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

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Received 17 October 2017; revised 12 July 2018; accepted for publication 10 August 2018

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.


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 interpreted (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
Crocodylia, and *Hylaeochampha 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, 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 *Tharkutosuchus* Ósi 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; Mannoni 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, *Woodbonesuchus byersmaurici* 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 Alloposuchidae) 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 taxon *Pietrarosiasuchus* (Early Albian, Italy), *Pachycheilosuchus* (Albian, United States) and *Iisisfordia* (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 *Hylaeochampha* 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, Bernissarttiidae, 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 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 *Tudzhikosuchus 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 *Tharkutosuchus* (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
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 crocodyliforms 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).

**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 (=Stenosaurus) bollensis (Antunes, 1967). The Late Jurassic outcrops provided an apparent peak in crocodylomorph diversity, with seven known taxa: Machimosaurus hugii von Meyer, 1837, Lisboaosaurus estesi Seiffert, 1970, 1973, Lusitanisuchus mitracostatus Seiffert, 1970 (Schwarz & Fechner, 2004) Knoetschkesuchus guimaroa (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 Vise, near Aveiro (Sauvage 1897–98). The Cenomanian of Portugal has a rich record that 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).

**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,
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, 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 *Rhynchosostreon*, *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*, *Pseudaspidoceeras* 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


Neosuchia Gervais, 1871 (*sensu* Benton & Clark, 1988)

Eusuchia Huxley, 1875

Crocodylia? Owen, 1842 (*sensu* Benton & Clark, 1988)

*Portugalosuchus* gen. nov.

urn:lsid:zoobank.org:act:8EB46DEB-0C2B-4A63-8E4E-862530D43AB7

**Etymology:** *Portugal* 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
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 posteroventral margin of the orbit. This ridge is anterior to the postorbital bar, which is flush with the lateral surface of the jugal.

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.
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-mandible 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-mandible 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.
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
The 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 unknown 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...
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 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.)
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 cannot 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 pterygoid 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 postero-medially, 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 posterodorsally, 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 anterior-most 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* Nopcesa, 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*, *Hylaeochampa*, *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*, *Hylaeochampa* and *Iharkutosuchus* are successive sister taxa to each other. The relationships within *Alloadoaposuchidae* have also changed, with *Arenysuchus* and *Alloadoaposuchus* 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 brain-case 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 *Alloadoaposuchidae*, 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-crocodilian eusuchian cannot be ignored or discarded.

Taking into account the unusual position, size, shape and configuration of the external mandibular fenestra...
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 → 7; 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, Iharukutosuchus, Agaresuchus, Lohucoesuchus, 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 throughout 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, Iharukutosuchus makaditi, Alloidosuchus subjuniperus (now Agaresuchus subjuniperus Narváez et al., 2016) and Allodaposuchus cf. precedens (now Lohucoesuchus 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 gaseabadiolorum 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.
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*, 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–quadratejugal contact at dorsal angle of infratemporal fenestra (also present in *H. vectiana*, allodaposuchids,
**Borealosuchus**, planocraurids, tomistomines, and some alligatorooids and crocodyloids). A foramen *internam- dibrularis 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 sloping skull table surface; pterygoid processes small and posteriorly projected; palatine-maxillary suture intersection at anteriormost limit of the sub-orbital 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 super- ior edge strongly sloping anteriorly (also common in cai- mans, *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 dyro- saurids 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 *Prodyrosuchus*); 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 posterodorsally or- iented, 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 gavi- aloids, *Tharkutosuchus* 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 basis- phenoid rostrum (shared with the allodaposuchid *Agaresuchus* and *Crocodyloidea*). *Portugalosuchus* also differs from Allodaposuchidae in several charac- ters. One of the most important differences is the ab- sence of a shallow fossa at the anteromedial corner of the supratemporal fenestra, which is usually con- sidered 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 mem- bers of Allodaposuchidae. The size relationship be- tween 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 analy- ses, 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 struc- ture is absent in most neosuchians closely related to Eusuchia and non-crocodylian eusuchians, such as *Shamosuchus*, *Bernissartia*, some goniopholidids, *Theriosuchus*, *Pachychelosuchus*, 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 composing the posterodorsal and anterodorsal margins and the surangular 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-gavialoid 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 Eothoracosaurus 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 evolution 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–S25). With this assumption, both maximum-parsimony and maximum-likelihood-Mk1 methods show a high probability (67%) for the absence of small fenestra as the ancestral character of Eothoracosaurus, and 50% uncertainty (Fig. S21).

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 Eothoracosaurus, 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% 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

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**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: ang, 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, Massalaiosuchus) (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) and Allodaposuchidae (with record from the Barremian) 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 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.

Moreover, 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. 

ACKNOWLEDGMENTS

Eduardo Puértolas Pascual is the recipient of a postdoctoral grant (SFRH/BPD/116759/2016) funded by the Fundação para a Ciência e a Tecnologia (FCT-MCTES). The authors wish to thank, most especially, the precious contribution of Dr Matilde Azenha, head of the Portuguese Teachers Association of Biology and Geology (APPBG), for the donation of the crocodile remains to the paleontological collections of the Museum of Lourinhã, as well as for field-work support and later collaboration. We also thank László Makádi from the Magyar Állami Földtani Intézet (Hungary), Zoltán Szentesi, Márton Szabó and Attila Ősi from the Magyar Természettudományi Múzeum (Hungary), Vlad Codrea from the Babeş-Bolyai University (Romania) and José Ignacio Canudo from the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) for access to specimens in their care. We thank Joana Bruno for the illustrations, Allan O’Connor and Marco Marzola for editing of the manuscript, and Christopher Brochu for the comments on the specimen. We thank Pedro Godoy and the anonymous reviewer for all their comments that have improved the article. Many thanks to Alexandra Fernandes for editing the text in English.

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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 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 aereum; 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 aereum and a linear and anteroposteriorly oriented surangular–articular suture. Abbreviations: an, angular; ar, articular; den, dentary; cor, coronoid; fae, foramen aereum; 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 craniocaudate passage. Abbreviations: cqp, craniocaudate passage; exo, exoccipital; fae, foramen aereum; 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 aereum; 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 (789 steps). Numbers of each node indicate the Bremer support and the bootstrap frequencies over 50%.

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.