well-defined longitudinal groove. This groove starts anteriorly at the height of the last dental alveolus and runs posteriorly to intersect the anterior margin of a small-sized and narrow, slit-shaped fenestra (Fig. 10). This fenestra, here interpreted as the external mandibular fenestra, is between the dentary–angular suture, with the dentary forming its anterior and dorsal margins, and the angular forming its posterior and ventral margins. The fenestra is not laterally coincident with the Meckelian fossa, as it is slightly more anterior than the latter. The preserved teeth are conical and ornamented with fine longitudinal striations ranging from the base to the apex. The mesial and distal carinae are very smooth and almost as lightly marked as the enamel striation.

The angular covers most of the ventral aspect of the mandible. At the lateral surface of the mandible, the surangular contacts the angular posterior to the dentary's posteriormost portion. In the medial view, and below the inferior process of the coronoid, the anterior process of the angular is visible. Although the surface is partially broken, this process extends dorsally towards a cavity, covered by matrix that is likely the foramen *intermandibularis caudalis*. The foramen is small, ellipsoidal and posteriorly placed relative to the Meckelian fossa, without reaching or surpassing the height of the anterior margin of the fossa.

The surangular is incomplete and only the anteriormost portion of the bone is preserved. This bone covers most of the dorsal aspect of the mandible posterior to the toothrow and reaches anteriorly to the posterior margin of the last tooth alveolus, without surpassing it. In the lateral and dorsal views, the surangular anterior processes are unequal in their contact with the dentary; the dorsal is much longer than the ventral. The surangular does not participate in the external mandibular fenestra. Dorsal to the mandibular adductor fossa, the surangular bears a conspicuous process that produces a dorsal concavity.

RESULTS AND DISCUSSION

Phylogenetic analyses

The early evolution of eusuchians and crocodylians is poorly understood, in part due to a lack of comprehensive phylogenetic analyses and despite important contributions by Clark (1994), Brochu (1999), Sereno *et al.* (2001) and Pol *et al.* (2009). However, during the last five years, a great amount of new eusuchian taxa have been discovered, leading to several new phylogenetic studies focused on providing a better understanding of the relationships among Crocodylia and non-crocodylian eusuchians (e.g. Buscalioni *et al.*, 2001, 2011; Salisbury *et al.* 2006; Delfino *et al.*, 2008a, 2008b; Martin, 2010; Puértolas *et al.*, 2011; Brochu *et al.*, 2012; Blanco *et al.*, 2014, 2015; Puértolas-Pascual *et al.*, 2014; Martin *et al.*, 2016; Narváez *et al.*, 2015, 2016), and between Eusuchia and non-eusuchian neosuchians (e.g. Turner, 2015; Turner & Pritchard, 2015).

To perform our cladistic analysis, *Portugalosuchus azenhae* was included in the dataset by Narváez *et al.* (2016), mainly based on the matrix by Brochu (1999), as it includes most of the new eusuchian taxa discovered in recent years. Character 60 was modified with the addition of a new character state, which is autapomorphic (*) for *Portugalosuchus*.

Character 60. 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) or mandibular fenestra between dentary and angular, no surangular participation on the fenestra (2*).

In addition, the codings for *Allodaposuchus precedens* Nopcsa, 1928, *Iharkutosuchus makadii* Ösi *et al.*, 2007, *Agaresuchus subjuniperus* Puértolas-Pascual *et al.*, 2014 and *Arenysuchus gascabadiolorum* Puértolas *et al.*, 2011 were modified from the original matrix by Narváez *et al.* (2016), based on first-hand observations of the specimens (see Supporting Information for the complete list of changes).

With the new taxon, the dataset included 107 taxa, which were coded for a total of 189 craniodental and postcranial characters. The taxon *Goniopholis simus* was used as the outgroup taxon. In TNT v.1.5 (Goloboff & Catalano, 2016), tree-space was searched using a heuristic search algorithm (traditional search method), with tree-bisection-reconnection (TBR) branch swapping, random seed set to 1 and 1000 random addition replicates holding 10 most parsimonious trees for each replicate. To recover all trees, a second search using the overflowed trees retained in the memory was performed. All characters were equally weighted and multistate characters were unordered. Bremer supports and bootstrap frequencies (1000 bootstrap replicates searched) were calculated to assess the robustness of the nodes.

The analysis found 4464 most parsimonious trees (MPTs) of 789 steps (ensemble consistency index, CI = 0.314; ensemble retention index, RI = 0.789; rescaled consistency index, RC = 0.248). The bootstrap frequencies and the Bremer supports (decay index) were summarized in the strict consensus tree (Fig. 11; for the complete cladogram with all the taxa used in the analysis, bootstrap frequencies over 50%, and the Bremer support see Supporting Information, Fig. S16).

With the inclusion of *Portugalosuchus*, the strict consensus topology is quite different from that of the original dataset of Narváez *et al.* (2016). The main differences are related to the loss of resolution among non-Crocodylia eusuchians and gavialoids.

In the strict consensus tree from the original dataset by Narváez *et al.* (2016), *Theriosuchus* is the sister taxon of Eusuchia and *Pachycheilosuchus*, *Shamosuchus*, *Pietraroiasuchus*, *Acynodon iberoccitanus*, *Hylaeochampsa*, *Iharkutosuchus* and *Acynodon adriaticus* are successive sister taxa to each other, forming a clade within Eusuchia. However, with *Portugalosuchus* included, *Bernissartia* is found as the sister taxon of Eusuchia, and Hylaeochampsidae is the sister clade of the unresolved node composed of *Pachycheilosuchus*, *Shamosuchus* and *Pietraroiasuchus*. Within Hylaeochampsidae, *A. iberoccitanus*, *A. adriaticus*, *Hylaeochampsa* and *Iharkutosuchus* are successive sister taxa to each other. The relationships within Allodaposuchidae have also changed, with *Arenysuchus* and *Allodaposuchus* forming the sister clade of the node composed by *Agaresuchus* and *Lohuecosuchus*. The relationships at the base of Gavialoidea are also slightly different, with *Thoracosaurus* and *Eothoracosaurus* forming a polytomy with the rest of the gavialoids. In our analysis, *Portugalosuchus* is located as the sister taxon to all other non-gavialoid crocodylians.

The position of *Portugalosuchus* is supported by the following unambiguous synapomorphies: absence of splenial process between the angular and coronoid (character 59, state 1); external mandibular fenestra placed between the dentary and angular without participation of the surangular (character 60, state 2); maxilla broadly separates the ectopterygoid from the maxillary tooth row (character 104, state 1); and braincase wall lateral to the basisphenoid rostrum smooth, without sulcus (character 162, state 1).

To test the robustness of *Portugalosuchus* within Crocodylia, we performed an alternative analysis forcing the position of *Portugalosuchus* outside Crocodylia (defining constraints in TNT), resulting in trees with only one extra step (790). The strict consensus tree (Supporting Information, Fig. S17) shows *Portugalosuchus*, the unresolved clade of Allodaposuchidae, and Crocodylia forming a polytomy. This suggests that the position of *Portugalosuchus* within Crocodylia is not robustly supported and the hypothesis of *Portugalosuchus* as a non-crocodylian eusuchian cannot be ignored or discarded.

Taking into account the unusual position, size, shape and configuration of the external mandibular fenestra

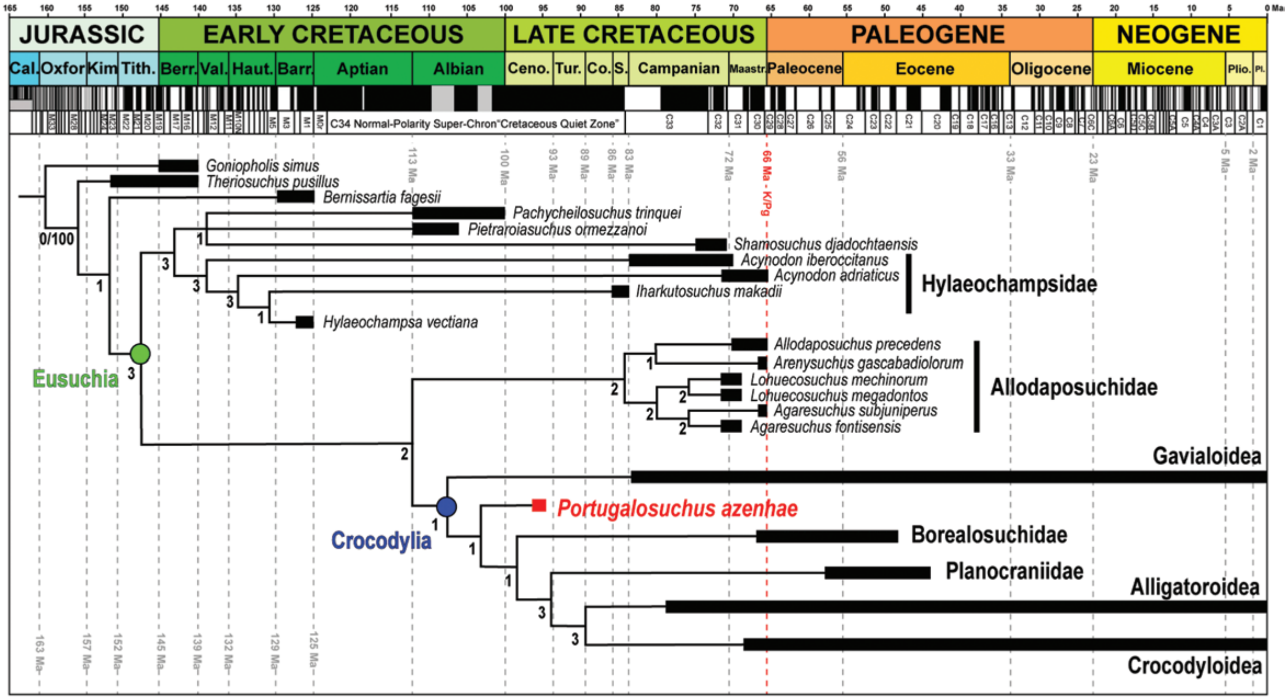

Figure 11. Phylogenetic relationships of eusuchians, depicting the position of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818) based on the matrix of Narváez *et al.* (2016). Stratigraphically calibrated and synthesized strict consensus tree of 4464 most parsimonious cladograms with 789 evolutionary steps. Black rectangles represent known minimal age ranges of each taxon (based on: Brochu *et al.*, 2012; Narváez *et al.*, 2016; Puértolas-Pascual *et al.*, 2016). Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

in *Portugalosuchus*, a last alternative analysis was performed, considering this fenestra as a different structure, non-homologous to the external mandibular fenestra present in Crocodylia (changes: char 60(2 →?); char 63(1 → 0)). The resulting analysis yielded trees with less one step (788). Yet, it resulted in a poorly resolved strict consensus (Supporting Information, Fig. S18), with *Portugalosuchus*, the unresolved clade of Allodaposuchidae and Gavialoidea, forming a polytomy with the rest of Crocodylia. This analysis demonstrates the importance of the presence or absence of the external mandibular fenestra in *Portugalosuchus* and is a key character to define phylogenetic position. Further studies on the development of this structure in eusuchians and crocodylians, as well as the recovery of new specimens, could be essential to resolve this part of the cladogram.

Another possible reason for the low degree of support and resolution primarily affecting the relationships of taxa such as Allodaposuchidae, *Borealosuchus*, Gavialoidea and *Portugalosuchus*, is the inclusion of several recently discovered non-crocodylian eusuchian taxa, such as allodaposuchids and hylaeochampsids (e.g. Buscalioni *et al.*, 1997, 1999; Buscalioni *et al.*, 2001; Salisbury *et al.,* 2006; Martin, 2007, 2010; Ösi *et al.*, 2007; Delfino *et al.*, 2008a, 2008b; Martin & Buffetaut, 2008; Puértolas *et al.*, 2011; Brochu *et al.*, 2012; Blanco *et al.*, 2014, 2015; Puértolas-Pascual *et al.*, 2014; Martin *et al.*, 2016; Narváez *et al.*, 2015, 2016). Most datasets used recently are mainly based (with some modifications) on Brochu (1999). This matrix was primarily elaborated to solve the phylogenetic relationships of the crown group Crocodylia, in a context where other eusuchians were very scarce and fragmentary. Since then, a large number of basal eusuchians have been discovered (e.g. *Acynodon*, *Iharkutosuchus*, *Agaresuchus*, *Lohuecosuchus*, *Arenysuchus* and *Musturzabalsuchus*). Therefore, all of these uncertainties around the base of Crocodylia could be influenced by the lack of diagnostic characters for these more recently described taxa. Another possibility related to these low supports could be that *Portugalosuchus* may belong to a previously unknown morphotype among Eusuchia, probably a member of a new, unknown clade. We have observed in the alternative analyses that minimum changes in some key characters, such as the presence of external mandibular fenestra, make this specimen act as a wildcard taxon thoroughout the tree. Further analyses on the skull (e.g. CT scan), findings of additional specimens and, above all, a better and more comprehensive dataset focused on the basal eusuchians, will allow a better coding that could alter these results in the near future and shed new light on the position of this taxon.

Due to all these issues, and to test the position of *Portugalosuchus* in a wider phylogenetic context within Crocodylomorpha, we performed another cladistic analysis based on the dataset of Turner (2015). This matrix takes into account the main clades within Crocodylomorpha, including sphenosuchians, protosuchians, notosuchians, thalattosuchians and neosuchians. The character list is adapted from Turner & Sertich (2010), Pol *et al.* (2009), Turner & Buckley (2008), Pol & Norell (2004a,b) and Pol & Apesteguia (2005), and includes characters from Clark (1994), Turner (2006), Brochu (1997), Pritchard *et al.* (2012) and Adams (2013).

According with our previous analysis based on Narváez *et al.* (2016), the codes for *Allodaposuchus precedens*, *Iharkutosuchus makadii*, *Allodaposuchus subjuniperus* (now *Agaresuchus subjuniperus* Narváez *et al*., 2016) and *Allodaposuchus* cf. *precedens* (now *Lohuecosuchus mechinorum* Narváez, Brochu, Escaso, Pérez-García & Ortega, 2015) were also modified from the original matrix by Turner (2015), based on photographs and first-hand observations of the specimens (see Supporting Information for the new codifications of these taxa). Finally, the taxa *Arenysuchus gascabadiolorum* and *Portugalosuchus azenhae* have also been added to the Turner (2015) matrix.

The taxon *Gracilisuchus* was used as the outgroup taxon. In TNT v.1.5 (Goloboff & Catalano, 2016), tree-space was searched using the same parameters as in the first analysis. All characters were equally weighted. According to Turner (2015), the characters 1, 3, 6, 10, 23, 37, 43–45, 49, 65, 67, 69, 73, 77, 79, 86, 90, 91, 96, 97, 104–106, 108, 126, 142, 143, 149, 167, 182, 197 and 226 were set as additive. Also according to Turner (2015), characters 5, 277 and 281 were considered inactive.

With all these changes, the inclusion of the new taxa resulted in a dataset of 103 active taxa, which were coded for a total of 319 active characters. The analysis resulted in 660 most parsimonious trees (MPTs) of 1659 steps (ensemble consistency index, CI = 0.241; ensemble retention index, RI = 0.704; rescaled consistency index, RC = 0.169). The bootstrap frequencies and the Bremer supports (decay index) were summarized in the strict consensus tree (Fig. 12; for the complete cladogram with all the taxa used in the analysis, bootstrap frequencies over 50% and the Bremer support see Supporting Information, Fig. S20).

With the inclusion of *Portugalosuchus* and *Arenysuchus*, the strict consensus topology is very similar to that obtained from the original dataset by Turner (2015). The main differences are related to the loss of resolution within Crocodylia, *Araripesuchus* and Allodaposuchidae. As with the matrix by Narváez *et al.* (2016), *Portugalosuchus* appears within Crocodylia, but most of the taxa in this clade appear to form a large polytomy.

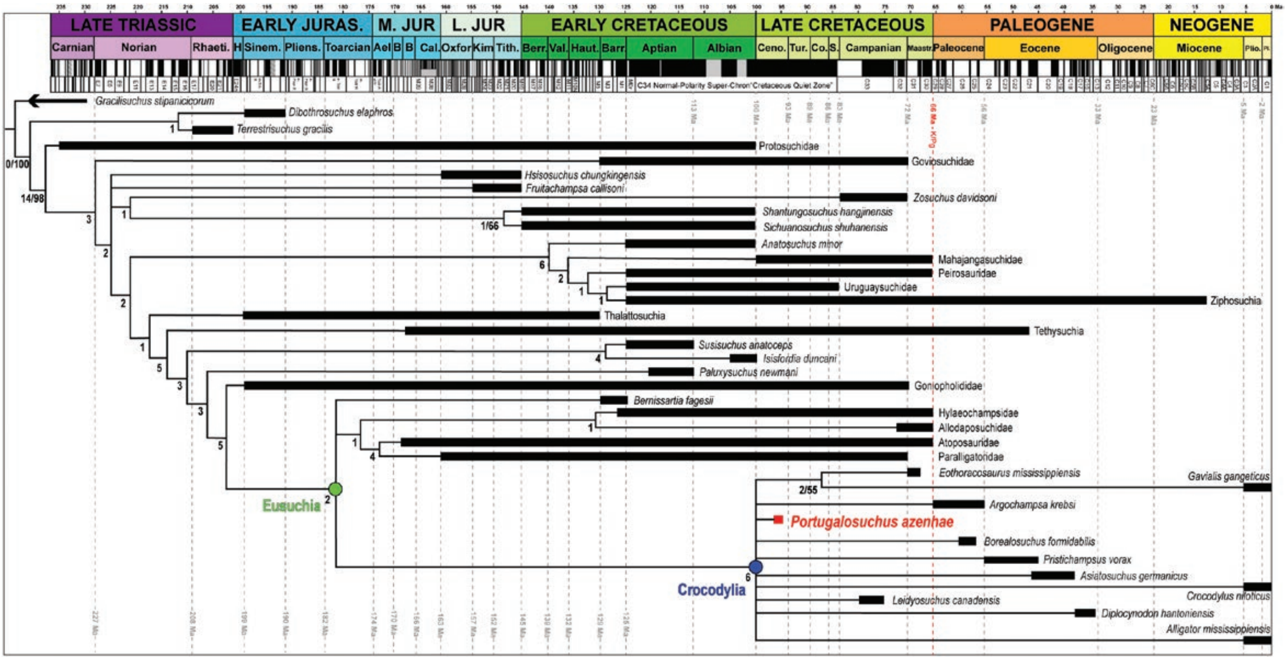

Figure 12. Phylogenetic relationships of eusuchians, depicting the position of ***Portugalosuchus azenhae* gen. et sp. nov.** (ML1818) based on the matrix of Turner (2015). Stratigraphically calibrated and synthesized strict consensus tree of 660 most parsimonious cladograms with 1659 evolutionary steps. Black rectangles represent known minimal age ranges of each taxon (based on: Brochu *et al.*, 2012; Turner, 2015; Turner & Pritchard, 2015; Narváez *et al.*, 2016; Puértolas-Pascual *et al.*, 2016). Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

The position of *Portugalosuchus* is supported by the following unambiguous synapomorphies: postorbital bar transversely flattened (character 26, state 0); jugal portion of postorbital bar, relative to lateral surface of jugal, flush with lateral surface (character 167, state 0). Also, it is characterized by the following ambiguous synapomorphies: pterygoid ramus of quadrate with deep groove along ventral edge (character 50, state 1); absence of palpebrals (character 65, state 0); supratemporal fenestrae relatively large, covering most of surface of skull roof (character 68, state 0); lateral surface of the anterior region of surangular and posterior region of dentary with a longitudinal depression (character 118, state 1); dorsally robust splenial posterior to symphysis (character 161, state 1); cheek teeth not constricted at base of crown (character 162, state 0); maxilla broadly separates ectopterygoid from maxillary toothrow (character 264, state 1).

To check the importance of the external mandibular fenestra for the position of *Portugalosuchus* within Crocodylia, another alternative analysis was performed. Again, this analysis was performed considering that *Portugalosuchus* lacks external mandibular fenestra: char 70(0 →?); char 75(0 → 1). The analysis yielded trees with one step less (1660) and the strict consensus topology was the same as the first analysis (Supporting Information, Fig. S20). These results reinforce the hypothesis that *Portugalosuchus* is within Crocodylia, since, in a broader phylogenetic context, its inclusion in the clade is not only influenced by the presence or absence of the fenestra.

COMPARISONS

The position of *Portugalosuchus* within Crocodylia, as the sister taxon to all other non-gavialoid crocodylians, is supported by several synapomorphies. For example, *Portugalosuchus* shares many characters related to the postorbital with most gavialoids: the presence of a massive postorbital bar (also shared with hylaeochampsids and some allodaposuchids and tomistomines); large, nearly circular supratemporal fenestrae separated by a very narrow intertemporal bar; a postorbital bar with a process that is prominent and dorsoventrally broad (also present in *Hylaeochampsa vectiana*, some allodaposuchids and *Borealosuchus wilsoni* Mook, 1959); ventral margin of the postorbital bar flush with the lateral jugal surface (also shared with non-crocodylian eusuchians and several non-eusuchian neosuchians); postorbital–quadratojugal contact at dorsal angle of infratemporal fenestra (also present in *H. vectiana*, allodaposuchids, *Borealosuchus*, planocraniids, tomistomines, and some alligatoroids and crocodyloids). A foramen *intermandibularis caudalis* that does not reach or surpass the level of the anterior margin of the Meckelian fossa is also present in some gavialoids, such as *Gavialis* and *Eosuchus*, and in the allodaposuchid *Lohuecosuchus*. However, *Portugalosuchus* lacks several characters typical of Gavialoidea, such as: the presence of a ventral margin of the orbit with a prominent notch; ventrally slopping skull table surface; pterygoid processes small and posteriorly projected; palatine-maxillary suture intersection at anteriormost limit of the suborbital fenestra (also present in hylaeochampsids and some allodaposuchids); and telescoped orbital margins.

Yet, *Portugalosuchus* also shares several characters with *Borealosuchus*, such as: a coronoid with its superior edge strongly sloping anteriorly (also common in caimans, *Leidyosuchus canadiensis* Lambe, 1907 and *Tomistoma schlegelii* (Müller, 1838)); external mandibular fenestra present as a narrow slit (present in *Borealosuchus wilsoni*, *B. threeensis* Brochu *et al.*, 2012, *Thoracosaurus*, *Deinosuchus*, and some dyrosaurids and pholidosaurids); and margin of the orbit flush with the skull surface (also present in several non-crocodylian eusuchians and some crocodylians). *Portugalosuchus* differs from *Borealosuchus* due to the large supratemporal fenestra in relation with the orbit; round anterior rim of the orbit; narrow posterior ramus of jugal; posterior maxillary toothrow curved medially (concavity in the medial margin); and choanae near the posterior margin of the pterygoid. Unfortunately, as the specimen is incomplete, *Portugalosuchus* lacks most diagnostic characters of *Borealosuchus* (Brochu, 2000; Brochu *et al.*, 2012), such as the presence of slender limb bones; the posterodorsal extension of the surangular through the retroarticular process; rectangular unkeeled dorsal osteoderms with a broad anterolateral process (also present in gavialoids and *Bernissartia*); bipartite ventral osteoderms (also present in *Diplocynodon* and *Leidyosuchus*); the nasals broadly separated from the external naris; the dentary teeth occluding in deep pits between the maxillary alveoli; the fourth and fifth maxillary alveoli similar in size (also present in other extinct crocodylians such as *Leidyosuchus*, most *Diplocynodon*, *Pristichampsus* and *Prodiplocynodon*); or the presence of two confluent enlarged caniniforms in the dentary (also present in diplocynodontines and *Leidyosuchus*).

The new taxon shares several similarities with Allodaposuchidae. Some of these similarities are related to the postorbital bar and have already been mentioned in the comparisons with Gavialoidea. With Allodaposuchidae, *Portugalosuchus* shares the presence of a secondary choana posteroventrally oriented, without a septum and flush with the pterygoid surface (also shared with gavialoids and most non-crocodylian eusuchians); postorbital–squamosal suture ventrally oriented (also present in some gavialoids, *Iharkutosuchus* and some *Diplocynodon*); frontoparietal suture linear and deeply entering within the supratemporal fenestra (also shared with Hylaeochampsidae and *Diplocynodon*); and the presence of a smooth braincase wall lateral to the basisphenoid rostrum (shared with the allodaposuchid *Agaresuchus* and Crocodyloidea). *Portugalosuchus* also differs from Allodaposuchidae in several characters. One of the most important differences is the absence of a shallow fossa at the anteromedial corner of the supratemporal fenestra, which is usually considered very diagnostic for Allodaposuchidae. The anteromedial corner of the supratemporal fenestra of *Portugalosuchus* is not totally smooth and presents two small longitudinal grooves (Fig. 7), but not as the shallow depression present in *Bernissartia*, the Glen Rose Form, some goniopholidids and Allodaposuchidae. Another important difference is the presence of an external mandibular fenestra, which is absent in all members of Allodaposuchidae. The size relationship between the orbits and the supratemporal fenestra is also different from the allodaposuchids. *Portugalosuchus* has very large fenestrae, even slightly larger than the orbits, and a very narrow intertemporal bar, while the orbits and fenestrae in allodaposuchids are smaller, as the orbit is bigger than the fenestra. However, *Portugalosuchus* does not preserve important parts of the skull that are diagnostic for Allodaposuchidae, such as the otic region or the paroccipital processes, making further comparisons difficult.

In addition, the overall morphology of the skull of *Portugalosuchus* presents some characters that are reminiscent of Tethysuchia (Pholidosauridae and Dyrosauridae), such as the shape and size of the orbits and the supratemporal fenestrae, the skull table, the postorbital bar or the external mandibular fenestra. However, only the presence of a choana showing the eusuchian condition is enough to rule out its relation to any of these clades.

THE IMPORTANCE OF THE EXTERNAL MANDIBULAR FENESTRA IN *PORTUGALOSUCHUS*

As suggested by the results of our phylogenetic analyses, the presence or absence of the external mandibular fenestra in *Portugalosuchus* is key for understanding and resolving its phylogenetic position among non-crocodylian eusuchians and crocodylians. This structure is absent in most neosuchians closely related to Eusuchia and non-crocodylian eusuchians, such as *Shamosuchus*, *Bernissartia*, some goniopholidids, *Theriosuchus*, *Pachycheilosuchus*, Hylaeochampsidae and Allodaposuchidae (Brochu *et al.*, 2012). As all crocodylians (with this region of the mandible preserved) have an external mandibular fenestra, the most parsimonious hypothesis would be that the presence of this structure is a synapomorphy of Crocodylia.

Although we acknowledge that this scenario could be more complex if the gavialoid *Eothoracosaurus* lacks the fenestra [as pointed out by Brochu *et al.* (2012)], making the fenestra plesiomorphically absent for Crocodylia, and it was gained independently at least twice in the group (in Gavialoidea and in non-gavialoid crocodylians). However, it is very likely that *Eothoracosaurus* had an external mandibular fenestra. Brochu (2004; Fig. 9) illustrates that both mandibular rami of the holotype of *Eothoracosaurus mississippiensis* have a broken area at exactly the part where the fenestra would be located. This could be explained by the presence of a tiny fenestra in that region, creating a more fragile and breakable area. Finally, if present in *Eothoracosaurus*, the fenestra should be considered synapomorphic for Crocodylia.

Another problem is the position, shape and size of the fenestra throughout Crocodylia. Most crocodylians present a medium to large-sized elliptical fenestra, with the dentary splitting posteriorly to form both anterodorsal and anteroventral margins and the surangular and the angular composing the posterodorsal and posteroventral margins, respectively. Nevertheless, some crocodylians, such as *Borealosuchus threeensis*, *B. wilsoni*, *Deinosuchus*, *Mekosuchus*, *Portugalosuchus* and maybe *Eothoracosaurus*, present a small, narrow and slit-shaped external mandibular fenestra. The presence of a small fenestra in *Eothoracosaurus*, *Deinosuchus* and *Portugalosuchus* could indicate that this is the plesiomorphic condition for Crocodylia. In other non-gavialid gavialoids, such as *Thoracosaurus neocesariensis* de Kay, 1842 and *Thoracosaurus macrorhynchus* de Blainville, 1835, the fenestra is poorly known (Brochu *et al.*, 2012). A small fenestra in these latter taxa would reinforce this condition as plesiomorphic for Crocodylia. However, this scenario could be more complex given the small fenestrae and phylogenetic position of *Borealosuchus threeensis*, *B. wilsoni* and *Mekosuchus*. This raises two different hypotheses: either the fenestra was lost and later regained independently in these taxa, or it was simply reduced in size (Brochu, 2004; Brochu *et al.*, 2012).

Taking into account this structure in *Portugalosuchus*, a series of problems also arise. Its position and its bones composition are exclusive to this taxon within Crocodylia. The fenestra is anteriorly located and not mediolaterally coincident with the Meckelian fossa. In addition, it is located between the dentary–angular suture, without the involvement of the surangular.

As previously discussed, it is possible that this fenestra is not homologous to the external mandibular fenestra present in Crocodylia. However, our hypothesis of homology can be supported by the following:

1. As in most crocodylians, the fenestra of *Portugalosuchus* is anteriorly coincident with a longitudinal groove present in the dentary (Fig. 10);
2. It is more parsimonious that this structure corresponds to the external mandibular fenestra than to a new analogous fenestra.

A progressive posterodorsally enlargement of this fenestra (Fig. 13G) allows us to observe the different development states of this structure in crocodylians. Therefore, the position, size and configuration of the fenestra in *Portugalosuchus*, without participation of the surangular, may correspond to the most primitive state of this character within Crocodylia.

To test all of these evolutionary history hypotheses, we have performed several ancestral state reconstruction analyses (see Supporting Information, Figs S20–S25), where the fenestra went from small to larger or vice versa (character 63). The ancestral states were reconstructed using our dataset based on Narváez *et al.* (2016), by maximum-parsimony and maximum-likelihood-Mk1 methods in MESQUITE (Maddison & Maddison, 2018). These analyses were carried out for three different assumptions and obtained different results:

1. The presence, size and morphology of the external mandibular fenestra is unknown for *Eothoracosaurus* (character 63 →?) (Supporting Information, Figs S20, S23). With this assumption, both maximum-parsimony and maximum-likelihood-Mk1 methods show a high probability (67%) for an ancestral state of character 63 corresponding to a small-sized and narrow slit-shaped external mandibular fenestra for Crocodylia;
2. *Eothoracosaurus* lacks an external mandibular fenestra (character 63 → 0) (Supporting Information, Figs S21, S24). In this case, the maximum-parsimony method shows a 50% probability of the presence of small fenestra as the ancestral character of Crocodylia, and 50% uncertainty (Fig. S21). Nevertheless, the maximum-likelihood-Mk1 method shows probabilities of 33% for the absence of fenestra, 22% for the presence of small fenestra and 45% uncertainty for the ancestral state reconstruction of this character in Crocodylia (Fig. S24);
3. *Eothoracosaurus* presents a small, narrow, slit-shaped fenestra (character 63 → 1) (Supporting Information, Figs S22, S25). With this assumption, both maximum-parsimony and maximum-likelihood-Mk1 methods show a 100% of probability for an ancestral state of character 63 corresponding to

a small, narrow, slit-shaped external mandibular fenestra for Crocodylia.

Therefore, these results seem to support the hypothesis that the slit-like opening in the mandible is an early stage of the external mandibular fenestra and its presence is a synapomorphy of Crocodylia. Observing this structure in different developmental stages through Crocodylia, we can infer an evolutionary pattern (Fig. 13), from a small-sized and narrow slit-shaped aperture with a minimal participation of the surangular in the fenestral margin and the dentary covering most of the dorsal margin (e.g. *Borealosuchus wilsoni*, Fig. 13B), to a posterior enlargement of the opening reducing the participation of the dentary in the dorsal margin with the posterodorsal margin is occupied by the surangular (e.g. *Alligator mississippiensis*, Fig. 13F).

Palaeobiogeographical and chronological implications

The palaeogeography of Europe during the Late Cretaceous was controlled by an increase in oceanic expansion due to the creation of a new crust in the mid-Atlantic ridge. The oceanic expansion peaked in the middle of the Cretaceous, producing some of the highest sea-levels during the Late Cretaceous. This phenomenon led to a significant increase in epicontinental seas and flooding of the cratonic areas of Europe, resulting in a large archipelago surrounded by shallow seas (e.g. Haq, 2014; Csiki-Sava *et al.*, 2015 and references therein).

Within this scenario, many works suggest a putative radiation of Crocodylia during the latest Cretaceous of Europe (e.g. Buscalioni *et al.*, 2003; Martin & Delfino, 2010; Puértolas-Pascual *et al.*, 2016). The situation was similar in North America, where the oldest records of Crocodylia also date from the Campanian–Maastrichtian, with specimens belonging to *Borealosuchus*, Alligatoroidea, Crocodyloidea and Gavialoidea (Brochu, 1997; Buscalioni *et al.*, 2003; Martin & Delfino, 2010; Puértolas *et al.*, 2011; Wu & Brinkman, 2015; Puértolas-Pascual *et al.*, 2016). The joint presence of crocodylians in both North America and Europe suggests that the common ancestor of Crocodylia evolved in one of these continents, at pre-Campanian times (Buscalioni *et al.*, 2003) and spread from one continent to the other through sporadic palaeobiogeographic bridges in the North Atlantic (Puértolas *et al.*, 2011). These connections have also been observed in other continental vertebrates from the Late Cretaceous, such as marsupials, theropod

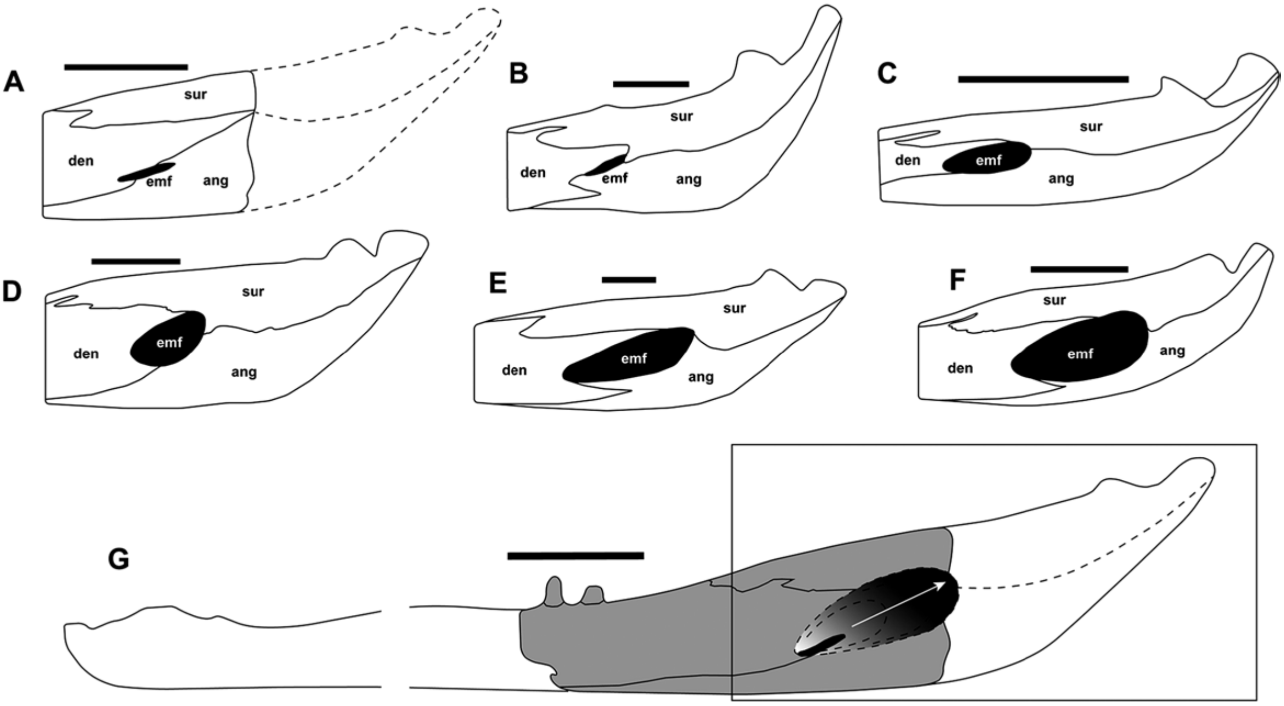

Figure 13. Schematic drawings of the different degrees of development of the external mandibular fenestra (emf) through Crocodylia in lateral view. A, ***Portugalosuchus azenhae* gen. et sp. nov.**; B, *Borealosuchus wilsoni*; C, *Gavialis gangeticus*; D, *Crocodylus niloticus*; E, *Borealosuchus formidabilis*; F, *Alligator mississippiensis*; G, reconstruction of the left mandible of ***Portugalosuchus* gen. nov.** (preserved bones in grey colour) showing a possible growth pattern of the fenestra within Crocodylia. Abbreviations: and, angular; den, dentary; emf, external mandibular fenestra; sur, surangular. Scale bar = 5 cm.

dinosaurs and hadrosaurs, and snakes (e.g. Le Loeuff, 1991; Martin *et al.*, 2005; Pereda-Suberbiola, 2009; Prieto-Marquez & Wagner, 2009; Sues & Averianov, 2009; Benton *et al.*, 2010; Puértolas *et al.*, 2011).

However, the newest phylogenetic hypotheses propose a different palaeobiogeographic scenario, since European taxa previously assigned to Alligatoroidea (*Acynodon*, *Musturzabalsuchus*, *Massaliasuchus*) (Buscalioni *et al.*, 1997, 1999; Delfino *et al.*, 2008a; Martin & Buffetaut, 2008; Martin, 2007, 2010) and Crocodyloidea (*Arenysuchus*) (Puértolas *et al.*, 2011) may actually be non-crocodylian eusuchians within the endemic European clades Hylaeochampsidae and Allodaposuchidae (e.g. Salisbury *et al.*, 2006; Brochu, 2011; Buscalioni *et al.*, 2011; Martin *et al.*, 2016; Narváez *et al.*, 2015, 2016; Turner & Pritchard, 2015). These new results imply that, except for the marine taxon *Thoracosaurus* (Gavialoidea) that was present in both continents and with a probable higher capacity for the dispersion between epicontinental seas (Puértolas-Pascual *et al.*, 2016), there would be no true members of Crocodylia in the Late Cretaceous of Europe.

Considering this more recent phylogenetic framework, there would be a completely different palaeobiogeographic scenario. In this case, eusuchians would probably have arisen in Laurasia, at some point during the Lower Cretaceous (the earliest Eusuchia is *Hylaeochampsa*, from the Barremian of England) and would have diversified between the Early Cretaceous and the Late Cretaceous (Brochu, 1999; Buscalioni *et al.*, 2001, 2003, 2011; Salisbury *et al.*, 2006; Martin & Delfino, 2010; Puértolas *et al.*, 2011). At this point, Eusuchia would have had vicariant evolution on each continent resulting in Crocodylia (with record from the Campanian) in North America, and Hylaeochampsidae (with record from the Barremian) and Allodaposuchidae (with record from the Campanian) in Europe. The presence of Crocodylia in the European Paleocene, with taxa such as Planocraniidae, alligatoroids such as *Diplocynodon* or crocodyloids such as *Asiatosuchus*, would be better explained by dispersal processes from North America or Asia to Europe after the K/Pg extinction event (Martin *et al.*, 2014; Csiki-Sava *et al.*, 2015; Puértolas-Pascual *et al.*, 2016).

Taking into account all of these previous palaeobiogeographic hypotheses, and the phylogenetic results obtained after adding the new taxon *Portugalosuchus azenhae*, we can establish new preliminary hypotheses about the origin of Crocodylia. *Portugalosuchus* is one of the earliest records of Eusuchia and probably the earliest known record of Crocodylia, helping to fill a gap from the Barremian to the Campanian. Previous hypotheses pointed to a pre-Campanian origin of Crocodylia, probably during the middle of the Cretaceous (e.g. Brochu, 2003; Buscalioni *et al.*, 2003; Blanco *et al.*, 2014). However, until now, it was not possible to trace a more accurate temporal range for the origin of the crown group Crocodylia. The presence of *Portugalosuchus* in the Cenomanian of Europe, being the sister taxon to all other non-gavialoid crocodylians, indicates that the most likely origin of Crocodylia was during the Early Cretaceous, with a divergence from Gavialoidea before or during the Early Cenomanian.

The presence of the first eusuchians and crocodylians in Europe points to a more plausible European origin for both clades. Therefore, the discovery of the new taxon indicates a Laurasian origin for Eusuchia before the Barremian, probably in Europe, and that the common ancestor of all crocodylians evolved during the Early Cretaceous around the Tethys Sea (Holliday & Gardner, 2012; Rabi & Sebök, 2015) or the Protoatlantic Ocean, with a later divergence that began before the Late Cenomanian. Then, the first crocodylians dispersed throughout Europe and North America, resulting in the main lineages of Crocodylia. In order to test all these hypotheses, further studies, including palaeobiogeographic analyses, are necessary.

CONCLUSIONS

Portugalosuchus azenhae, described here, is the only well-documented and currently valid eusuchian species for the Cenomanian of Europe. Moreover, except for the Barremian *Hylaeochampsa vectiana*, *Portugalosuchus azenhae* is the oldest known occurrence of an eusuchian crocodylomorph so far.

The results of the phylogenetic analysis place this taxon within Crocodylia, as the sister taxon to all other non-gavialoid crocodylians. *Portugalosuchus* is also the only Late Cenomanian Crocodylia known for Portugal and, until now, the oldest member of the group worldwide. However, due to the low support in its phylogenetic position, a placement outside of Crocodylia should not be ruled out.

Morover, this taxon presents a series of novel features related to the shape and position of the external mandibular fenestra, which provide new clues on the evolution of this structure throughout Eusuchia. According to our analyses, the morphology of this fenestra in *Portugalosuchus* is very likely to represent the ancestral condition for Crocodylia.

Palaeobiogeographically, the age of this taxon indicates a pre-Cenomanian or Cenomanian origin for Crocodylia, around the Tethys Sea or the Protoatlantic Ocean, probably in Europe. Therefore, the discovery of this new taxon sheds light on the origin of Eusuchia and Crocodylia and helps fill a gap in the crocodylomorph fossil record during the Cretaceous.

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SUPPORTING INFORMATION

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

Figure S1. Detail of the dentition and occlusion pattern of *Allodaposuchus precedens* (PSMUBB V 438). The arrows indicate the position of the occlusion pits. Abbreviations: mx, maxilla; n, nasal; pmx, premaxilla. Grey colour represents broken surfaces.

Figure S2. Detail of the preorbital region of *Allodaposuchus precedens* (PSMUBB V 438). The black arrow marks posterior process of maxilla. Abbreviations: fr, frontal; la, lachrimal; mx, maxilla.; na, nasal; pfr, prefrontal. Grey colour represents broken surfaces.

Figure S3. Different degrees of closure of the supratemporal fenestra. A, *Agaresuchus subjuniperus*; B, *Arenysuchus gascabadiolorum*; C, *Allodaposuchus precedens*; D, *Caiman yacare*; E, *Osteolaemus osborni*; F, *Melanosuchus niger*; G, *Paleosuchus trigonatus*; H, *Paleosuchus palpebrosus*; I, *Iharkutosuchus makadii*. Scale bar = 5 cm.

Figure S4. Ventral view of *Allodaposuchus precedens* holotype (MAFI Ob3131), exhibiting the capitate process orientation and the exit for the cranial nerve in different coronal planes. Abbreviations: cap, capitate process; olf, olfactory nerve exit. Grey colour represents broken surfaces.

Figure S5. Ventral view of *Agaresuchus subjuniperus* holotype (MPZ 2012/288). Interpretation of the right choanal margin. Abbreviations: cho, choana.

Figure S6. Posterior view showing the relationships between basioccipital, basisphenoid and pterygoid in: A, *Agaresuchus subjuniperus* holotype (MPZ 2012/288); B, *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184); C, *Alligator mississippiensis*; D, *Crocodylus porosus*. Abbreviations: bo, basioccipital; bs, basisphenoid; pt, pterygoid. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

Figure S7. Ventral view of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184). The black arrow marks the real suture between the palatine and the pterygoid. Abbreviations: pa, palatine; pa-pt, palatine–pterygoid contact suture; pt, pterygoid. Grey colour represents broken surfaces.

Figure S8. Lateral view of the left (A) and right (B) otic regions of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184). The white lines show where the posterior otic area is eroded. Abbreviations: q, quadrate; qj, quadratojugal; sq, squamosal.

Figure S9. Posterior view of the occipital region of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184) showing the ducts of the pneumatic system within the parietal and the lateral carotid foramen laterally opened to the basisphenoid. Abbreviations: bs, basisphenoid; car fo, duct of the carotid foramen.

Figure S10. Medial view of the left mandible of *Iharkutosuchus makadii* (MTM V 2012.29.1). Abbreviations: ar, articular; fae, foramen aerum; fo, anterior perforation for mandibular ramus of cranial nerve V; sp, splenial.

Figure S11. Dorsal view of the left mandible of *Iharkutosuchus makadii* (MTM V 2012.29.1) showing a greater coronoid–angular contact at the lateral margin of the Meckelian fossa, location of the foramen aerum and a linear and anteroposteriorly oriented surangular–articular suture. Abbreviations: an, angular; ar, articular; den, dentary; cor, coronoid; fae, foramen aerum; sp, splenial.

Figure S12. Dorsal view of the skull holotype of *Iharkutosuchus makadii* (MTM 2006.52.1) showing the length/width ratio of the external naris with black lines.

Figure S13. Ventral view of the skull of *Iharkutosuchus makadii* (MTM 2006.53.1). The red areas represent depressions and the yellow areas represent elevations. Abbreviations: bo, basioccipital; ch, choana; ect, ectopterygoid; exo, exoccipital; lsf, laterosphenoid; mef, median eustachian foramen; mx, maxilla; pa, palatine; pmx, premaxilla; pt, pterygoid; q, quadrate; qj, quadratojugal. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article.)

Figure S14. Lateral (A) and posterior (B) views of the skull of *Iharkutosuchus makadii* (MTM 2006.54.1) showing the relations of the cranioquadrate passage. Abbreviations: cqp, cranioquadrate passage; exo, exoccipital; fae, foramen aerum; q, quadrate; qj, quadratojugal; sq, squamosal

Figure S15. Posterior view of the skull of *Iharkutosuchus makadii* (MTM 2006.53.1). Abbreviations: bo, basioccipital; bs, basisphenoid; bs tub, basioccipital tubera; exo., exoccipital; exo pro, exoccipital ventral process; fae, foramen aerum; fm, foramen magnum; pt, pterygoid; q, quadrate; sq, squamosal, su, supraoccipital.

Figure S16. Phylogenetic relationships of *Portugalosuchus azenhae* based on the matrix of Narváez *et al.* (2016). Strict consensus tree of 4464 most parsimonious cladograms with 789 evolutionary steps. Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

Figure S17. Phylogenetic relationships of *Portugalosuchus azenhae* when the taxon is forced outside Crocodylia, based on the matrix of Narváez *et al.* (2016). Strict consensus cladogram (790 steps).

Figure S18. Phylogenetic relationships of *Portugalosuchus azenhae* when we consider that *Portugalosuchus* lacks external mandibular fenestra, based on the matrix of Narváez *et al.* (2016). Strict consensus cladogram (788 steps). Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

Figure S19. Phylogenetic relationships of *Portugalosuchus azenhae* based on the matrix of Turner (2015). Strict consensus tree of 660 most parsimonious cladograms with 1659 evolutionary steps. Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%. Crown group Crocodylia in blue colour.

Figure S20. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → ?).

Figure S21. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → 0).

Figure S22. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → 1).

Figure S23. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → ?).

Figure S24. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → 0).

Figure S25. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez *et al.* (2016) (*Eothoracosaurus*; character 63 → 1).

Figure S26. Pictures of *Portugalosuchus* during the laboratory preparation work. Ventral (A) and lateral (B) views of ML1818, below, the same pictures with coloured bones differentiating the skull (in red) and the mandible (in blue). Thick black arrows show the slight rotation of the mandible. Abbreviations: ang, angular; emf, external mandibular fenestra; den, dentary; sur, surangular; ju, jugal; la, lachrymal; mx, maxilla; pfr, prefrontal; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal.

SUPPLEMENTARY INFORMATION

A new eusuchian crocodylomorph from the Cenomanian (Late Cretaceous) of Portugal reveals novel implications on the origin of Crocodylia

Supplementary Information from the article:
Octávio Mateus, Eduardo Puértolas-Pascual, Pedro M Callapez; A new eusuchian crocodylomorph from the Cenomanian (Late Cretaceous) of Portugal reveals novel implications on the origin of Crocodylia, *Zoological Journal of the Linnean Society*, , zly064, https://doi.org/10.1093/zoolinnean/zly064

1) Comments and modifications on the anatomical characters of basal eusuchians from the original matrix of Narváez et al. (2016)

Several character scorings of some taxa belonging to Allodaposuchidae and Hylaeochampsidae have been modified after first-hand observation of several specimens, such as *Allodaposuchus precedens*, *Arenysuchus*, *Agaresuchus subjuniperus* and *Iharkutosuchus*. These changes are detailed and justified below.

Changes in *Allodaposuchus precedens*

Character 92 (2 to 0): 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).

The specimen PSMUBB V 438 shows occlusion pits placed lingually to the toothrow (Fig. S1), exhibiting an overbite rather than interfingering in the dentition. Except for the position between the sixth and seventh maxillary teeth where an interalveolar pit is located.

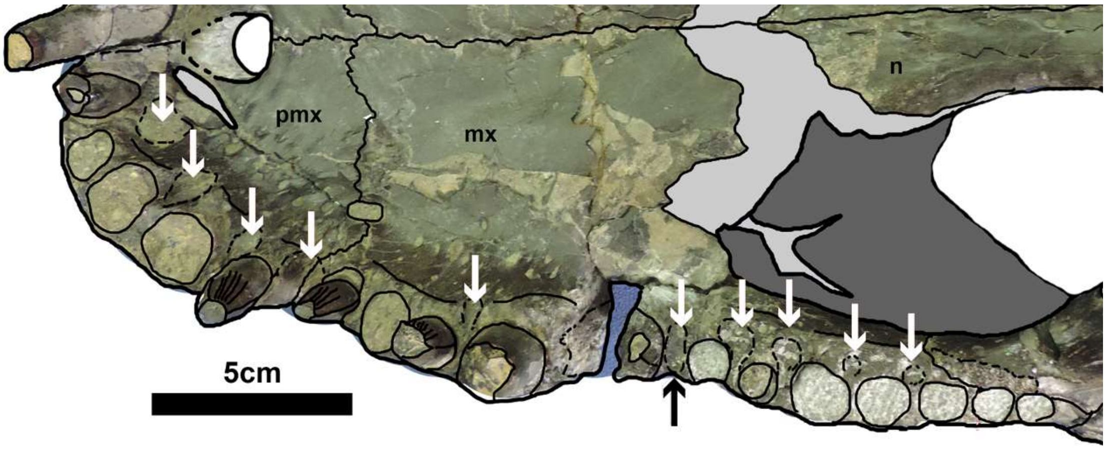

Figure S1. Detail of the dentition and occlusion pattern of *Allodaposuchus precedens* (PSMUBB V 438). The arrows indicate the position of the occlusion pits. Abbreviations: mx., maxilla; n., nasal; pmx., premaxilla. Grey color represents broken surfaces.

Character 128 (? to 1): 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) or prefrontal extending an anterior process that separates the nasal from the lacrimal (3). State of character (3) from Aguilera *et al*. (2006).

In PSMUBB V 438, a posterior process of maxilla, within the left lachrymal, is observed (Fig. S2).

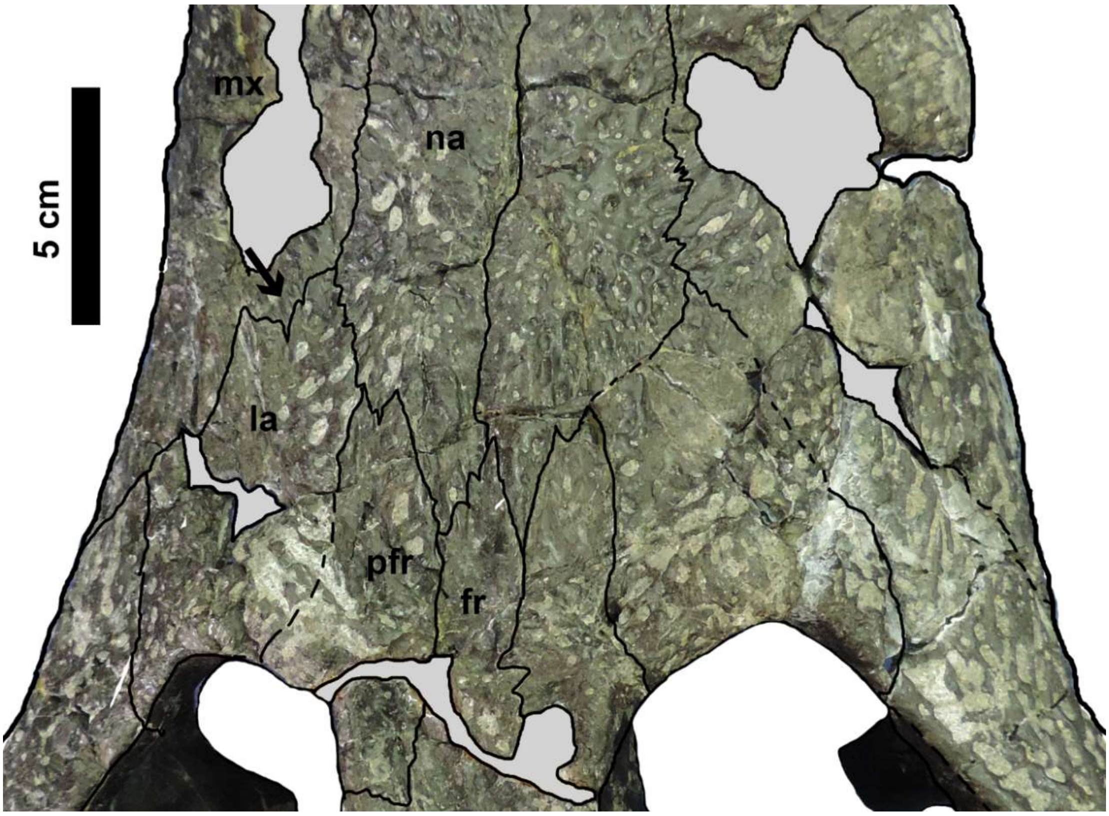

Figure S2. Detail of the preorbital region of *Allodaposuchus precedens* (PSMUBB V 438). The black arrow marks posterior process of maxilla. Abbreviations: fr., frontal; la., lachrimal; mx., maxilla.; na., nasal; pfr., prefrontal. Grey color represents broken surfaces.

Character 131 (? to 0): Anterior tip of frontal (0) forms simple acute point or (1) or forms broad, complex sutural contact either with the nasals or prefrontals. State of character (1) modified by Salas-Gismondi *et al*. (2015).

In PSMUBB V 438, the anterior process of the frontal forms an acute tip (Fig. S2).

Character 152 (1 to 0): Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae small, with a circular or nearly circular shape (1) or supratemporal fenestra closes during ontogeny (2) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (3). State of character (3) from Cidade *et al*. (2017). This character has also been changed from state 1 to 0 in *Lohuecosuchus*, *Agaresuchus* and *Arenysuchus*; and from state 1 to 2 in *Paleosuchus*. The small overlap observed in Allodaposuchidae (Fig. S3A-C) cannot be considered to be the same state as observed in caimans, *Osteolaemus* and other taxa, such as *Voay* and *Baryphracta*. In these latter taxa, the dermal bones surrounding the fenestra (squamosal, parietal, postorbital) have laminae that clearly project over (and even hiding) the supratemporal fossa (Fig. S3D-F). We have also changed this scoring in *Paleosuchus* (from 1 to 2), since the supratemporal fenestra of this taxon is closed during ontogeny, as it is in *Iharkutosuchus* (Fig. S3G-I).

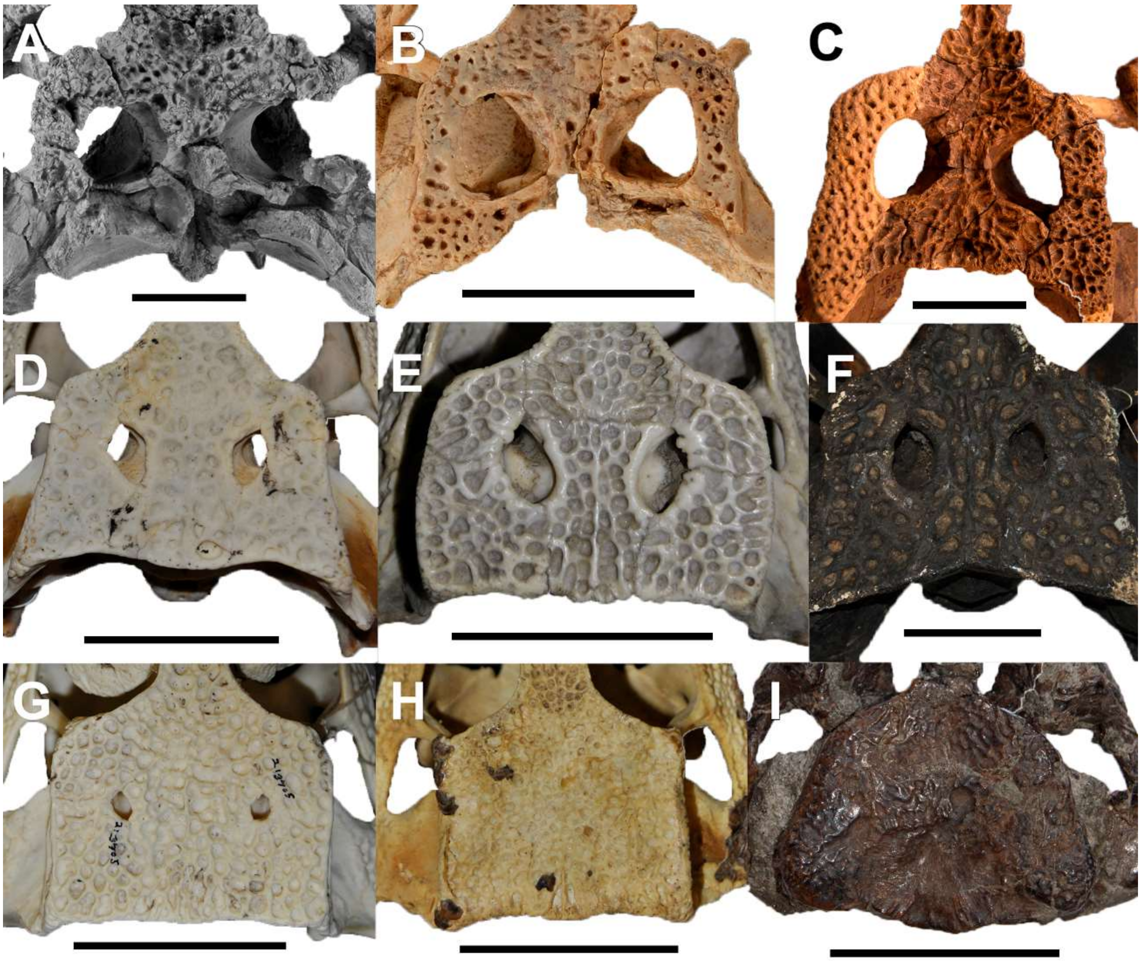

Figure S3. Different degrees of closure of the supratemporal fenestra. A. *Agaresuchus subjuniperus*; B. *Arenysuchus gascabadiolorum*; C. *Allodaposuchus precedens*; D. *Caiman yacare*; E. *Osteolaemus osborni*; F. *Melanosuchus niger*; G. *Paleosuchus* *trigonatus*; H. *Paleosuchus palpebrosus*; I. *Iharkutosuchus makadii*. Scale bar = 5 cm.

Character 166 (0 to 1): Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

The capitate process was originally coded as laterally oriented in *A. precedens*. Indeed, the lateral branch of the capitate process in *A. precedens* seems to be laterally oriented (as in most eusuchians). However, the original description of this character by Brochu (1997) refers to the relationship between this lateral branch and the exit of the olfactory nerve. In most eusuchians (including *A. precedens*), the exit of the olfactory nerve is anteriorly placed in relation to the capitate process (Fig. S4). While in a few taxa such as gavialoids, the exit of the olfactory nerve and the capitate process are in the same coronal plane.

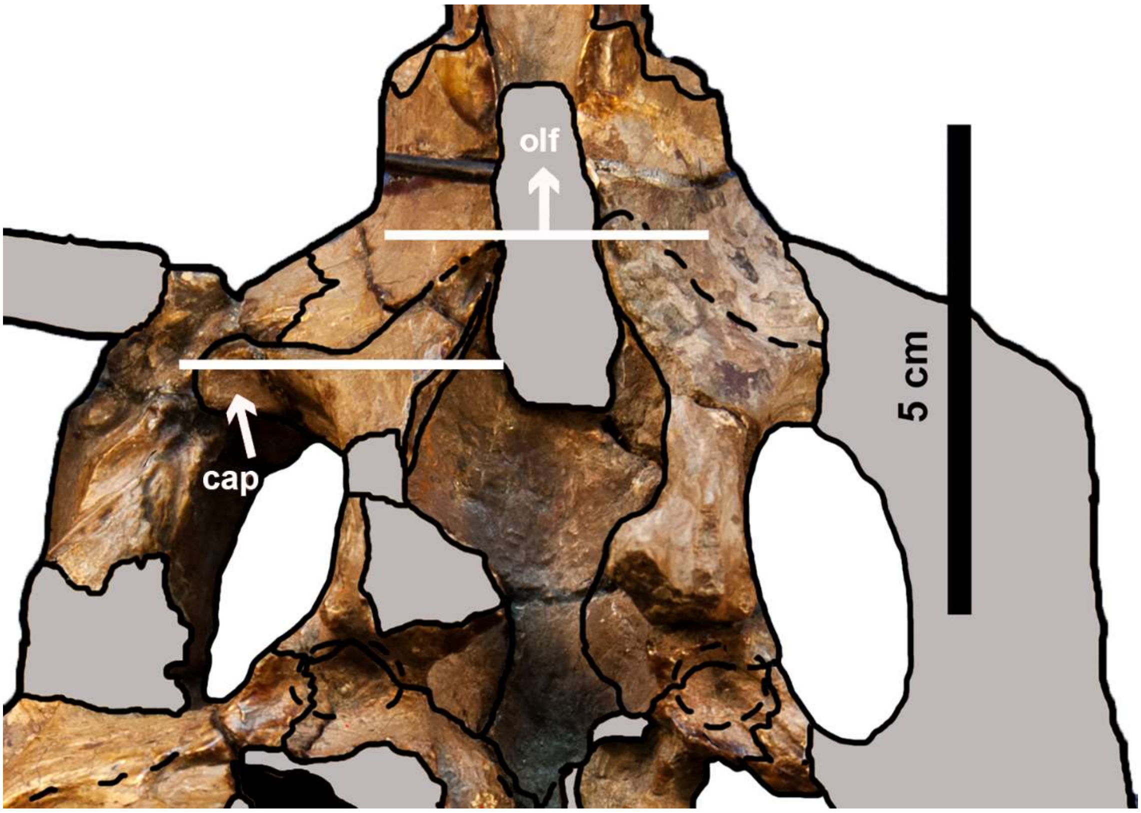

Figure S4. Ventral view of *Allodaposuchus precedens* holotype (MAFI Ob3131), exhibiting the capitate process orientation and the exit for the cranial nerve in different coronal planes. Abbreviations: cap., capitate process; olf., olfactory nerve exit. Grey color represents broken surfaces.

Changes in *Agaresuchus subjuniperus*

Character 124 (? to 0): Posterior rim of internal choana not deeply notched (0) or deeply notched (1).

Although the choana is not well preserved in *A. subjuniperus*, the right margin is conserved (Fig. S5), and the notch present in caimans is not observed.

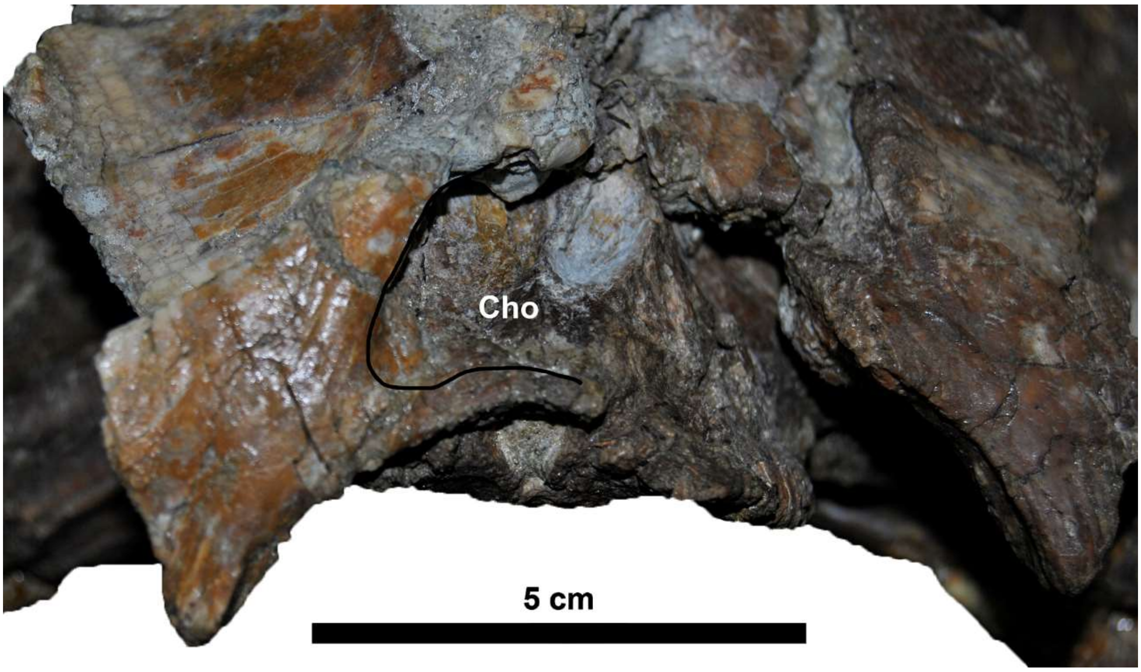

Figure S5. Ventral view of *Agaresuchus subjuniperus* holotype (MPZ 2012/288). Interpretation of the right choanal margin. Abbreviations: cho., choana.

Character 152 (1 to 0): Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1) or supratemporal fenestra closes during ontogeny (2).

This change of character is justified in the *A. precedens* section.

Character 173 (1 to 0): 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).

The basisphenoid is not broadly exposed and the pterygoid is short ventral to the median eustachian opening (Fig. S6A), presenting less exposure than what is observed in most alligatoroids (Fig. S6C).

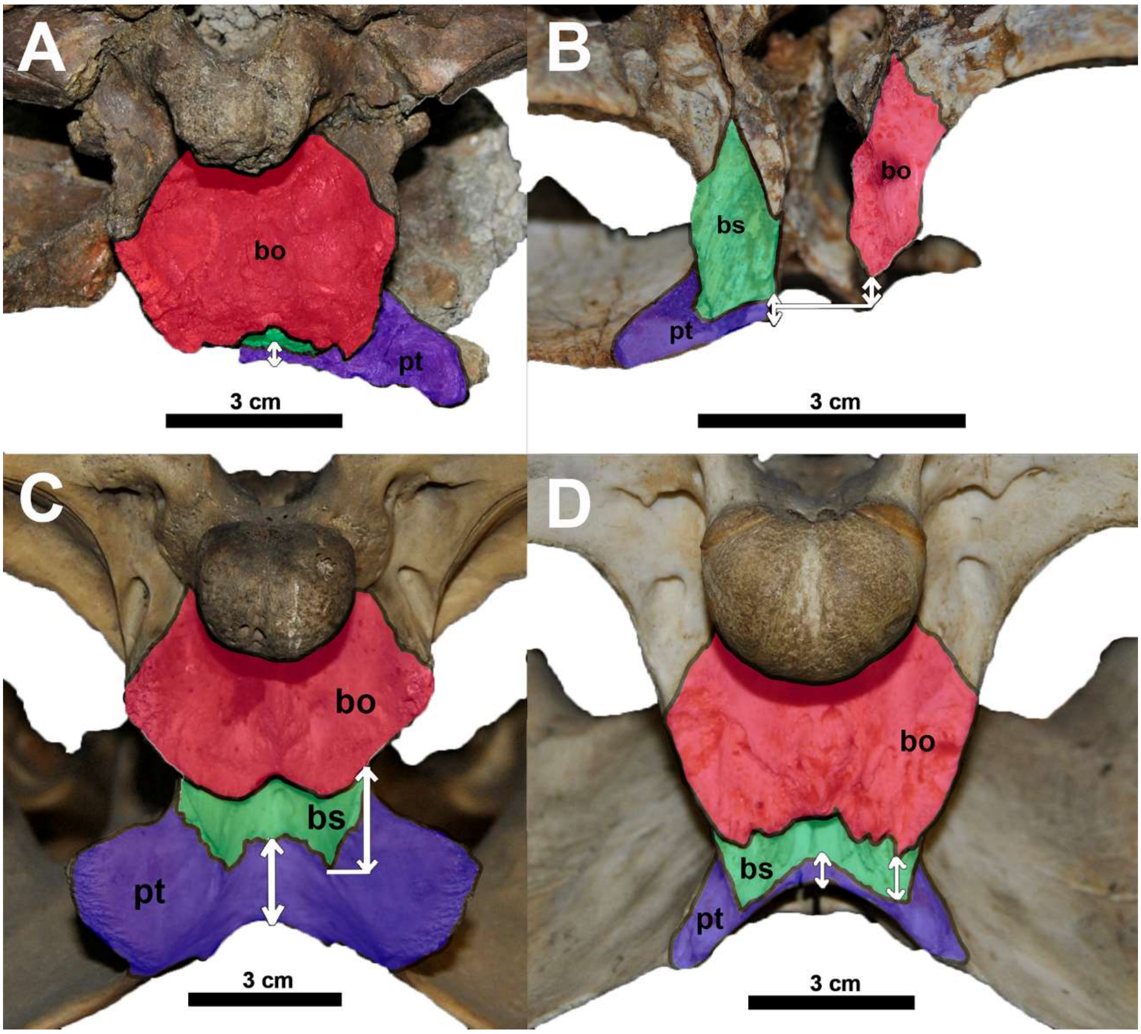

Figure S6. Posterior view showing the relationships between basioccipital, basisphenoid and pterygoid in A. *Agaresuchus subjuniperus* holotype (MPZ 2012/288); B. *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184); C. *Alligator mississippiensis*; D. *Crocodylus porosus*. Abbreviations: bo., basioccipital; bs., basisphenoid; pt., pterygoid. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article).

Changes in *Arenysuchus gascabadiolorum*

Character 79 (? to 0): Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2).

Although most of the teeth have not been preserved, *Arenysuchus* retains three teeth and most of the dental alveoli, so that the circular shape of the alveoli can be determined with certainty.

Character 118 (? to 1): Palatine-pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra.

Although on the left side the suture cannot be determined due to poor preservation, on the right side the palatine-pterygoid suture is visible and clearly not placed in the most posterior angle of the suborbital fenestra (Fig. S7).

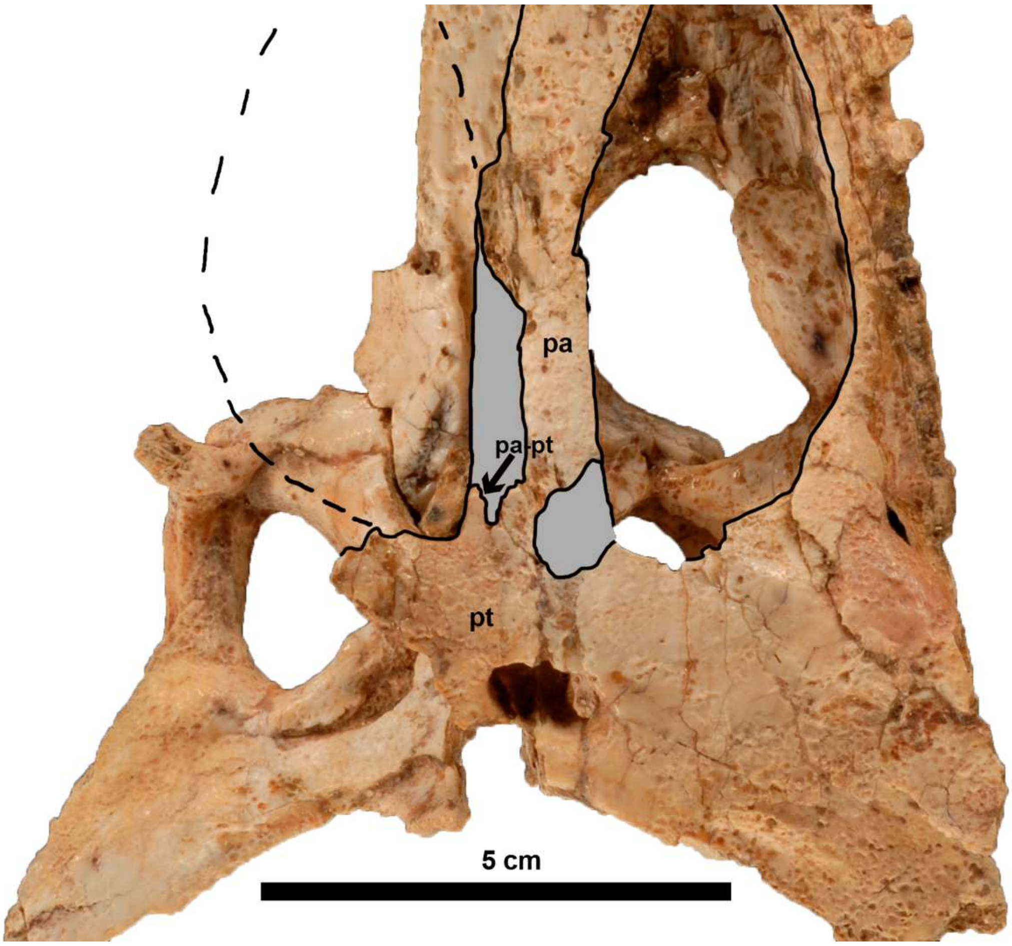

Figure S7. Ventral view of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184). The black arrow marks the real suture between the palatine and the pterygoid. Abbreviations: pa., palatine; pa-pt., palatine - pterygoid contact suture; pt., pterygoid. Grey color represents broken surfaces.

Character 132 (? to 0): Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).

As in *A. subjuniperus*, the sutures in this area are not well marked, but an ascending process of the ectopterygoid on the medial side of the postorbital bar can be observed.

Character 148 (0 to ?): 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 posterior margin of the external auditory meatus (1) or extends only to the caudoventral corner of the external auditory meatus (2).

The posterior region of the external auditory meatus is not well preserved (Fig. S8), therefore this character and the **character 149 (0 to ?)** cannot be codified.

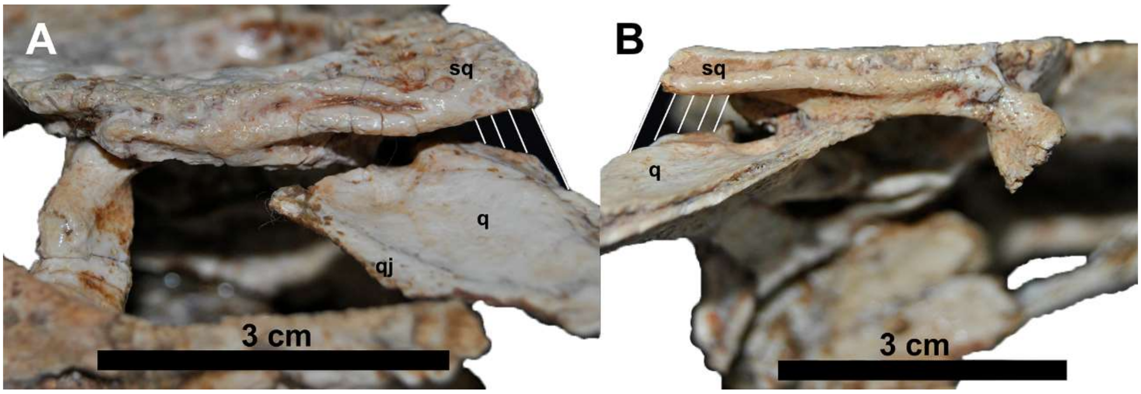

Figure S8. Lateral view of the left (A) and right (B) otic regions of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184). The white lines show where the posterior otic area is eroded. Abbreviations: q., quadrate; qj., quadratojugal; sq., squamosal.

Character 152 (1 to 0): Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1) or supratemporal fenestra closes during ontogeny (2).

This modification is justified in the *A. precedens* section.

Character 158 (0 to ?): 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).

As most of the posterior region of the skull in *Arenysuschus* is partially eroded, the posterior extension of the squamosals and its relation with the paroccipital processes cannot be determined.

Character 167 (? to 0): Parietal with recess communicating with pneumatic system (0) or solid, without recess (1).

Due to damage in the occipital region, several ducts that could correspond with the pneumatic system of the parietal can be observed (Fig. S9).

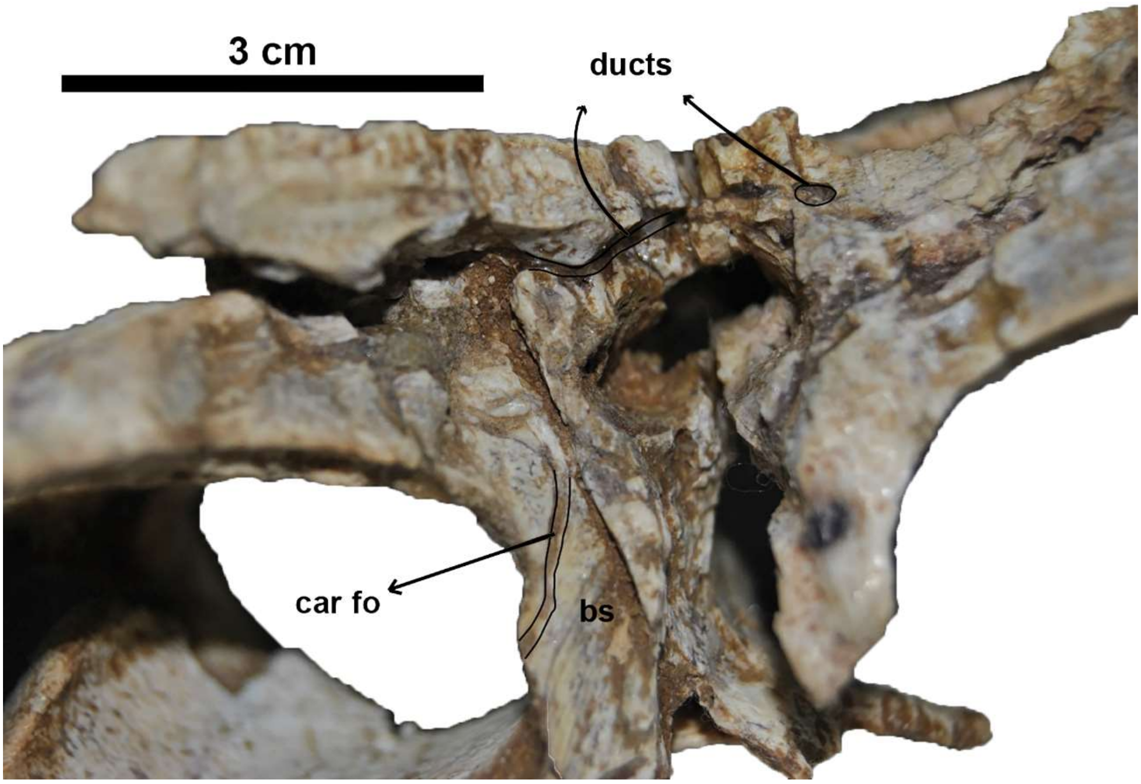

Figure S9. Posterior view of the occipital region of *Arenysuchus gascabadiolorum* holotype (MPZ 2011/184) showing the ducts of the pneumatic system within the parietal and the lateral carotid foramen laterally opened to the basisphenoid. Abbreviations: bs., basisphenoid; car fo., duct of the carotid foramen.

Character 170 (? to 1): External surface of basioccipital ventral to occipital condyle oriented posteroventrally (0) or posteriorly (1) at maturity.

Part of the right basioccipital has been preserved (Fig. S6B) and a posterior orientation can be determined.

Character 173 (1 to ?): 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).

Although part of this area of the occipital region has been preserved (Fig. S6B), the exposure of the basisphenoid cannot be safely determined.

Changes in *Iharkutosuchus makadii*

Probably because the codings for *Iharkutosuchus* proposed by Narváez *et al*. (2016) are mainly based on the original codings of Ösi *et al*. (2007), and some new cranial elements were discovered after the Ösi *et al*. (2007) publication, we have been able to codify many characters that originally appeared as (?).

Character 52 (? to 0): Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1).

In the best preserved mandible MTM V 2012.29.1, the splenial has an anterior perforation for the mandibular ramus of cranial nerve V (Fig. S10).

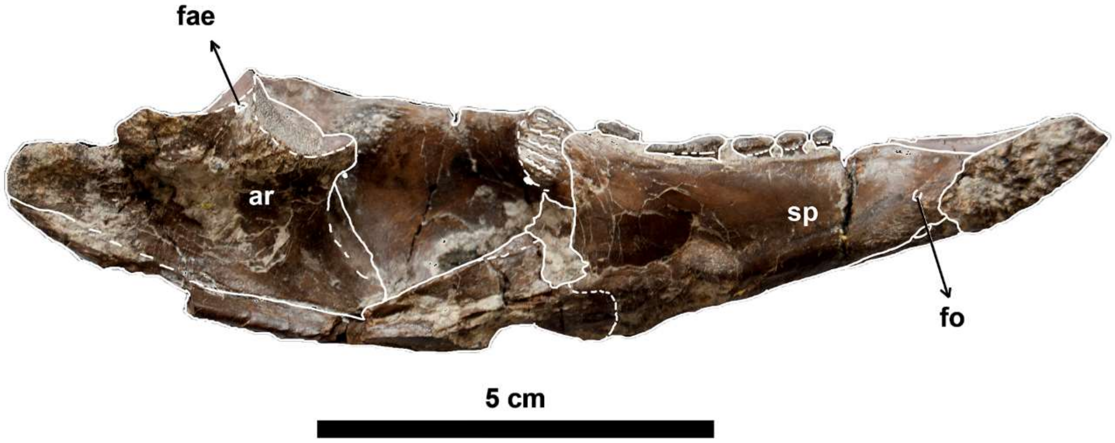

Figure S10. Medial view of the left mandible of *Iharkutosuchus makadii* (MTM V 2012.29.1). Abbreviations: ar., articular; den., fae., foramen aerum; fo., anterior perforation for mandibular ramus of cranial nerve V; sp., splenial.

Character 53 (? to 0): 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).

No perforations are observed on the medial surface of the splenial (Fig. S10).

Character 54 (? to 0): 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).

In the specimen MTM V 2012.29, the splenial shows a small participation in the symphysis, being adjacent to about 2 or 3 alveoli.

Character 57 (? to 0): Inferior process of coronoid overlaps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

Although the coronoid has not been preserved in MTM V 2012.29, the contact surfaces with the angular can be observed. The contact area between the coronoid and the angular is much more developed in the lateral margin of the Meckelian fossa (Fig. S11), therefore *Iharkutosuchus* would present the state 0.

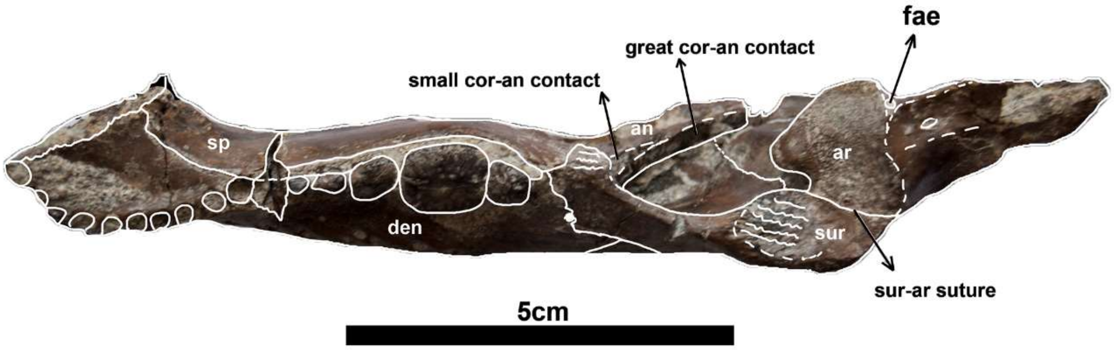

Figure S11. Dorsal view of the left mandible of *Iharkutosuchus makadii* (MTM V 2012.29.1) showing a greater coronoid - angular contact at the lateral margin of the Meckelian fossa, location of the foramen aerum and a linear and anteroposteriorly oriented surangular - articular suture. Abbreviations: an., angular; ar., articular; den., dentary; cor., coronoid; fae., foramen aerum; sp., splenial.

Character 69 (? to 0): Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1).

In the specimen MTM V 2012.29, this foramen can be observed and perforates the surangular entirely.

Character 70 (? to 0): Foramen aerum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1).

In the specimen MTM V 2012.29, the foramen can be distinguished and located at the lingual margin of retroarticular process (Fig. S11).

Character 71 (1 to 0): Retroarticular process projects posteriorly (0) or projects posterodorsally (1).

Probably, this character was originally codified with state (1) based on the incomplete specimen MTM V 2006.63.1 published by Ösi et al. (2007), from which the retroarticular process was interpreted. Nevertheless, taking into account the more complete specimen MTM V 2012.29, the retroarticular process is posteriorly projected

(Fig. S10) rather than posterodorsally.

Character 73 (? to 0): Surangular-articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

In the specimen MTM V 2012.29, the surangular-articular suture is linear and anteroposteriorly oriented (Fig. S11).

Character 83 (? to 1): Naris circular or keyhole-shaped (0) or wider than long (1) or anteroposteriorly long and prominently teardrop-shaped (2).

Taking into account the holotype MTM 2006.52.1, whose external naris is complete, it can be seen that it is clearly wider than long (Fig. S12).

Character 99 (? to 0): Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary-maxillary suture (1).

In the holotype MTM 2006.52.1, the palate is entirely preserved and no vomer is observed.

Character 103 (? to 0): Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1).

In the holotype MTM 2006.52.1 and in the specimen MTM 2006.53.1, most of the palate region is preserved and there is no foramen for the palatine ramus of the cranial nerve V (Fig. S13).

Character 123 (0 to 2): 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).

In the specimens MTM 2006.53.1 and MTM 2006.56.1, where the choanal area is best preserved, the choana is associated with a series of depressions resulting in a neck around the aperture (Fig. S13). In the holotype MTM 2006.52.1, these structures are not so obvious.

Character 129 (1 to 0): Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1).

In the holotype MTM 2006.52.1 and in the specimen MTM 2006.53.1, a wide anterior process of the frontal separates the prefrontals (Fig. S12).

Figure S12. Dorsal view of the skull holotype of *Iharkutosuchus makadii* (MTM 2006.52.1) showing the length / width ratio of the external naris with black lines.

Character 135 (? to 0): Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1).

In *Iharkutosuchus*, the dorsal margin of the jugal does not present the typical elevation in this area, therefore the postorbital bar insertion is at the same level with the lateral jugal surface.

Character 143 (? to 1): 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).

In the specimens MTM 2006.52.1, MTM 2006.53.1, MTM 2006.54.1, MTM 2006.55.1, this contact can be observed, being the quadratojugal the element that contacts the postorbital (Fig. S13).

Figure S13. Ventral view of the skull of *Iharkutosuchus makadii* (MTM 2006.53.1) . The red areas represent depressions and the yellow areas represent elevations. Abbreviations: bo., basioccipital., ch., choana; ect., ectopterygoid; exo., exoccipital; lsf., laterosphenoid; mef., median eustachian foramen; mx., maxilla; pa., palatine; pmx., premaxilla; pt., pterygoid; q., quadrate; qj., quadratojugal. (For proper interpretation of the coloured sutures and structures in this figure, the reader is referred to the web version of this article).

Character 146 (? to 0): Postorbital-squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

In the specimens MTM 2006.52.1, MTM 2006.53.1, MTM 2006.54.1, MTM 2006.55.1, this contact is visible, being the postorbital-squamosal suture ventrally oriented.

Character 148 (? to 0): 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 posterior margin of the external auditory meatus (1) or extends only to the caudoventral corner of the external auditory meatus (2).

Character 149 (? to 0): Posterior margin of otic aperture not defined and gradually merging into the exoccipital (0) or smooth and continuous with the paroccipital process (1) or posterior margin of otic aperture inset (2).

Referring to the characters 148 and 149, the posterior area of the otic aperture is best preserved in MTM 2006.54.1. This specimen shows the typical condition observed in *Hylaeochampsa* and allodaposuchids, with the quadrate and squamosal not in contact posteriorly to the external auditory meatus and the posterior margin of the otic aperture merging into the exoccipital, showing a laterally open cranioquadrate passage, more verticalized and ventrally oriented than in Allodaposuchidae (Fig. S14).

Character 159 (? to 0): Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paroccipital process.

In the specimens where this area is preserved, such as MTM 2006.53.1 and MTM 2006.54.1 (Fig. S14A), the squamosal does not extend to the lateral extent of the paroccipital process.

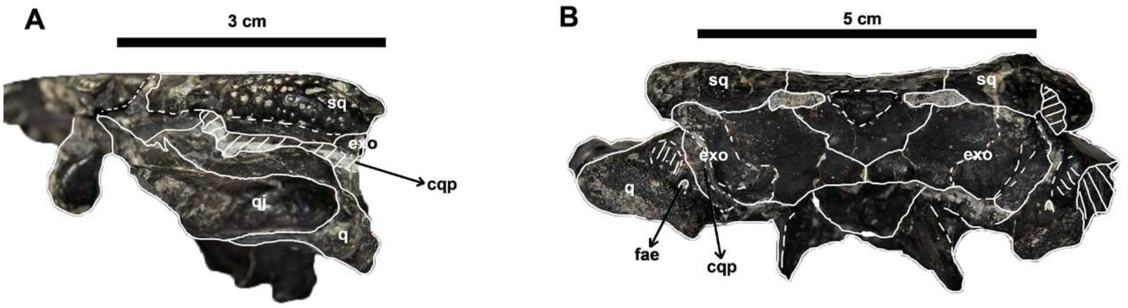

Figure S14. Lateral (A) and posterior (B) views of the skull of *Iharkutosuchus makadii* (MTM 2006.54.1) showing the relations of the cranioquadrate passage. Abbreviations: cqp., cranioquadrate passage; exo., exoccipital; fae., foramen aerum; q., quadrate; qj., quadratojugal; sq., squamosal

Character 168 (? to 0): Significant ventral quadrate process on lateral braincase wall (0) or quadrate-pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1).

In the specimens MTM 2006.53.1 and MTM 2006.54.1, this sutural contact can be observed in ventrolateral view, and the quadrate sends a ventral process (Fig. S13), with the quadrate-pterygoid suture not linear posterior to the trigeminal foramen.

Character 176 (0 to 2): Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust processes ventrally and participate in basioccipital tubera (1) or send slender processes ventrally to basioccipital tubera (2).

This area is well preserved in the specimen MTM 2006.53.1, and a long ventral extension of the exoccipital to the basioccipital tubera can be observed (Fig. S15).

Character 177 (? to 1): Quadrate foramen aerum on mediodorsal angle (0) or on dorsal surface (1) of quadrate.

Character 178 (? to 0): Quadrate foramen aereum is small (0), comparatively large (1), or absent (2) at maturity.

The region related to characters 177 and 178 is well-preserved in specimens MTM 2006.53.1 and MTM 2006.54.1, in which the foramen aereum is clearly small and dorsally placed (Figs. S14B, 26).

Other minor changes from the original matrix of Narváez et al. (2016)

Eothoracosaurus mississippiensis

Character 63 (0 to ?): 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).

According to Brochu (2004) and Brochu et al. (2012) the presence of the fenestra in this taxon is not certain, and the area where this fenestra is usually placed is broken (see Brochu 2004, Fig, 9).

Purussaurus neivensis

Character 152 (1 to 3): Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae small, with a circular or nearly circular shape (1) or supratemporal fenestra closes during ontogeny (2) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (3). State of character (3) from Cidade *et al*. (2017).

We have added a new state of character (3), based on the work of Cidade *et al*. (2017), which is applicable to the taxon *P. neivensis*.

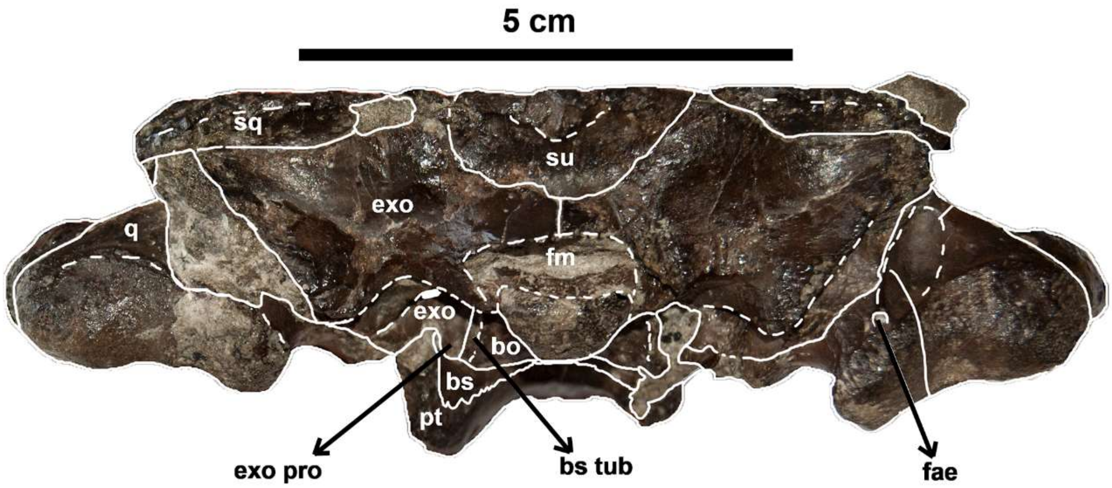

Figure S15. Posterior view of the skull of *Iharkutosuchus makadii* (MTM 2006.53.1). Abbreviations: bo., basioccipital; bs., basisphenoid; bs tub., basioccipital tubera; exo., exoccipital; exo pro., exoccipital ventral process; fae., foramen aerum; fm., foramen magnum; pt., pterygoid; q., quadrate; sq., squamosal, su., supraoccipital.

2) Modifications and new taxa on the original matrix of Narváez et al. (2016)

These are the new codes of the taxa modified from the original matrix of Narváez et al. (2016), used in our first analysis.

Portugalosuchus azenhae (based on holotype partial skull ML1818)

???00?12011?0?????????????
00????????????????01?0???10001???0?0??011010000?1?0?00000100????1?00???0101
0010??001?0???0?10?1??????0????0000?

Allodaposuchus precedens (based on holotype skull table MAFI Ob3131; and complete skull PSMUBB V 438)

??0
0010?0000001020000100?100000????0000001101 0?0???1000?1?1110???01?0?00001
000?10100?????1?101?1001010000???0000?

Agaresuchus subjuniperus (based on the holotype complete skull MPZ 2012/288)

??0
0110?00100?0020000100?000000????00010011010000???00?00?1110?000100000001
000?10????????1???10000?010000???0010?

Arenysuchus gascabadiolorum (based on holotype nearly complete skull MPZ 2011/184 (ELI-1))

??0
00?0?00?0000??00001???0?0?000???0?0??011010000?110000101110????1?000??010
00?10????0???10?0100?????00????00?0?

Iharkutosuchus makadii (based on holotype nearly complete skull MTM 2006.52.1; and nearly complete skull MTM 2006.53.1; three partial skulls MTM 2006.54.1-2006.56.1; complete left mandible MTM V 2012.29.1; nearly complete right mandible MTM V 2006.63.1; fragmentary mandibles MTM V 2006.59.1, MTM V 2006.61.1, MTM V 2006.64.1, MTM V 2006.70.1, MTM V 2006.71.1, MTM V 2006.72.1, MTM V 2006.74.1; partial maxilla MTM V 2006.57.1; parietal MTM V 2006.67.1; 148 isolated teeth MTM V 2006.80.1)

??10124000??0???110???0000001???
?00011?0000011061000100??00110????00000010011200012011001010 0?1?0100000
0?12???10002?????1?0?100000210110???1010?

3) Cladistic analyses based on the matrix of Narváez et al. (2016)

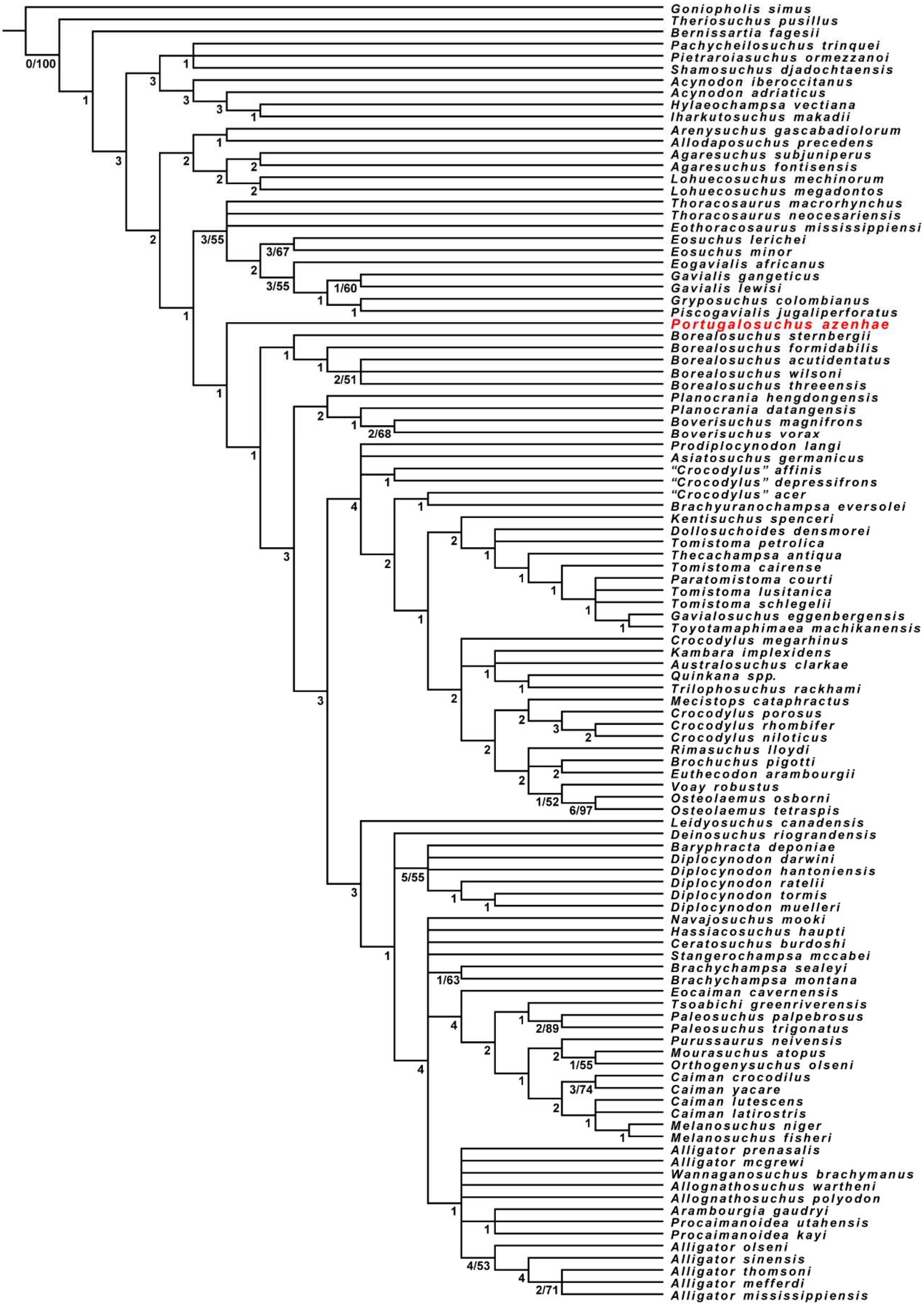

Figure S16. Phylogenetic relationships of *Portugalosuchus azenhae* based on the matrix of Narváez et al. (2016). Strict consensus tree of 4464 most parsimonious cladograms with 789 evolutionary steps. Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

Figure S17. Phylogenetic relationships of *Portugalosuchus azenhae* when the taxon is forced outside Crocodylia, based on the matrix of Narváez et al. (2016). Strict consensus cladogram (790 steps).

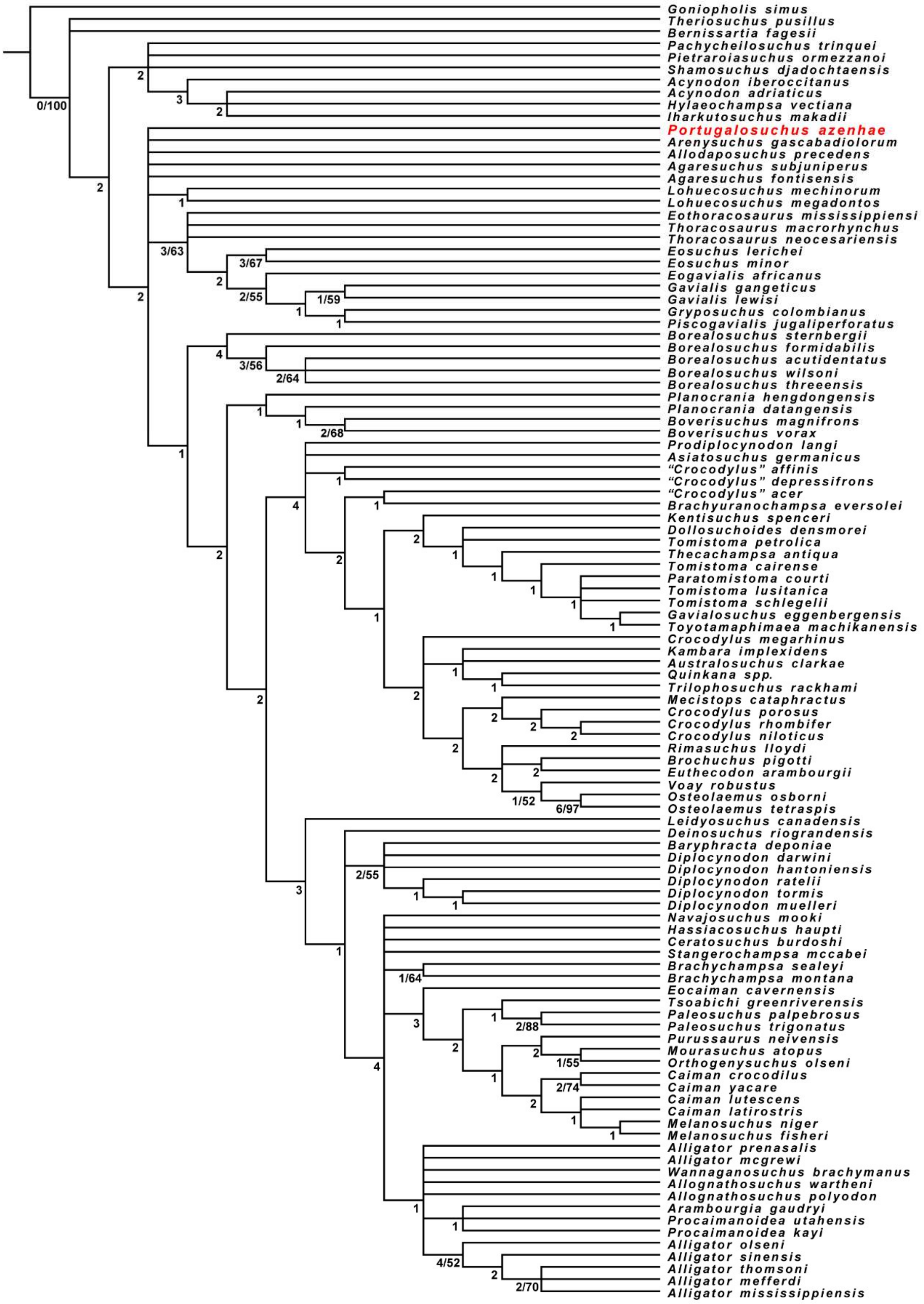

Figure S18. Phylogenetic relationships of *Portugalosuchus azenhae* when we consider that *Portugalosuchus* lacks external mandibular fenestra, based on the matrix of Narváez et al. (2016). Strict consensus cladogram (788 steps). Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

4) Sinapomorphies of the main involved clades based on the matrix of Narváez et al. (2016)

In our results Eusuchia is only weakly supported (Bremer = 3; bootstrap < 50%), and it is characterized by the presence of the following unambiguous synapomorphies: procoelous presacral vertebral centra (character 21, state 1); wide and rounded olecranon process of the ulna (character 29, state 1); pterygoid ramus of ectopterygoid bowed, posterolateral margin of fenestra concave (character 119, state 1); non-septate choanae (character 125, state 0); and thin and rod-like posterior cervical neural spines (character 189, state 1).

The clade formed by Crocodylia is poorly supported (Bremer = 1; bootstrap < 50%), and characterized by the following unambiguous synapomorphies: external mandibular fenestra present as narrow slit, no discrete fenestral concavity on angular dorsal margin (character 63, state 1); and exoccipital with small or no boss on the paroccipital process (character 174; state 1).

The position of *Portugalosuchus* is supported by the following unambiguous synapomorphies: absence of a splenial process between the angular and coronoid (character 59, state 1); external mandibular fenestra placed between the dentary and angular without participation of the surangular (character 60, state 2); maxilla broadly separates the ectopterygoid from the maxillary tooth row (character 104, state 1); and braincase wall lateral to the basisphenoid rostrum smooth, without sulcus (character 162, state 1).

5) Modifications and new taxa on the original matrix of Turner (2015)

These are the new codes of the taxa modified from the matrix of Turner (2015), used in our second analysis.

Portugalosuchus azenhae (based on holotype partial skull ML1818)

20??????2????1110001001101001000???2110?012??11?11?11???010?1100?3000???0
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????????110?01?0???1?1?00??0002?????0?0??0101?0100?01??0??0????00??00???0??
?000?0?100?0???0?00?0??001?0?0???????110??1??????000???00?00?00?00??01???
00000?0????0???1??0

Allodaposuchus precedens (based on holotype skull table MAFI Ob3131; and complete skull neotype PSMUBB V 438)

203?2111?0?????1?0?10[01]1111001000?0021101012 0?110011?10000?0?1?00131???
??????0[12]????????????11???????????0100??00???????0010?131100?100000010001?
1?1100???????????1001022?01?1??0?1?00?11???0???0?1010?10??0??10000010?0000
?????0?0000000?1?0000000?0??00000100?10?????000110?0????0010???100?0???0?0
000?01?0?0?000000001110?1010

Lohuecosuchus mechinorum (based on the holotype complete skull MDE/CM-616)

203?211120000??110010[01]111?001000?0021101012?1110?11?1??00?0?1?00
131?????????01????????????????????????0100??00???????0010?131100??000000101
0101???00????????????001022?01?1??0?1000?11???0???0?1010010???1?1000001 0?0
000?????0?0000000?10001000000??00000100?10?????00011010????0210???100???0
0000?00?0??000000000001111?1010

Agaresuchus subjuniperus (based on the holotype complete skull MPZ 2012/288)

203?211120000?1100010[01]11110010?0??0211010120?110011?10000?0?11?01310?
???????01?????????????????????????0200??00???????0010?131100??0000001000101
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?0000?01?0?000000?00?1111?1?10

Arenysuchus gascabadiolorum (based on holotype nearly complete skull MPZ 2011/184 (ELI-1))

203?2?11?00?011100010[01]111?0010?0???211010120?11?01??1???0?0????01310???
??????1?????????????????????????0?00??00???????0010?1?11?0??00??0010?010??1?

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Iharkutosuchus makadii (based on holotype nearly complete skull MTM 2006.52.1; and nearly complete skull MTM 2006.53.1; three partial skulls MTM 2006.54.1-2006.56.1; complete left mandible MTM V 2012.29.1; nearly complete right mandible MTM V 2006.63.1; fragmentary mandibles MTM V 2006.59.1, MTM V 2006.61.1, MTM V 2006.64.1, MTM V 2006.70.1, MTM V 2006.71.1, MTM V 2006.72.1, MTM V 2006.74.1; partial maxilla MTM V 2006.57.1; parietal MTM V 2006.67.1; 148 isolated teeth MTM V 2006.80.1)
203?211021?0011?10010?111?001?0?10021101012011100 11?1010010?110013?0?310
01?001???????????????????????000100??10?????000000?141000?0000[01]011000000
00000???101?01101000002001??0?0?0000?0?010200?0010000100011?10000000?000
000???1?0000000?100000000000?0000010??00????200?01010????00000??100000000
00101?0101111110000000021?1101

6) Cladistic analysis based on the matrix of Turner (2015).

Figure S19. Phylogenetic relationships of *Portugalosuchus azenhae* based on the matrix of Turner (2015). Strict consensus tree of 660 most parsimonious cladograms with 1659 evolutionary steps. Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%. Crown group Crocodylia in blue color.

7) Sinapomorphies of the main involved clades based on the matrix of Turner (2015).

In this analysis, Eusuchia is moderately supported (Bremer = 3; bootstrap < 50%) and it is characterized by the presence of the following unambiguous synapomorphies: first caudal vertebra biconvex being the other procoelous (character 94, state 1). Also it is characterized by the following ambiguous synapomorphies: nasal contribution to narial border (character 13, state 0); choanal groove undivided (character 69, state 0); cheek teeth constricted at base of crown (character 162, state 1); presence of exposure of supraoccipital in skull roof (character 171, state 1).

The clade formed by Crocodylia is moderately supported (Bremer = 6; bootstrap < 50%) and characterized by the following unambiguous synapomorphies: insertion area for M. pterygoideous posterior extends onto lateral surface of angular (character 76, state 1); rodlike posterior cervical neural spines (character 90, state 1); presence of hypapophyses in cervical vertebrae (character 91, state 1); proximal end of radiale expanded symmetrically, similarly to the distal (character 117, state 0); absence of shallow fossa at anteromedial corner of supratemporal fenestra (character 265, state 1); boss small or absent on paroccipital process, process lateral to cranioquadrate opening long (character 268, state 1). In addition it is characterized by the following ambiguous synapomorphies: primary pterygoidean palate completely encloses choana (character 43, state 1); Prefrontal pillars longitudinally expanded in their dorsal part and columnar ventrally (character 182, state 2).

The position of *Portugalosuchus* is supported by the following unambiguous synapomorphies: postorbital bar transversely flattened (character 26, state 0); jugal portion of postorbital bar, relative to lateral surface of jugal, flush with lateral surface (character 167, state 0). Also it is characterized by the following ambiguous synapomorphies: pterygoid ramus of quadrate with deep groove along ventral edge (character 50, state 1); absence of palpebrals (character 65, state 0); supratemporal fenestrae relatively large, covering most of surface of skull roof (character 68, state 0); lateral surface of the anterior region of surangular and posterior region of dentary with a longitudinal depression (character 118, state 1); dorsally robust splenial posterior to symphysis (character 161, state 1); cheek teeth not constricted at base of crown (character 162, state 0); maxilla broadly separates ectopterygoid from maxillary toothrow (character 264, state 1).

8) Reconstruction of ancestral states of character

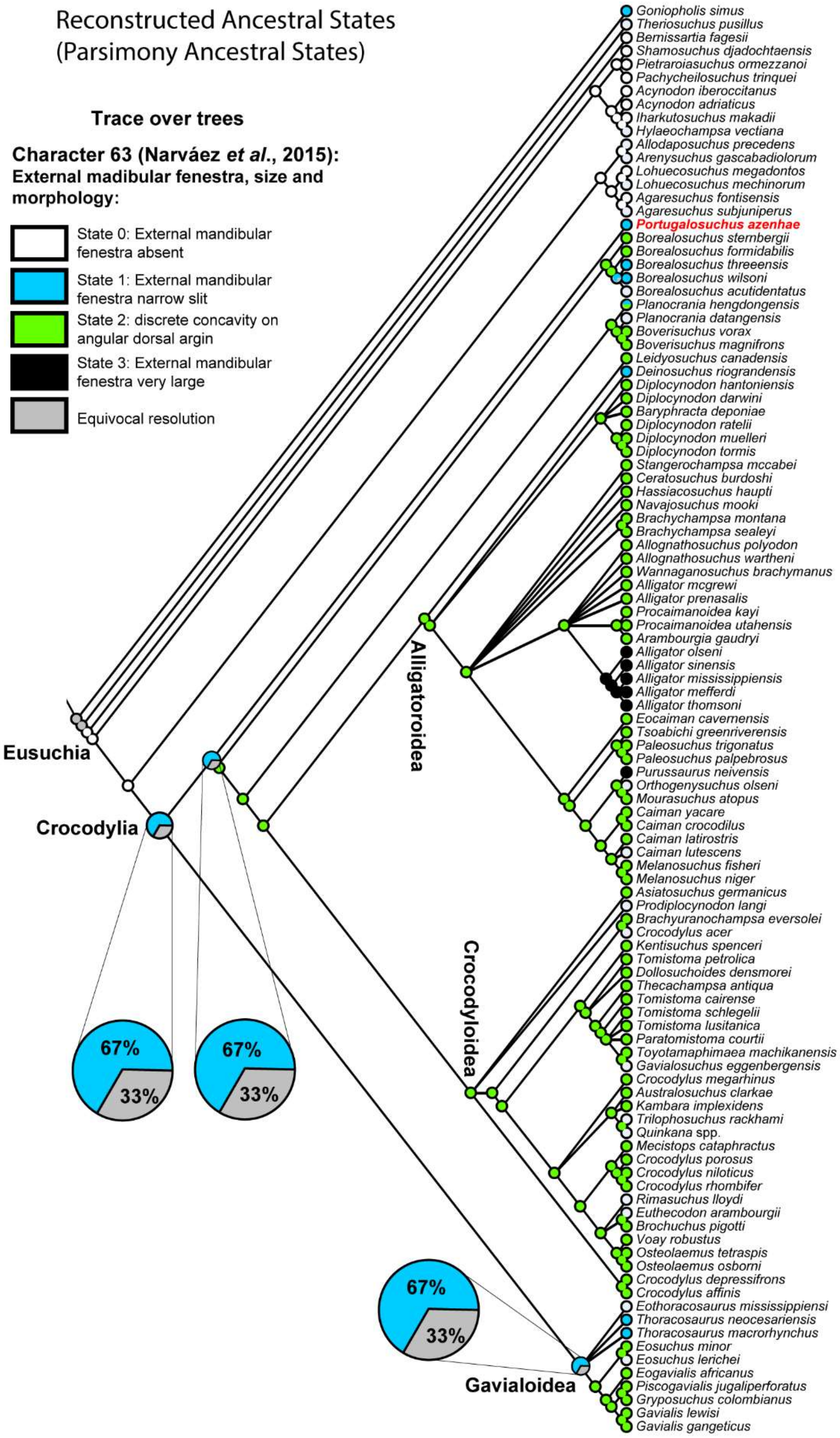


Figure S20. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → ?).

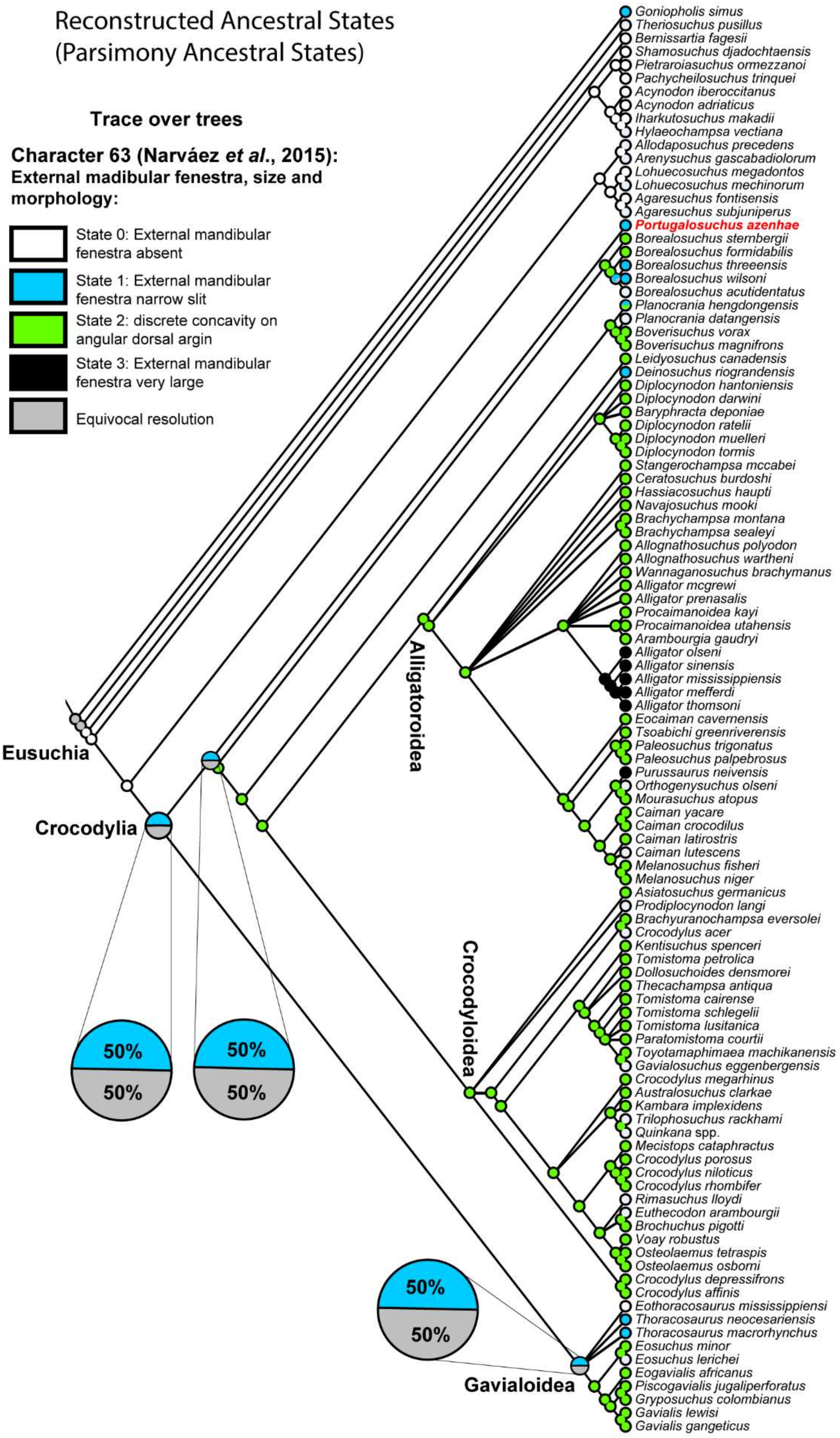


Figure S21. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → 0).

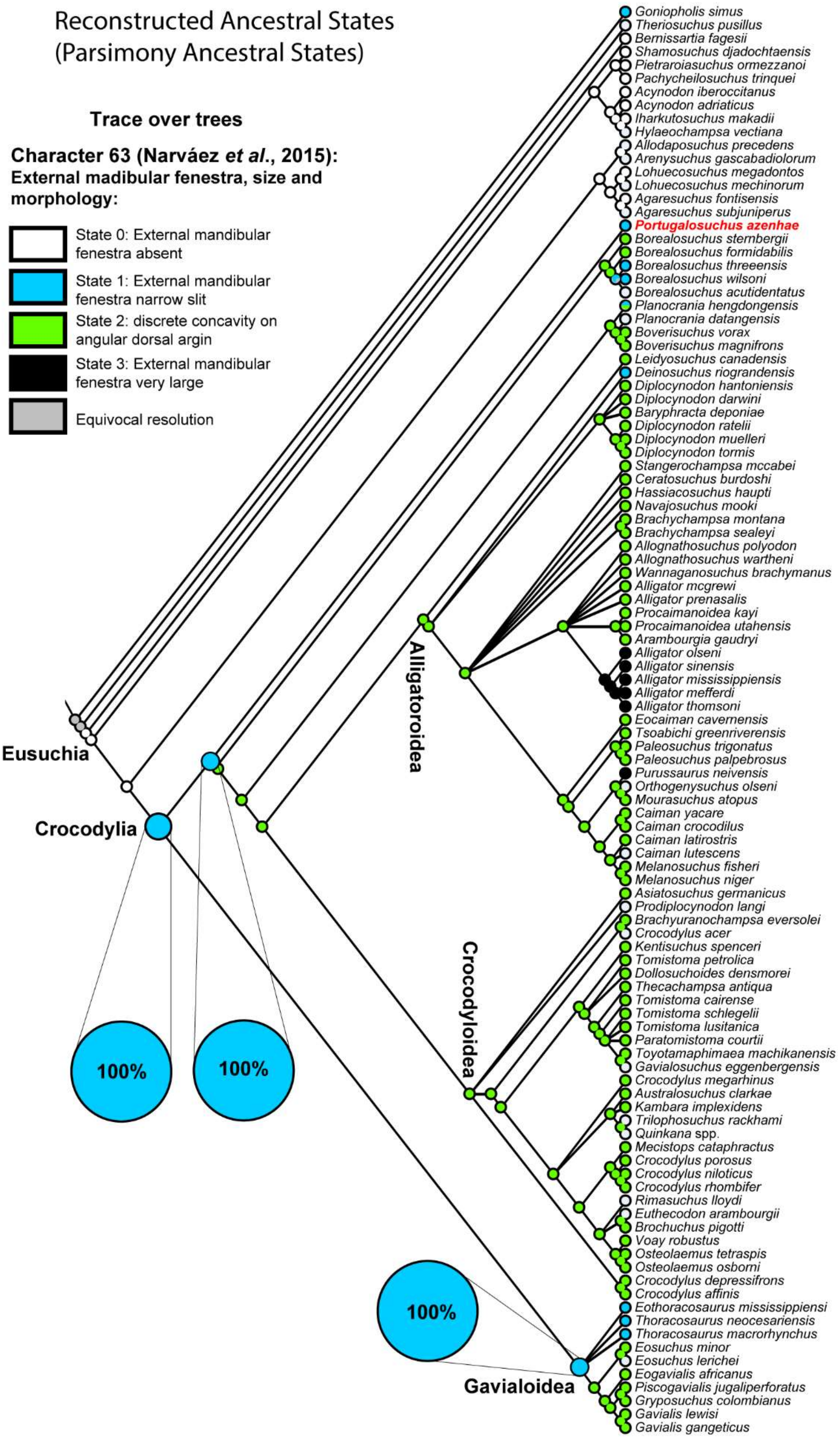


Figure S22. Maximum-parsimony reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → 1).

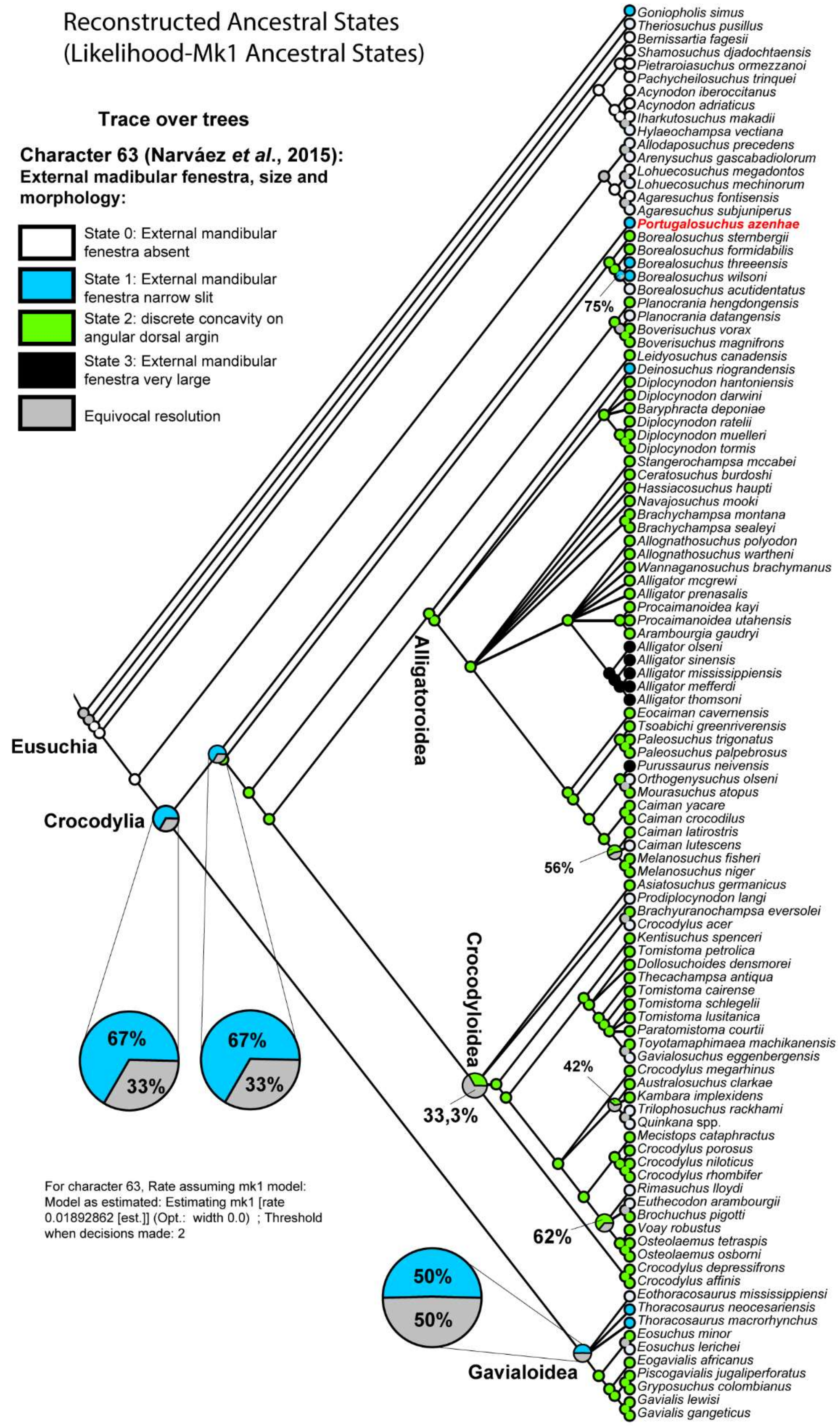
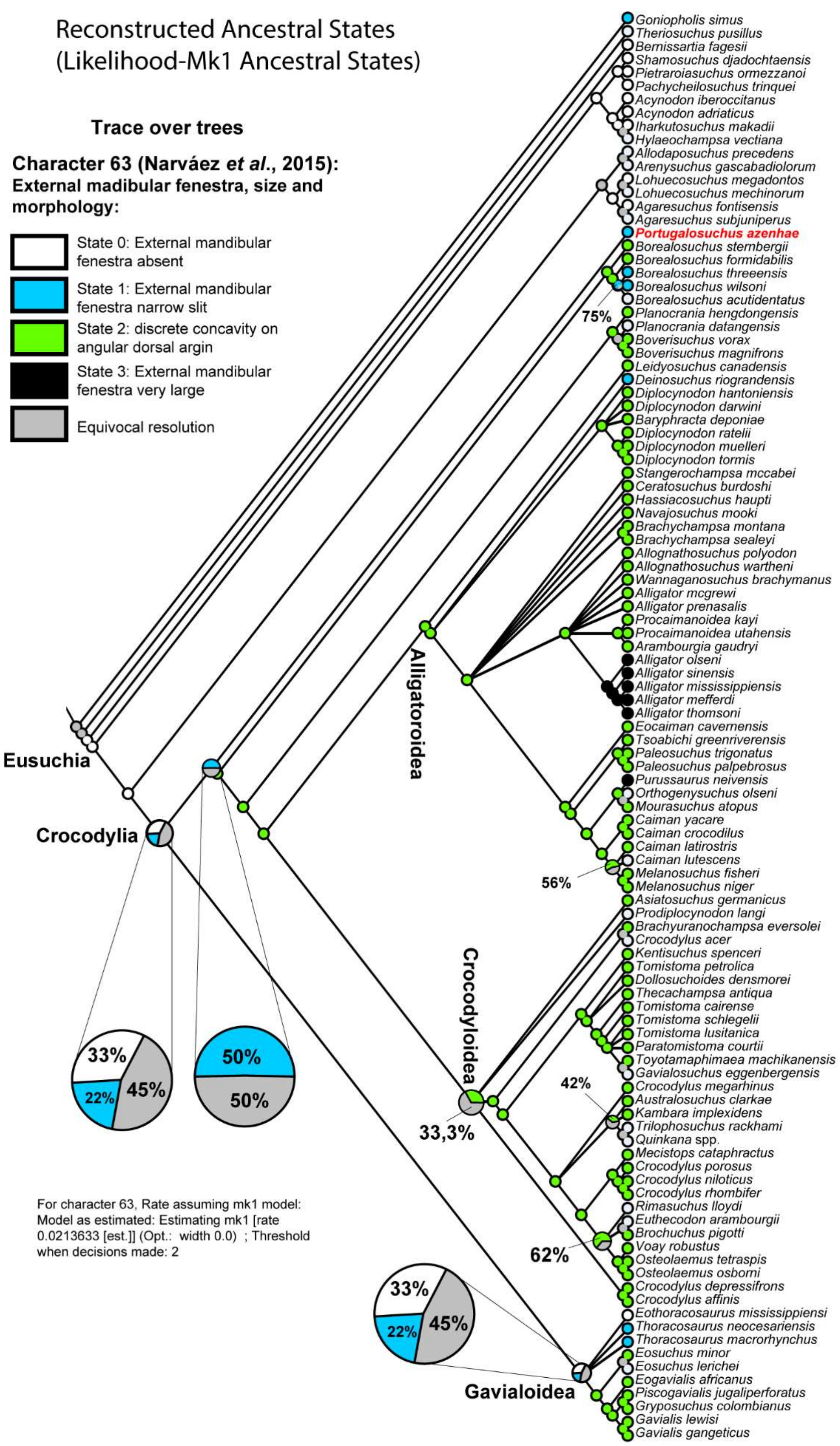


Figure S23. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → ?).



For character 63, Rate assuming mk1 model: Model as estimated: Estimating mk1 [rate 0.0213633 [est.]] (Opt.: width 0.0) ; Threshold when decisions made: 2

Figure S24. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → 0).

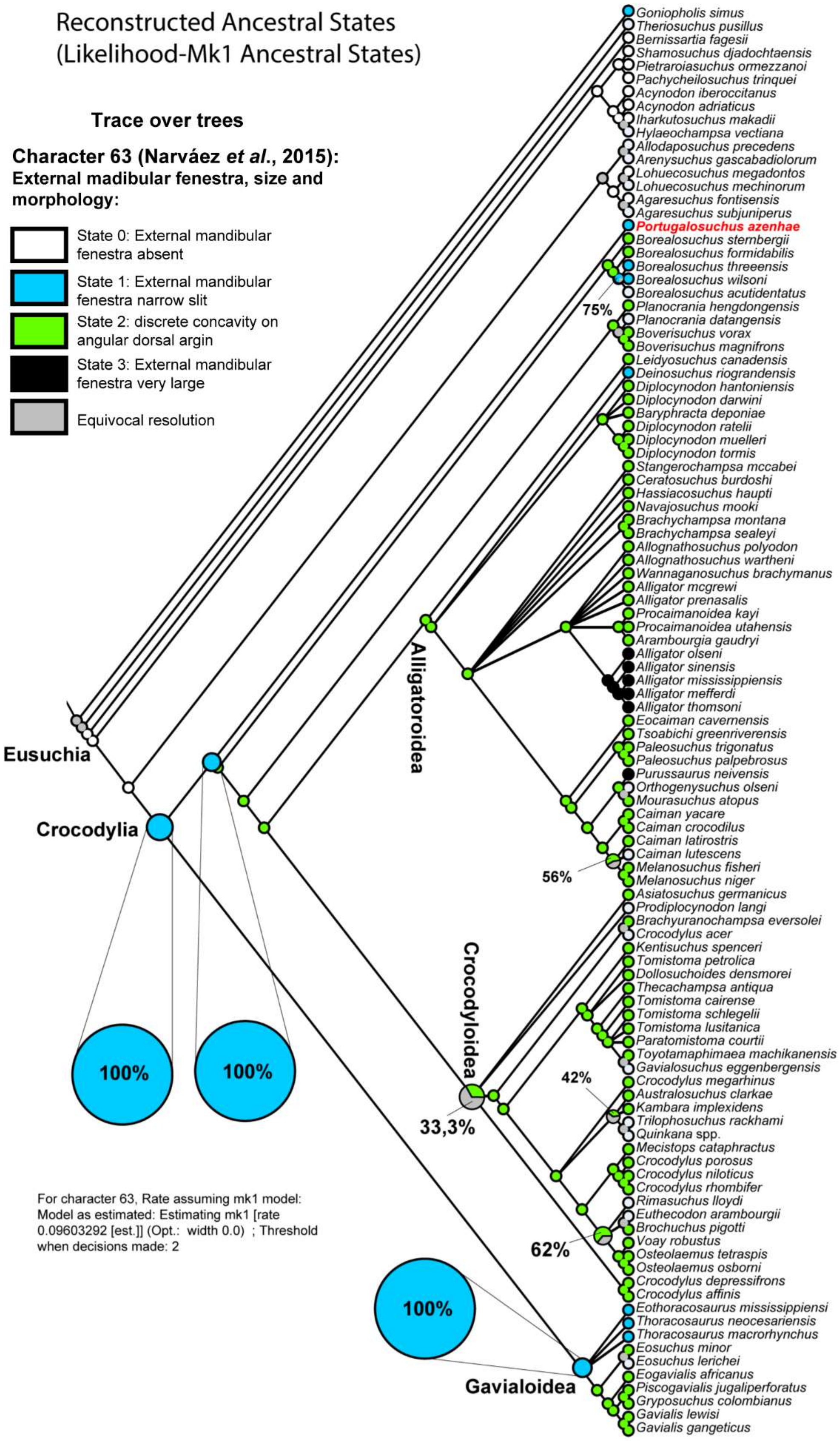


Figure S25. Maximum-likelihood-Mk1 reconstruction of ancestral states of character 63 of 4464 most parsimonious trees traced over the strict consensus tree and using our matrix based on Narváez et al. (2016) (*Eothoracosaurus*; character 63 → 1).

9) State of preservation of the specimen ML1818

As can be observed in Figure S26, the block contained a partial skull and mandible in anatomical association. As can be seen in ventral view (Fig. S26A), the mandible is slightly rotated medially at its anterior margin in relation to its original anatomical position. However, in lateral view (Fig. S26B), it is observed that the mandible fits perfectly with the associated skull. Therefore the association of both bones to the same individual is undoubted.

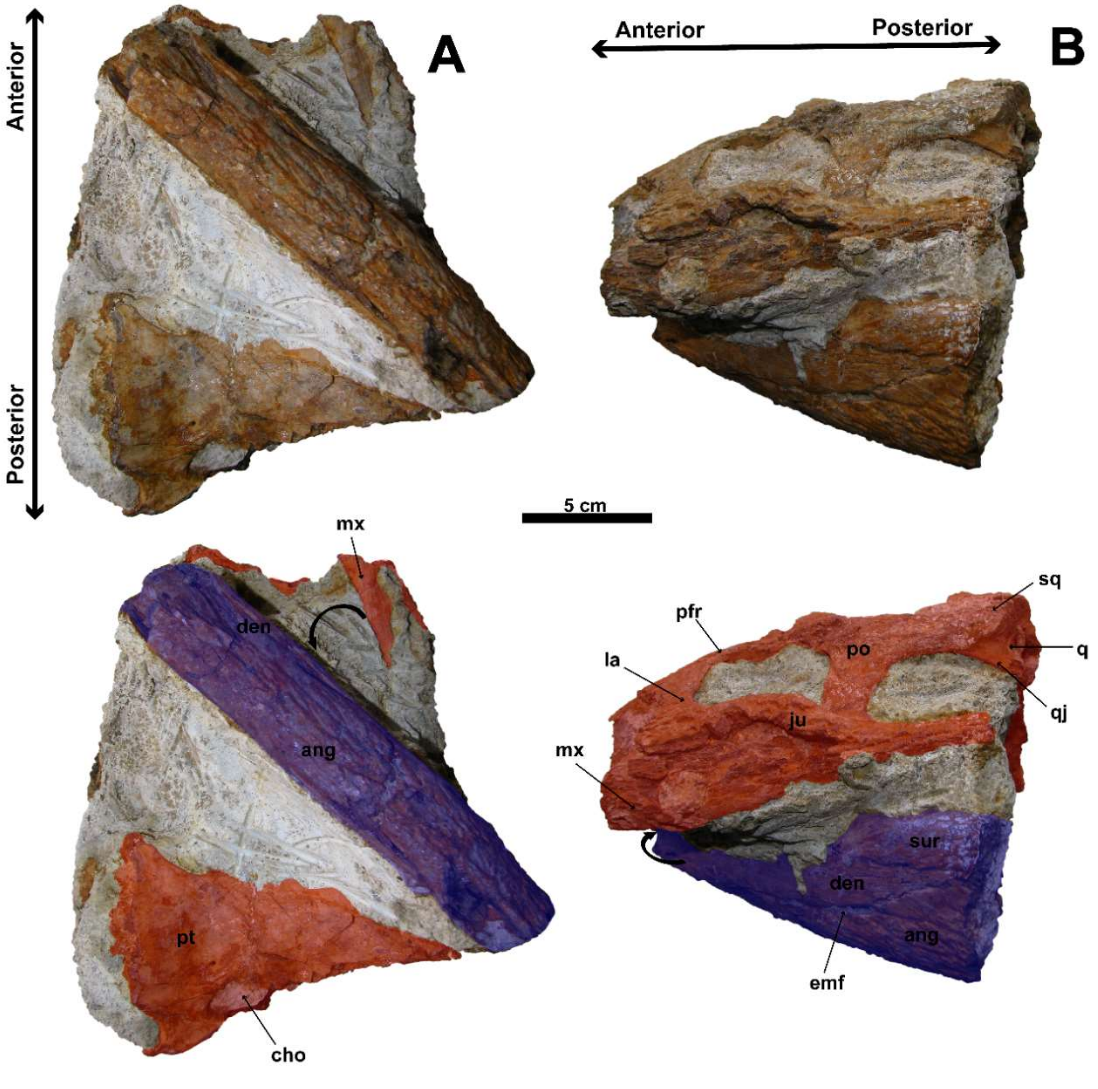


Figure S26. Pictures of *Portugalosuchus* during the laboratory preparation work. Ventral (A) and lateral (B) views of ML1818, below, the same pictures with coloured bones differentiating the skull (in red) and the mandible (in blue). Thick black arrows show the slight rotation of the mandible. Abbreviations: ang., angular; emf., external mandibular fenestra; den., dentary; sur., surangular; ju., jugal; la., lachrymal; mx., maxilla; pfr., prefrontal; po., postorbital; q., quadrate; qj., quadratojugal; sq., squamosal.

10) References

Aguilera OA, Riff D, Bocquentin-Villanueva J. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the Upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology* 4(3): 221-232.

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?????0???0?0???????????????????0??0??0?0???0?001????????????????????????0?0???
??0?????0????????00??????????????0?????000???????????????????????????
Mahajangasuchus_insignis
203?1[1,2]?1021??01211001011110011000100211010010111 2011?10100101110??212
11101000011 11?1121??140000100??01301[1,2]00?10101?01011010?131100100 01000
12101110000 1???1011110100000210 01000?1?0000110?0100010010100100011100000
10?0000000??02?00000001101000000000000000100?01????0111?10?0?1?00010?0?1?
1110?0000000 1?0010000000000000?0??11?100????????????????????
Kaprosuchus_saharicus
[1,2]03112?1?21?001?11?01011110011000103211 01?01???1201111010????????0212
13100011121 1????????????????????1101300??01?????01001011311010000?0001210
1110000 0???101?1101000000100 1100?1?1001?1010000010010?00?10001?100001000
00000???020?00000?1100000001 0100??10100?00????00?100?1?0???0000000??11110
1?00000?1?00100000000001 0000?011?000????????????????????
Stolokrosuchus_lapparenti
20200001120000111000101111000110010 1211?1?0?0111201111010010?1?0?021?0???
?0011[1,2]?????????????????????1??0100??00??????10011010110110000000 1200
1110100 1??01???0111000021001100?0?0??010100?000?00?011?100101?1000010?0
0000????0?0010000?1?000000010?000000100?00????011011?1????0000?10??1?001
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?0??0000??01?0??000000000000-?1?1?0???????????????????
Hsisosuchus_chungkingensis
211?0???????000000100001100011000?022?101001[1,2]??12?11?10000?0?1?0[2,3]
?11114?00[0,1]01?1??10???????000?1000???0?01?1021?1?????01101?????0?0000?
?000?2011?1??001????10???0??0?00020?010???000?0?000000?00?10??[0,1]00?000
11111100[0,1]?0000?0000?0???000?0?10??0???0??000?0001?0?00???00?00???????
?1000??00?0??00000010?00??000???0?0??000020??---??????????????????????
Pelagosaurus_typus
202?[0,1]111?20011020101[0,1]00000000000[0,1]1002110100000011011?1001001?
10001201?300000200001101?1?00000012000111?012002100???101?001??1??10000??
00001010110??[0,1]00???100000??0001102000100?000200?0??0?0?00001011010000
11000001??00000000??0???10?00?10[0,1]000000210001100110?00??????1000?1???
?10000000?0?????000000000?000??000000000010?001-0?0???????????????????
Steneosaurus_bollensis
[0,1,2]02?[0,1]111?20011020100[0,1]00010000000110021101000?0011011?100101
1?1?00120103?000?20000110111100000?120001[0,1]1?012?02100[0,1]001001001??
10?10000??0?0010?1??0??00000110000010000110?0001001000200?0?000000000101[
1,2]01000[0,1]1100010010?0000000000?0010?00?100000000?1000010?0[0,1]0100?
?00??1000?01?0?1000000?0??????000000000?000????000??0?100001-0?0????????
???????????
Metriorhynchus_superciliosus
[0,1,2]02?1211020011?20100100010000000110021101000?0011011?1001011?1?0012
01?30001020000??01111?0000??????0?0?013?02?100001?11001??10?10000??0?0010
????0???000????0000?0000110?00?00010?0200?0?000000000101101000?1100000010
?000000???0?0010000?100000000200111111010100???????00????????000??0??????
??00??00000??000?0?0000000?10??01???????????????????????
Metriorhynchus_casamequelai
0?2?1??10?0011?20?0010?010??00?????02?101001?0??1?1??????0?????0?1201????
010?0000????????????????????0?01??0??10??????1001??1??1?0??????0010??????
??0?????????0???00110??0?0?????0??0?0?0??0?00?0???1????0?1?00??001????0??
????0???1?????1?0?00?00???111?110?0?00???????00???????????0?0????????????
00000?0???????0????0?10??01???????????????????????
Cricosaurus_araucanensis
002012?1020011120100100010000000110021101000000?1101??10010[0,1]1?1?000200
?3?001020000????????0000????????0?013?0?01000???11001??10?1001???0?0010?[
0,1]2?00??00???0?0?0010000110?00000010?0??0[0,1]0?00?000?00???1?1000?1?00
0?0010?000000???0?0010000???0000000211111110?1?00????0??00?????????000000
-????0??????00000?0????0??0?0000?10???????????????????????????
Cricosaurus_suevicus
0?2012?10???11??01?0100010?000001?00????????????????????????????00[2,3]0?
?3??01020000??????????????????????0?[2,3]?0??1?????011001??1??1??????0?00
10?02?0???0?0010??000??00110????0???0?0??0?0????0????0?????????00??1?0??00
?0?000?00???0?0?10?0????0?00000???11?11?0?1?00????0??00????????000??0????
????????????0?????????0????0?10???????????????????????????
Dakosaurus_maximus
001?12?1???11??0??010?0??00?001?????????????????????????????????01?0?????
01??0000????????????????????????3?0??1??????1?10???1??1??????0?0012??????
??????????000??00011?????????0?0????0????0????0????????????00???????????0
0???0?0???00?????00001??1?1????011100????0??0????????????????????????????
????0?0???????000?0??0????????????????????????????
Dakosaurus_andiniensis
001????1020011?200001000100000001?002?10100?00??1?1?????[0,1]0???1?00?200
???0010?0000????????????????????0?013?0??10?????11101??1??1?01???01001211
2?0???00001??0?00??000110?00?00??0?0??0?0????0???00???[0,1]?1?0001?00??00
???000?0????0???1000??1????0001?111111110?1?00????0??00????????000?00????
?????0??00000??00?000?000000?00??01-??0???????????????????
Rhabdognathus
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202??????200??11100010011011010011012110100[0,1]01112011?1011010?1?11?302
??????????0????????????????????????1?10??00???????000?????00??000??0[0,1]
10020?001?00?????1?????0?01[0,1]22000?0??0?000000????0??00?1010010??01?10
00001?0000??????0???000???112?1???010??00000000?11?????0000111?0???000000
0??1?0?0?000000?1?01?0002000?000011??01-?00???????????????????
Sokotosuchus_ianwilsoni
2?2??21112??10????001001???101001?012?1??????1112?11?1?11??0???1?1?0?????
????01????????????????????????????2?0?????????0???????0????????0?10??????
??0??????????????0?????????????1?????????0????????0??????????????1???????
????0???????????2??000?????0??001?0?11???????????????????????????????????
0000?????????????????1?0??????????????????????????
Dyrosaurus
202?12?102?010?11??010011??101001?012?101000?1112011?1011?10?101113021???
00?2?000??????????00???????????1?10??00???????00??????00???00??0010020?0?
??0??????1000?00001?0200?????0?0?00?0????00000010?0??000?1??00?001??00000
0???0?0?0??00?1120100010??000000?0??1????0010011100???00000?0????????0000
00001?0110002000?000010??11-?00???????????????????
Hyposaurus_rogersii
?02?12?102??1???????1????0?101??????2????????1?12011?101??10?1?1??3?????0
???2?000??112?????00??????????01??0???0???1?0100???????????????0?1002??0?
??00???1?1000100?0????00???0?0??????0?000000?00???0?????????0???01?????0?
????0???????????2?????0?????0???0????1???00??0?1???????000??00??10000????
00001?00?0?0?000??0?011???????????????????????????
Pholidosaurus_purbeckensis
212?121102??1??1110?10011??0010001012110100?01112?11?101??10?100?131[1,2]
???0???2?0????1?2???0??0??200?????????0??0????????0?0??1?110?????0?00100?
??????00??????000?0000102?100????0?0000?0???000?00?10?0?10??01?110?0010??
?0??????0???0???0?10??1????1???0?0001?0?00???????00?????????0????????????
??????????0????0??00?0010110??????0???????????????????
Sarcosuchus_imperator
203?12?10200101?100010011001010001012?10100101?12?1??10100?0?100?131213??
000210101?112????[0,1]00?1200?00??011[0,1]0??00[0,1]001?0?001??121100??00
000010010?1???00???110?0[0,1,2]11010[0,1]022[0,1]00?0000?000000?000000?00
?01001000?1?110?0010?00000000?0?0100000?100011110100?0?000100?10???00110
?1100?0?0001000??1?00000000000??011000?00000000110001-000????????????????
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Terminonaris_robusta
202?[0,1]2?1020010?11??01001???1010001012?101001??????11?1010??0??0??13[0
,1][1,2]13?000?2100011112??00000?1200?10??0?110210?1001001001??1??10??0??
0?0010????1???000011100?0???101[0,1]2[1,2]10?????0?0000?0?0000?0001?0?00?
0?0?11100?00?0??00???00?0?0100?00?1020111101?0?0?00?100??00???00?10111?00
01000000001?0100?000000??000000[1,2]00000110100011-?01???????????????????
?
Elosuchus_cherifiensis
203?12111100001?1??010???11????01012????????????????????0??????????1?????
???112?????????????????0????????0????0??????0???1????010????????????0?11?
??????????????0?1??02?0????????1????1???????????????????????1????????????
???????0?????????2??001?????????1?????????0?100?1100??10000100??1?0000000
0000??00?000200000?10100011-001???????????????????
Meridiosaurus_vallisparadisi
2?2?121111??11???????????????????????????????????????????????????1???????
????12??????????????????????????010???????????1??0?11????????0?0010??????
???????????????010???????????0?1????11???0??????????????????0????????????
??????00???0????20?001??????????1?????????????0???0?????????????1?????0??
00????0??????0000?0????0-???0?0???????????????????
Oceanosuchus_boecensis
202?12110100101????11001???101??01012???????????????????0??????????1?????
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???1?00???1?????????????????????0????0??????0???1???110??????????????????
??????????????0?1??0???????????0????0????????????????????????????????????
???????0????????2??001??????????1?????0????0100?0?0??0?000??00??1??0000??
00??0?0??????000000101000???0?1???????????????????
Vectisuchus_leptognathus
202?????????????01?1?0111110011?0?002110?001?1?????1????00?0??????[2,3]02
14000001?[1,2]?????????0?[2,3,4]00?1200?10??00?0021?01???101001??1???00??
?0?0001202101??00???010?0?11??0?022?0??????0??000???0?00???0010??01000?11
1???000??000010?10?????0?0??00??????0?00?0??001?0?10?????00????1????10000
000????0000?00?00?1?0??0000?00?0??0?????????????????????????????
Paluxysuchus_newmani
203??11?20010110100100111010100010021????0?11112011110100000?1?0??31?1?1?
010??200???????????????????????0?00??00?????01100??101100?00000001001101?
1?00????0??00110?01022100?0??0?1000111???0?0?00?0100100001?10000010000000
0???0???000?00?00?1???0000?00000100?00?????0000101?????0000000??1?00000??
00??0?00?0?00000?001011????-??0???????????????????
Goniopholis_simus
203?1211120010111000100111?0010001002?101000?1110011?1010?10?1?021312?410
0[0,1]0[1,2]02011?1??1??0?00?1200?11?300100210010?1101001??101100?0000100
10001?1???00001110003110001022100?10?001000111??0000000101001000011110?00
1000000000000?0000000?10000[0,1]000000?0?000100?00?????000??????????20100
??01?000??000?????0??00?00000001?11??01-??0???????????????????
Goniopholis_simus_pea2013
203?1211120010111000100111?0010001002?101000?1110011?1010?10?1?021312?410
0[0,1]0202011?1??1??0?00?1200?11?300100210010?1101101??101100?00001001000
1?1???00001110003110001022100?10?001000111??0000000101001000011110?001000
0000000?0?00000?1?10000[0,1]00000??0?000100?00??????000?????????201?0??01
?000?????????????00000000001??????????????????????????????
Goniopholis_stovalli
203?121111??101?1000100111?0010001001?1??000?1110011?10?0??0?1?021312?410
????02????????????????????????00200??00???????001??1?1100??000?0010001?1?
??00?????0?????0001022?00????0?1??0?11??00??00?10?0??0??01?1100001000000?
????0?0000000?1?00000000???0?000100?00?????0?0010?100??000?00010??0000???
00001?0??00?0000000?0?????????????????????????????
Amphicotylus_lucasii
203?121111??101?1000100111?0010001001?1??000?1110011?10?0??0?1?021312?410
????02????????????????????????00100??00???????001??1?1100??000?0010001?1?
??00?????0?????0001022?00????0?1??0?11??00??00?10?0??0??01?1100001000000?
????0?0000000?1?00000000???0?000100?00?????0?0010?120??020?000101?00000??
00?00001?00?000000010110-?1-000???????????????????
Calsoyasuchus_valliceps
203?0201110?10?110?01021111001000?001?1???00?1110?11??0?0??0?1?0?111[1,2]
????????01??????????????????????0??0100??00????????01??11110?0???0?001000
1?1???00????????????001022?001?????1????01???0??00?????????????1100?01000
00???????000000000??000000??0?100?0?100?00?????0?1010??0??1000???0??0?0?0
?0??0??00?0??0???00000??000??-?-0?0???????????????????
Calsoyasuchus_new
203?0201110010?110?01021011001000?001?1???00?1110?11??0?0??0?1?0?111?????
????01??????????????????????0??0100??00???????101??11110?0???0?0010001?1?
??00????????????001022?001?????1????01???0??00?????????????1110?0100000??
????000000000??000000??0?100?0?100?00??????0?1010??0??1?00???0??1?0?0?0??
0?????000???00000??000??-?-0?0????????????????????
Sunosuchus_junggarensis
203?0201111?10?1100010011110010001002110100011110011110100?0?11011312?410
00110201??1111?0?20001200?11?????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????
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?000??01??????00000?0200-01-?00???????????????????
sunosuchusnew
203?0201111?10?1100010011110010001002110100011110011110100?0?11011312?410
00110201??1111?0?20001200?11?????????????????????????????????????????????
????????????????????????????????????????????????????????????11???????????
??????????????????????????????????????1????0??011???00??3?1000????0000000
?0?0000???????00000?0200-01-?00???????????????????
Eutretauranosuchus_delfsi
203??????10010111000100111?00?0001001110?000?1110011?1010??0?1?0?121204?0
0001020111???1??0??0?1???????3??100??00?????0?001????110???????0??00???1?
??0????11???[0,1,2]?1??01022100?1????10?0??1???00000010?0??000?1?110??01?
0000000???0?000?00??100?0?000?00?0??00100?00??0?1010010??0???0001000?0??0
00?00000001?01000?00000000011??-1-?00???????????????????
EutreALL
203-02?11100101110001001111001000100111010000111001111010010?110?13120410
0001020111???1??0000?12??????000100??0010???0?001????1100-000000010001110
0?00???10??00100001022100-10?0?1000111000000000101001000?11110?0010000000
000?0-0?00000-100000000?00-00000100?00??-?10100001?2???0200000?01-0000000
00000?00000000000000011??-1-?00???????????????????
Eutretauranosuchus_amnh
203??????100??1110?01001111001000100111010000?11001111010010?110??312????
??????0???????????????12???????0?00??00???????001?????10???00?1??10001110
0?00????0??????0?01022100????0???001?1???0??????01?010???1?111?00???0?00?
?00?0???000001?0?0?????????0000?100?00????0?0?00???2???02?0??0??1?0?0???0
00??0?0?????00000000011??-1-??0???????????????????
Goniopholis_baryglyphaeus
20??1????10010111000?0?11110010?0??02?101??001110??????10??0???0?131??4??
01?102??????????0?0001200?11??00??0???0???????0??0?1011??????0?00100?????
??00?????????31?00010?2?0??1????1?????1????????10??????0????10???10??????
????????????????000?000??????000?????0??????????????????????????????00??0
00?0??0??000?0000000?10???1???????????????????????
Alligatorium
?0??????1?0000?1000010?111??0?100?1????0??00??11??1??1000???????20?1????0
0101?101?011211000???1?00100????????????10??1??????????????????0?????????
?????????????1???????????????????????????0????????????????????????0??????
????????????????????0???????????1???00?????????????????????????0?????????
??????0????0??0000???10???????????????????????????
Theriosuchus_pusillus
201101111201001100001101111001100110211010001?11?01111000?????1?20211-410
01010201101121100011[1,2]1200100130?1002?0?10?110100[0,1]001?1100?00?0?00
120??01??0?00??10[0,1]00210100[0,1]02200?100?0?10001110[0,1]?0??0?0101?01
00001?100000?00000?20???000?00000-100?0000000??000??100?00??0?0?0011?1??0
?1000000001?0000?0000000?00?0000?000110011??01-?00????????????????????
Theriosuchus_sympiestodon
2?1????1?2?????????01101????????0110?1101001????0????????0?0??????311????
?????1??????????????????????-????00???????????0?0????????-?????00????????
?????????????????0???2???-??????0???01???0?????1?1?0?0???1??00????0???0??
????0?????????1?0?????0?????00001??????????0??0?????????0????0?????????00
00?0??0??????00??0100?????1-?0????????????????????
Theriosuchus_guimarotae
201101?1121?00??01?011?11??????10?00??101???1????????1?00???????202110???
00??1101??1?????0100?120???01???100??0?10?1?0?100001???0[0,0,0]????000?12
?00??0????010??????1?1011022?011?0?0??0???11???0??0??10??01000?1??00????0
0?00??????0????1??0??00?0?00???0?0????1?0?00?1010?0????1???01000?000?????
????????????0???00??000?1?0?????1-?0????????????????????
Wannchampsa_kirpachi
203?0???121?001100001111110001000110211010011111201111000000?1?0??310??10
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0111?211??????????11?????????300?0021001???101100????1100?000?00?10001000
1?00???100?13101?0?022011?00?0?1000110001000?001010010?00101000001??00002
0???0???000?00100?0???000??00000100?00??1?20001?00?????0001000??110000100
00001?0100000?00?1??010??11-?00???????????????????
Shamosuchus_major
213??[1,2]1102??00????0011?1???0010001002?101?01?1?????1?10000?0?1?0??312
?????????2??1?????????????1????-???0[1,2]00???0???????001??111100-0000?00
10?????????????????????00010?2??1-???0?1?00?11???0?????101???0???1?1000??
?0??2-???0??0??00?000-100??00000??-0?000100??0?????00????0?????1??11?0?11
?0?1?0000000000?????000000110????01-100???????????????????
Shamosuchus_djadochtaensis
203????10?1??0111000110111000100011021101?0011110?1111000000?110??310?410
0101?1???????1101[3,4]11[0,1][1,3]1?0?10?[0,3]00[1,2,3]002?00[0,1]????010
00??1?11?0?0000000100011101?00000??0?0?10?000021[0,1]?0?1??0?1000?100000?
0?001010010?001?10?0001000200200?10???000?0?100?0??00?00?000001?0?0001?1?
0?01101??0001111011?1?0010000000001?01000?0000001?110??01-?00????????????
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Shamosuchus_gradilifrons
20301[1,2]11020000??1000110111?001000110211010011111001111000000?110?0312
-1100101020?????21???[2,3,4]000[1,3]1???10-000100??00[0,1]0???01001011111
00-0000000100010101000???0100000001001021?11-10?0?1000?1100000000010100100
001110000010?0200200?10-0?00000?100000000?00-0000100?00??1?100010001-000
1101111?110001?0000000100?000000000111110001-100???????????????????
Shamosuchus_gradilifronsholo
203012?10???00??10001101???00100011 0?1??????[2,1]1110011?1000000?1?0?031?
-1100101020??????1???[2,3,4]000[1,2]1???10-000100??00[0,1]????01001011?11
?0-0000000100010101?00???010?00001001021?1?-10?0?1?00?110000?0?00?010???0
0???10?0?010??200200?10?0?0000???0000000??0?00000100?00????1000100?????0
[0,1]10?111???001???0000100??0?0?000001?111???????????????????????????
Shamosuchus_tersus
203??[1,2]?10?0000??10?011?10??001000100?11?1???11110011?1010000?110??31[
1,2]???????[1,2]02????????????????1????0-0?0?10??000?????10010?1?11?0-000
?00012001010100 0???0???????1001021?11-???0?1?00?110??10??0??010?????11?10
?00010?0200??0??0?0?000???1?0000000???-000001?0?00????100?100?????0010???
1???00?1????0000000??0?0??00?01?111???1???????????????????????
Shamosuchus_ancestralis
2???????????????10?011011??0010?0?00??????????????????????????????31?????
???????????????????00???????-??????????[0,1]?????1?01???????0??00?00??0?0
1?10????????1??????1?0?021???????0??000??????0????0?01?0??????1????00????
20??????0???000????0??0???0????0?0001?0?00??1??0?10??0?????010???1?1??0?1
????000???????0???0?0??111???????????????????????????
shamoancestralis
203??[1,2]11020000??1000110111?0010001002110100[0,1]1111001111010000?110?
?312?110010102??????21???[2,3,4]000[1,3]1???10-000?[0,1]0??0000???010010?
101100-000?0001200101010 00???0100000?1001021?11-1??0?1000?110?000?0001010
010000111000000 10?0200200?10-0?000?0-100000000?00-0000100?00??1?10001000?
-000[0,1]101101?110011?00000000000?00000000???1??????????????????????????
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Shamosuchus_ulanicus
203???1??2???0??1000110111?0010001002110100[0,1]1111001111010 0?0?110??312
-1100101?2???????21???[2,3,4]000[1,3]1???10-000?00??00[0,1]0???01001??1111
00-0???0001?001010 1000???0100000???01022?11-1??0?10?0?110?000?0001?100100
001?1000001 0?0200200?10-??000?0-100?0???0?00-0000100?00???10000000?-000
1101101??10011?0000???00??0?0?000?01?1?1??01-??0????????????????????
Shamosuchus_ulgicus
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Rugosuchus_nonganensis
203??[1,2]?1?20?00??1??0110111????00011[0,1]2110?000?1110?11?1000000?1?0?
?31??4?0010102???????????????21[1,2]0??0?[0,3]0?100???0?????01?01??1?1000
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1?100?0010?000020???0?0?00000?1?0??0000000?00000100?01????0??????????????
1111???1?0000??000001?0?0000000000?0011??0?-?00???????????????????
Batrachomimus_pastosbonensis
2030???1021-00??100010?1100010????2110100011?0???????????????????03?2-410
?10102??????????????????????-???100??0??????01001?11?1000-??0000012101?10
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0???01??000?0-100?00000100-0????1???00???????????1?0??1101110???1?0000?00
00?0?00?0?0000000?00?00??01-?00???????????????????
Glen_Rose_Form
2030001112??0011???0100111?001100???2110?001??11??11?10?00?0?1?030310????
01?10211?????????????????????3??100??00?????01000?0131?00?0000??010?0???0
1??????10??13101001022??1?10?0?10?0?1000?000??01?1?010?0?1?1000??000?0?2
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0000??00?0???0000?110100011-1?0???????????????????
Bernissartia_fagesii
203??21112??00111000?00111?001000?002?????0101112?11?10100?0?1???1?1??410
010102011?1?21??0200111101101300100??0????????0????1?????????0??0?10??01?
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0000?101100?0?0000??010??01-??????????????????????
Hylaeochampsa_vectiana
00???????21???11????1?01???0????0?002?1?1012????0????101??1??1????310????
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??????????????????00022?01??????00?1?????0???????????????????????????????
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????0?0??1101111?0?0000??-11?10???????????????????
Iharkutosuchus_makadii
203?1211021?0011?10010?111?001?0?1002110101201110011?1010010?110013?0?310
01?001????????????????????????000100??10????000000?141000?0000[0,1]011000
00000000???101?01101000002001??0?0?0000?0?010200?0010000100011?1000000?0
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000000101?0101111110000000021?11010???????????????????
Acynodon_iberoccitanus
203-021102??00?210?0100111?0010001002110?012?1110011?10100?0?1?001310-3??
11?10000????????????????????-3?1100??00?????0?1000-14110--00000-010101?1?
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00?01?01?1111100000001110-10010???????????????????
Acynodon_adriaticus
203-02?1020000??10?01001110011000?0021101012?11?0?1??1???0???1?001310-3?0
11?0000?2?????????1??[1,2]110??0-301100??0??????010000-141?0-??0000001211
1?1??00??000??0???000002110?-???0?0000?0-?000?-?0?1[1,0]10?1000?1110?000
?0?00000?0??0-0?0?0000100?00000???-000001?0?0?????????00?11?-?01000100?0?
?00???0000?0??01?1111?1100000110?-11?10???????????????????
Allodaposuchus_precedens
203??2111?0?????1?0?10[0,1]1111001000?00211010120?110011?10000?0?1?00131?
????????0[1,2]?????????????11??????????0100??00???????0010?131100?1000000
10001?1?1100???????????1001022?01?1??0?1?00?11???0???0?1010?10??0??100000
10?0000?????0?0000000?1?0000000?0??00000100?10????000110?0????00010?0??1
00?0???0?0000?01?0?0?000000001110?10100???????????????????Agaresuchus_sub
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juniperus
203?1211120000?1100010[0,1]11110010?0??0211010120?110011?10000?0?11?01310
????????01?????????????????????????0200??00???????0010?131100??0000001000
10101?00????????????0001?2?10??1??0?1000?11???0???0?1010010???1?1000010?0
000?????0?0000000?1?001000000??0000?100?10?????000110?0????0[0,2]010????1
?0?0?000?0000?01?0?000000?00?1111?1?100???????????????????
Lohuecosuchus_mechinorum
203-1211120000??110010[0,1]111?001000?0021101012?1110?11?1??00?0?1?00131?
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101???00?????????????001022?01?1??0?1000?11???0???0?1010010???1?1000010?0
000?????0?0000000?10001000000??00000100?10?????00011010????02010?0??100??
?00000?00?0??0000000000001111?10100???????????????????
Pachycheilosuchus_trinquei
203?????????????00??10?111???10001??????????01?1??????????????????2??????
01?0?0?0101111??021111[0,1]00??0?3???0021??1000?0?00???????????????0?1??0
???????????10?00010??0??2??????????01????1???00???0????????0??1?0????????
?????00?0???????????0???????????????[0,1]?????????[0,1]?????????001?????0
?10??00??0???00?0????0???000??????????????????????????????????
Pietraroiasuchus_ormezzanoi
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Unasuchus_reginae
2?3?12?102?????1?1?????11???????0??????????????????????????????????1?-?10
01?20?00????????????????????-3??1?0?????????0100?011????0???????01??01???
???0???10??001?1?0?????0???0?0??????0?00?000?00???????00????0??0??0?00??0
0???0?00??0?????00?0000?00??????1?0??????????1??????????0????0????0??0???
0110??0????0??1???????????????????????????????????
Glichristosuchus_palatinus
2???????????????????10[1,2]1?????10001??2?10??02??11??1????????0?1?0???1?
??????????????????????1???????????????????0??????????????????????????????
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????????????????0????????????????0?00??0?????????????????????????????????
?????????????0?????0?????????1?-??????????????????????
Susisuchus_anatoceps
203?12?10?1?00?11000100111?001000100??????????11?????????????1?0?131??3?0
????00??1?????????0002020110????100?10??00?1??000??1?11?0????000012011?0?
??00???????0????0?1022?01?0???10??0?0????0????0???0?1?00??110??00?0?00000
00000?0?0000???0000000?0??0?00?1?0000?????0?11?0?????01000??00?0?00?0????
0000?1?????0??00100?0112??????????????????????????
Isisfordia_duncani
203-120102000011100010011110010001002110100111112011?1010010?1?101312?310
001000001?1??????1000[1,2]010000-010100?1001?00?0?0010-131100-0??00001210
1?1?1000010?0?00000000000022101-1??0?00?000?-?00?00001?110100011110000010?0
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?00000001100?0000000010010112-?1??01??????????????????
Borealosuchus_formidabilis
203?1211120010111000100111?00100010021101011111121111010010?110?13100310
001102011111211113111?110?10?300100210?100100?001??11110??000000010001?1?
??0000110000310?00?022101??????1000[1,2]11??0000?001010010000111000001000
000000000?000???0?100??000000??00?001000000?0100010?111?00?0000000001?000
000000001101?00??000000101000-10000???????????????????
Argochampsa_krebsi
202?121112001011???110[0,1]101?0010001012110?012??112?11?10110?0?1?0?1300
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[1,2]0?0??00???????????0001022?01?1??0?00?020????0???0???1?010?????1000??
10?0?0??????0?0?00000?0??000?0010??0?000100??1???????1001?0????0000??0??1
00?0?0??0??00?0??000000?000101100-1?000???????????????????
Pristichampsus_vorax
200?02?1120000111000101111000100010021 10??1211112011?10100?0?1?1?1310?3??
?0?102011?112??0?311?1?????1?3?0100??001??1??1101??1?1100?00000001200101 0
0?000??[0,1]0??0300100002??01?1000?[0,1]001?1?00?000?001010010???11100000
1000000??0??0?0000000?100000000000??00000100?000011000111111???000???00?1
?000??0000000?01?00??000000101110-10000???????????????????
Eothoracosaurus_mississippiensis
[1,2]02?1211120010??11?[0,1]100111?001000100211 0??1?011?2??1?1?11????1?0?
131??3100??20000?????????[1,2,3,4]111[1,2]1????1?3001002?0?1?0??01?01??12
1100?0000?00100?1?????00???0000010?001022101??????0000???000000?00101?0?
000?1?10000010??000?00??0?0000?00??00010000100???000100?00????01010?110??
??0000000??1?000000000000?00000?0000000100010-10000???????????????????
Gavialis_gangeticus
212?121102001111110110111110010001002110101201112011110110101110113100310
0012000001112110131112111100?300100210?10010[0,1]?001??121100?00000001000
101?1?00001?00000100001022101?1?0000000[1,2]1??00000?00101001000011100000
1?00000000000?000??00?100010000[1,2]00?000001000101110010110110?001000001
0001000000000000?10110000000000101000-10001???????????????????
Leidyosuchus_canadensis
203112111200[0,1]0111000100111100100 0?0021101012?1112111110100?0?1?0?1310
031000110201?????????????20???10?300100??00?????01001??111100?00000001000
101?1?00???1[0,1]???31?1001022100?1000?1000211??0000?0010100100001?100000
10?000000???0?0000000?1000000000000?00000100?00???1001101111???00010?0??1
?000000000001?0010000000000101011-10000???????????????????
Asiatosuchus_germanicus
203?12111200001110001011 11?0010001002?10?012111?2?1??1??0????1?0?131003?0
00110?012?1?21??1?11??????????300100?10????1101001??1[1,2]1100???00001000
101???000??10000?10?001022?01?1????10?0?11000000?0?1?1001000?11100?0010?0
000?0???0?0000000?1?000000?000?0?000100?00101100010?111?0??000?000001?000
00???000??0??000000000??0101?-1??0????????????????????
Crocodylus_niloticus
203012111200[0,1]01110001021111001000100211 0?012111120111101001011101131 0
031000100201211121101311120211 00?3001002100100100?001??121100?00000001000
10101?00001?0000310?001022101?10001100021 1??00000001010010000111000001000
000000000?0000000?100000000?00?00000100000101100010 1111?001000000000 1?000
000000000101000000000 00101000-10000???????????????????
Diplocynodon_hantonensis
203?1211120010111000101111?00100010021 10?01211112011110100?0?110?13100310
0010020111112110131112021110?3001002?001??1?01001??111[0,1]00??0000001000
101?1?0000110000310?001022001?10?0?1000?11?00000?0010100100 0?11100?0010?0
0000000?0?0000000?100?00??0000?00000100?000011001101111?0010001100001?000
00??0000010??0000000000101010-10000???????????????????
Alligator_mississippiensis
203112?102?000111000102111100100 0?002110101211112011110100101110103120310
0010020121112111131112021100?30010021001001001001??111000?00000001000[1,2
]0101?000011?0003101001022000?100011000211??0000000101001000011100000 1000
000000000?0000000?100000000000?0000010000000111011111110001000110000 1?000
000000001101?0000000000100010-10000???????????????????
Portugalosuchus_azenhae

20???????2????1110001001101001000???2110?012??11?11?11???010?1100?3000???
00????????????????????????????????0??00?????10001???????0??00??0?10?010??
10??????????110?01?0???1?1?00??0002?????0?0??0101?0100?01??0??0???00??0
0???0???000?0?100?0???0?00?0??001?0?0???????110??1?????0000????00?00?00
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?00???01???00000?0????0???1??0????????????????????
Arenysuchus_gascabadiolorum
203??2?11?00?011100010[0,1]111?0010?0???211010120?11?01??1???0?0????01310
?????????1?????????????????????????0?00??00???????0010?1?11?0??00??0010?0
10??1?0????????????100102?????1??0?1000111???0?????10?0010??01?10??0010?0
000?????0?0?00000?100010000?0??0?0001?0?10?????00011?10????02010?0????0?0
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outgroup Gracilisuchus_stipanicicorum;


ccode  + 0 2 5 9 22 36 42.44 48 64 66 68 72 76 78 85 89.90 95.96 103.105
107 125 141.142 148 166 181 196 225*  ] 4 276 280 322.341;

taxcode - Candidodon_itapecuruense Trematochampsa
Stolokrosuchus_lapparenti Vectisuchus_leptognathus
Goniopholis_simus_pea2013 Goniopholis_stovalli Calsoyasuchus_new
sunosuchusnew Eutretauranosuchus_delfsi Shamosuchus_gradilifronsholo
Shamosuchus_tersus Shamosuchus_ancestralis shamoancestralis
Shamosuchus_ulanicus Shamosuchus_ulgicus Eutretauranosuchus_amnh
Pietraroiasuchus_ormezzanoi Unasuchus_reginae Glichristosuchus_palatinus;

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nstates 8 ;
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189 107
Goniopholis_simus
?0?0??????00000??00000000000?01000000?000000???01000000????00110000000000
1????00120?0000?0003000010000000000000000001000000010?000100000000000000?
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Theriosuchus_pusillus
?0??????0?000010?11000000000000000000?000010???11002000???0001?00000??010
1????00000?0000?01030000000?0000000?0?000000000000010?1011010101001?0210?
01100000010003?00000?000000?001?000????0000
Bernissartia_fagesii
??????0???0111102100000?0?000???0000?100010???0010?000???????10?0?00?001?
1????000?0?0000?00030?001?????1000????1?0000?000??0100?0???000100?0?0??0?
0?1010?0??00??0?????????000?0000?000??00000
Shamosuchus_djadochtaensis
????0????????0????1?01?????0?1??????0?11?????????????0??????1?0????0?10??
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011000?0?00????????????0?10?00??00??????011
Pietraroiasuchus_ormezzanoi
???????????????????1?000??0???????0?10021???111?3???????????10????????00?
?????00?21?00?0?01050???1?0??????0???????0???000000??2000?1?00?0???????0?
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Pachycheilosuchus_trinquei
????????????????0?01?00010?10??000??10???0???11?03?????????1?0???????????
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Allodaposuchus_precedens
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Lohuecosuchus_megadontos
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Lohuecosuchus_mechinorum
?????????????????????????????????????????????????????????????????????????
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Agaresuchus_fontisensis
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Agaresuchus_subjuniperus
?????????????????????????????????????????????????????????????????????????
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00001000?10????????1???10000?010000???0010?
Arenysuchus_gascabadiolorum
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0??01000?10????0???10?0100??????00????00?0?
Acynodon_iberoccitanus
??????????????????????????????????????????????10104101????????0???????0?0
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Acynodon_adriaticus
?????1?????????????01?100?1??????????010?10?????????01????????0???0??100?
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Iharkutosuchus_makadii
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Hylaeochampsa_vectiana
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Borealosuchus_threeensis
????0??????????????01???????0??????1?00??20???01002??1?????10?11?00000100
0????????????????????????????????????????????????????????????????????????
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Borealosuchus_formidabilis
000?000?0?11001001001000000101000001?000?20???0110200000?000?12000000100
001??00020?0000?00231000100?0000001000000010100100010100 2001?11000000?00?
011010100101000??????00100110000000??00001
Borealosuchus_wilsoni
??????0???????????10010000000101??00?1?000?20???01002??100?0?00110000020100
0????00020?0?0???02310001?????00001?0?0?0010100100010100200101100?000100?
?11110100101000 0?00???010011?0?0000??00001
Borealosuchus_acutidentatus
?????????????????????????????0???????????????????002???????????????000??????0
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0?111010?101000???????010??1?0?0000???0000?
Borealosuchus_sternbergii
000000000?110010?1001000000101000001?00???0???01102000000?00020000000100
000??00020?000000013100010001000001?0?000001110100010100000111100?000100?
011000100101000000?1?00100110000000??00001
Eothoracosaurus_mississippiensi
??????0??????????????01??000?????????00?00???0????122???3??????0?????00?011?
0????00120?000??102500001 0??000000???0000101001000???000?000100??01???
11100010?001?00????????10001000000 0??00001
Thoracosaurus_neocesariensis
??????0??????111?1?010????0011??0??0?00???0???1122???3?????????10?000?01?0
?????00120?0000?10250000100??000000?0?00001010010000?0000000000110?00010??
1?1000100001000000000?00100?10000000??00001
Thoracosaurus_macrorhynchus
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0????00120?00?0?10250000100??000000?0?0000101001000011000000000110?000100?
1110101 0?0010000???0??01000100000000???0000?
Eosuchus_minor
??????0???0??111???01?00?0?01???0000?000??0???1122??0300?0000?20?00000110
0????00120?0000?1025?000100?000000?00000001010010000?10000000110???0100?
11?100100001?0100??1???101010101003???00001
Eosuchus_lerichei
??????0???????01????01????????1?????????0?????????1122???3??????????????????0
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Piscogavialis_jugaliperforatus
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Gryposuchus_colombianus
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Gavialis_lewisi
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Gavialis_gangeticus
020000000?001111011010000000111000000?00000000112230030000000020000000110
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Boverisuchus_vorax
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Planocrania_hengdongensis
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Diplocynodon_muelleri
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Hassiacosuchus_haupti
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Procaimanoidea_utahensis
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Alligator_mississippiensis
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Eocaiman_cavernensis
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Tsoabichi_greenriverensis
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Paleosuchus_palpebrosus
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Purussaurus_neivensis
101?100?1?000010?0??1????011???????0?11???1???1?00??1?1010?11130110001100
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Mourasuchus_atopus
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Caiman_crocodilus
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Tomistoma_schlegelii
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Crocodylus_niloticus
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Crocodylus_porosus
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