



A new Late Cretaceous crocodyliform from the western margin of Gondwana (La Rioja Province, Argentina)



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ABSTRACT

The Cretaceous witnessed the greatest diversity of Gondwanan notosuchian crocodyliforms, which displayed high levels of diversity and a notable array of specialized forms that developed in different ecological niches. Among this diversity, the advanced notosuchians are a clade of mid body sized forms which displays a remarkable abundance but is restricted to two lithological units from the Late Cretaceous of South America, the Adamantina Formation in southeastern Brazil and the Bajo de la Carpa Formation in Patagonia (Argentina). The only exceptions known so far were the Late Cretaceous *Labidosuchus* from the Marília Formation in Brazil and *Yacarerani* from the Cajones Formation in Bolivia. Herein we report a new Cretaceous crocodyliform, *Llanosuchus tamaensis* gen. nov. et sp. nov., found in the Los Llanos Formation (Campanian?) in northwestern Argentina (La Rioja Province). The small specimen includes well preserved fragments of the cranium and mandible with an estimated skull size of about 9 cm lengths. This crocodyliform shares several derived characters with *Notosuchus terrestris* from the Bajo de la Carpa Formation (Patagonia) and it was found in a weakly developed sandy paleosol profile formed in wet local conditions but in a region characterized by semi-arid climate and active eolian sedimentation. The presence of a new advanced notosuchian in the Cretaceous of western Gondwana, and its intermediate geographical region between the known South American species (Brazil, Argentina and Bolivia), has interesting implications, and adds another record of an advanced notosuchian in deposits with inferred warm climates and semi-arid paleoenvironments. Finally, *Llanosuchus tamaensis* supports a Late Cretaceous age for Los Llanos Formation with important geological implications for La Rioja Province.

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1. Introduction

The Cretaceous of Gondwana witnessed the greatest diversity of crocodyliforms, and the notosuchians are the prime example of this diversification (de la Fuente et al., 2007; Pol and Gasparini, 2007; Pol et al., 2014). According to Pol et al. (2014), Notosuchia

comprises two distinct and major radiations, during the Early Cretaceous (peirosaurids + uruguaysuchids and ziphosuchians) and during the Late Cretaceous (South American peirosaurids, advanced notosuchians, and sebecosuchians). The most notable feature of the clade is the extraordinary array of specialized forms that exploited specific ecological niches (Carvalho et al. 2010; Ösi, 2013; Pol et al., 2014). Their diversification reached its peak in South America, where the majority of the advanced notosuchians are known from two units, in northern Patagonia (Argentina) and in Brazil (Candeiro and Martinelli, 2006; Pol and Gasparini, 2007; Nobre and Carvalho, 2013; Pol et al., 2014). In this contribution

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we use the term *advanced notosuchians* as it was used by Pol et al. (2014): a group that is deeply nested within Notosuchia and that includes *Mariliasuchus amarali*, *Labidiosuchus amicum*, *Notosuchus terrestris*, *Morrinhosuchus luziae* and Sphagesauridae (Pol et al., 2014). This informal grouping has been used by other authors recently and is usually recovered with high support in their analyses (e.g., Leardi et al., 2015a, 2015b). This clade also fits the phylogenetic definition of Notosuchidae given by Sereno (2005), although the latter was made based on analyses with reduced taxon sampling that did not include any member of Sphagesauridae. Despite the fact that the Cretaceous terrestrial ecosystems and their faunas are well known in these regions (Gasparini et al., 2007; Novas, 2009), the diversity of advanced notosuchians outside northern Patagonia and Brazil is virtually unknown, with the sole exception of the Late Cretaceous *Yacarerani boliviensis* from the Cajones Formation of Bolivia (Novas et al., 2009; Leardi et al., 2011a).

The Cretaceous vertebrate fossil-bearing beds in La Rioja Province, northwestern Argentina, remained poorly known and almost unstudied, aside from the Sanagasta neosauropod nesting site in Los Llanos Formation, being one of the most important recent findings (Grellet-Tinner and Fiorelli, 2010). Field works on the outcrops of the Los Llanos Formation (Tama locality, southeastern La Rioja Province, NW Argentina), lead to the discovery of a new terrestrial vertebrate assemblage. This fossil fauna includes representatives of three major dinosaur clades, and their association with microfossils suggests a Late Cretaceous age for the unit (Fiorelli et al., 2012; Hechenleitner et al., 2014).

Here, we report a new crocodyliform from the Los Llanos Formation that consists of skull and lower jaw fragments with incomplete but well-preserved dentition, which represents a new species of a small-bodied notosuchian crocodyliform. In this paper we describe the remains of this new notosuchian and test its phylogenetic relationships using a recently published dataset.

Institutional abbreviations—CRILAR Pv. Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Paleo-vertebrate collection, Anillaco, La Rioja, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MUCPV**, Museo de Geología y Paleontología, Paleo-vertebrate collection, Universidad Nacional del Comahue, Neuquén, Argentina.

2. Geological setting

The new taxon was discovered SW of Tama village in La Rioja Province, northwestern Argentina (Fig. 1), in exposures at the type locality of the Los Llanos Formation (Bodenbender, 1911; Bordas, 1941; Zuzek, 1978). This formation is composed of sandstones and locally conglomerate sandstones, which unconformably overlay upper Paleozoic deposits (Paganzo Group) and lower Paleozoic granitoids and metamorphic rocks (Ezpeleta et al., 2006; Basilici et al., 2014). The Los Llanos Formation is mostly exposed in the Sierra Brava region and on the eastern and western plains of the Sierra de Los Llanos with some isolated outcrops associated with the Sierra de Velasco (e.g., Sanagasta valley; Tauber, 2007; Fiorelli et al., 2012). Although Bodenbender named the “Estratos de Los Llanos” in 1911 the suite of Los Llanos Formation sedimentary succession with a Late Cretaceous age (“supracretaceous” sensu Bodenbender, 1911), subsequent authors correlated these strata with Cenozoic outcrops without further evidence, a very doubtful age, which is still used in some contributions (Ezpeleta et al., 2006; Dávila et al., 2007; Ruskin et al., 2011; Dávila and Carter, 2013; Dávila and Lithgow-Bertelloni, 2013, 2014). The Cretaceous age for Los Llanos Formation was re-established based on new finds of fossil vertebrates, charophytes and freshwater ostracods (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012; Carignano et al.,

2013; Hechenleitner et al., 2014) in different beds of this stratigraphic succession at Tama and other nearby localities. The associated vertebrate fossil fauna (ornithischians, titanosaurids, abelisaurian and coelurosaurian theropods, plus the notosuchian described here) and the microfossils, suggest a Late Cretaceous age for the unity in Los Llanos region.

In the Tama area, the Los Llanos Formation consists of a sedimentary succession more than 150 m thick with beds dipping 2–3° WNW constituted of poorly sorted, medium- to fine-grained sandstones with small pebbles, and secondarily conglomerate sandstones. It is characterized by a succession of cumulative paleosol profiles (Basilici et al., 2014). Although beds with high calcium carbonate content are present throughout the succession, they are particularly common in the lower section. Despite the absence of sedimentary structures, conglomeratic sandstone at the base of the formation shows ‘ghosts’ of cross-stratifications. The specimen presented here was recovered from a paleosol profile ~30 m above the contact with the underlying unit (see Supplementary Information for more details and discussions of the geology and sedimentology of Los Llanos Formation).

3. Systematic paleontology

Crocodylomorpha Walker, 1970 (*sensu* Clark, 1986)

Crocodyliformes Hay, 1930 (*sensu* Clark, 1986)

Mesoeucrocodylia Whetstone and Whybrow, 1983

Notosuchia Gasparini, 1971

***Lanosuchus tamaensis* gen. et sp. nov.**

Etymology. From *Llanos* (Los Llanos geographic region), the south east plains of La Rioja; also from *Sierra de Los Llanos* (Los Llanos mountain range), where the type outcrops of the Los Llanos Formation are located; and *souchos* (Gr.), crocodile; specific epithet *tamaensis* after the Tama village, La Rioja province, Argentina.

Holotype. CRILAR-Pv 502. The specimen includes fragments of the left and right maxilla (supporting the left palatal lamina), both with maxillary teeth, fragments of the left jugal, left pterygoid and ectopterygoid, right dentary with teeth, and a small fragment of right dentary with surangular (Figs. 2–7).

Type locality. The holotype comes from the Colozacán valley in the vicinity of Tunacata and Guasamayo, 4 km south of Tama village (Gral. Angel V. Peñaloza department), western slope of Sierra de Los Llanos mountain range in the southeastern region of La Rioja province (Fig. 1).

Stratigraphic horizon. The specimen was found in a paleosol of Los Llanos Formation approximately 30 m above the contact with the underlying unit (see Supplementary Information). A latest Cretaceous age (Campanian?) has recently been suggested for the Los Llanos Formation from an association of microfossils represented by charophytes and freshwater ostracods (Carignano et al., 2013; Hechenleitner et al., 2014).

Diagnosis. *Lanosuchus tamaensis* is a notosuchian crocodyliform with the following combination of relevant cranial characters (autapomorphic character is indicated by an asterisk): maxilla with six teeth; posterior margin of pterygoid flanges dorsoventrally thick with pneumatic spaces; anterior palatal fenestra present; evaginated maxillary alveolar edges present as a continuous sheet; posterior peg in mandibular symphysis located on the ventral surface of symphysis; splenial-dentary suture on the ventral surface of the mandibular ramus is posteriorly straight and forms an angle less than 60°; shape of the spleniads at the symphysis in dorsal view contacting each other obliquely, forming V-shaped

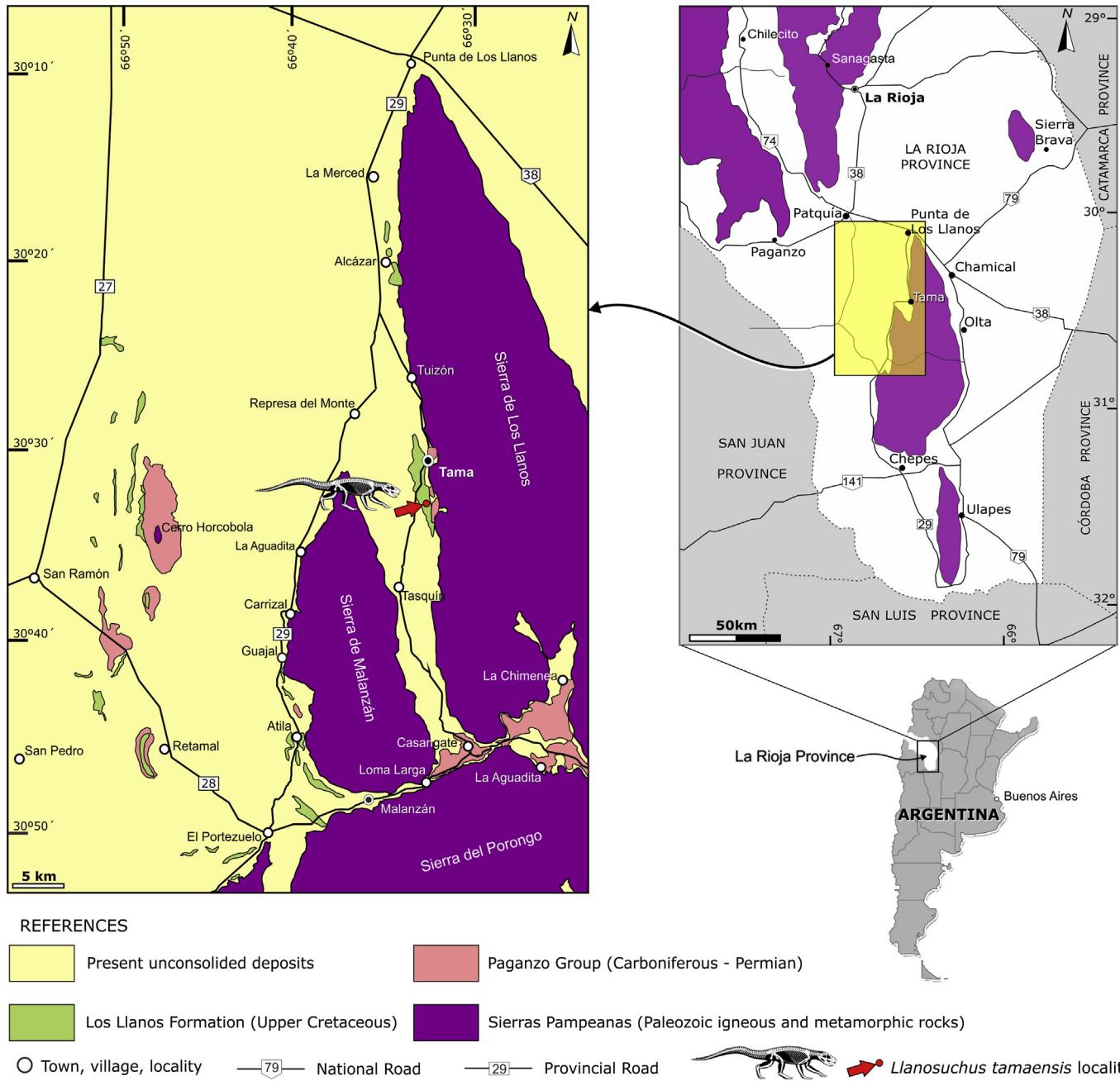


Fig 1. Geographical and geological setting of the studied area, Los Llanos region, southeast of La Rioja Province, Argentina, with the provenance of *Llanosuchus tamaensis* (CRIALR Pv 502). See [Supplementary Information](#) for more details on the geology and sedimentology of Los Llanos Formation, the stratigraphical section from the studied area. Maps drawn in Corel Draw Graphics Suite X6 based on Google Earth images and personal field observations.

anteriorly tapering process*; small subcircular depression on the lateral surface of the maxilla*.

4. Description

The holotype of *Llanosuchus tamaensis* is composed by associated fragments of the skull and mandible, including teeth (Fig. 2). The fragments are well preserved, with some of them replaced by amorphous silica, a diagenetic pattern observed also in other fossil remains of the Los Llanos Formation (Fiorelli et al., 2012). Both maxillae with teeth are preserved as well as the major portion of the palatal lamina of the left maxilla (Figs. 3 and 4). In general the

maxillae are very similar but smaller – approximately half the size – than in the largest specimens of *Notosuchus* (Fiorelli and Calvo, 2008), but have a similar size than those of *Mariliاسuchus* (Zaher et al., 2006) and other small-bodied advanced notosuchians, such as *Caryonosuchus* (Kellner et al., 2011a) and *Adamantinasuchus* (Nobre and Carvalho, 2006). Only a small fragment of the right premaxilla is preserved, attached to the maxilla by a butt joint (Fig. 3A–B). The articular facet for the premaxilla is visible across the right maxilla, while the alveoli and implantation of the first maxillary tooth can be observed in cross-section (Fig. 3D). There is a small neurovascular foramen located on the suture between the premaxilla and maxilla on the lateral surface of the rostrum. Also the wedge-like process of the maxilla present in peirosaurid taxa

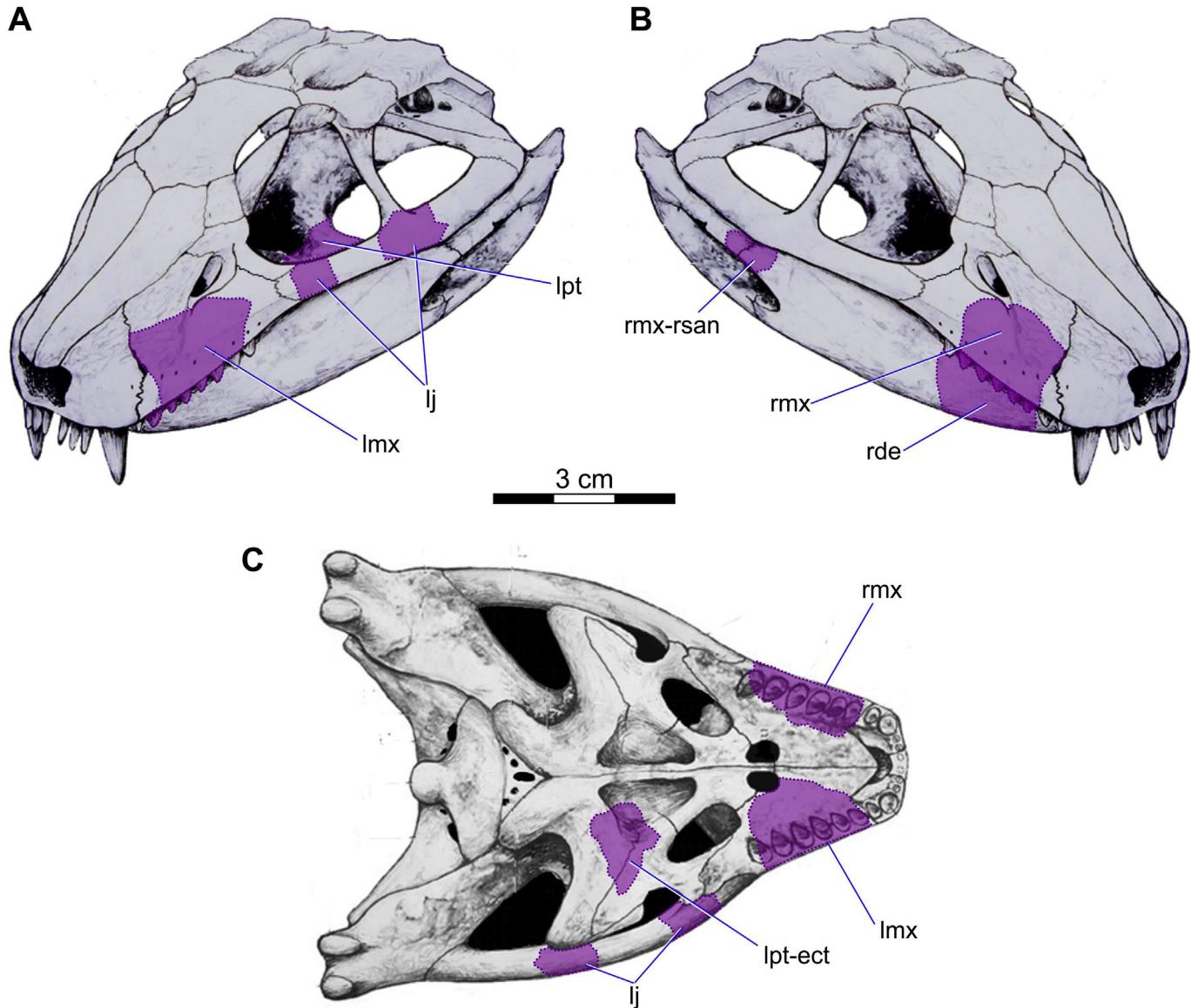


Fig 2. Different views of the skull restorated of *Llanosuchus tamaensis* (based on *Notosuchus terrestris*; drawing taken and modified from Fiorelli, 2005) showing the different elements of the type specimen CRIALR Pv 502 in **A**, anterolateral left; **B**, anterolateral right; **C**, ventral views. References: **lj**, left jugal; **lmx**, left maxilla; **lpt**, left pterygoid; **lpt-ect**, fragment of the left pterygoid and ectopterygoid; **rde**, right dentary; **rmx**, right maxilla; **rmx-rsan**, fragment of right maxilla and right surangular. Scale bar equals 3 cm.

(Gasparini et al., 1991; Turner and Buckley, 2008) is absent on the lateral surface of this suture. A transitional tooth is located at the contact between the premaxilla and maxilla, with both bones contributing to its alveolar walls.

Both maxillae of *Llanosuchus* preserve six molariform teeth (Figs. 3 and 4). Although not completely preserved, the shape and relative size of the antorbital fossa and fenestrae appear to be similar to those of *Notosuchus*, some advanced notosuchians, and basal mesoeucrocodylians (Figs. 3A and 4A). The ventral border of the antorbital fossa in both maxillae suggests a subcircular or almost rounded structure, unlike the anteroposteriorly elongated fossae of *Araripesuchus* (*A. wegneri*, *A. tsangatsangana*, *A. gomesii* and *A. patagonicus*) and basal crocodylomorphs. As in most notosuchians (Pol and Apesteguia, 2005), the maxillae have an unsculptured region along the alveolar margin on their lateral surface with a single row of neurovascular foramina of similar size (Figs. 3A and 4A). Furthermore, their external surfaces have a ventral region facing laterally and a dorsal region facing

dorsolaterally. The anterodorsal region of the maxillae of *Llanosuchus* is ornamented with small crests, pits and fine grooves (Figs. 3A and 4A). The lateral contour of snout in dorsal view is straight, whereas the ventral edge of maxilla in lateral view is slightly convex (Figs. 3D and 4D). There is a small subcircular depression on the lateral surface of both maxillae of *Llanosuchus* at the level of the third to fourth maxillary tooth, between the line of neurovascular foramina and ventral to the bulge of the anteroventral margin of the antorbital fossa (Figs. 3A and 4A). These depressions are so far unique for a notosuchian and do not represent homologous structures to those observed in neosuchians such as goniopholidids and pholidosaurids (see Martin and Buffetaut, 2012; Pritchard et al., 2012). However, more cranial material of *Llanosuchus* must be found to confirm the presence of such structures in the lateral surface of the maxilla tentatively accepted in this paper.

The left maxilla of *Llanosuchus* preserves the anterolateral margin of a maxillo-palatine fenestra (Fig. 4C–D), a feature also

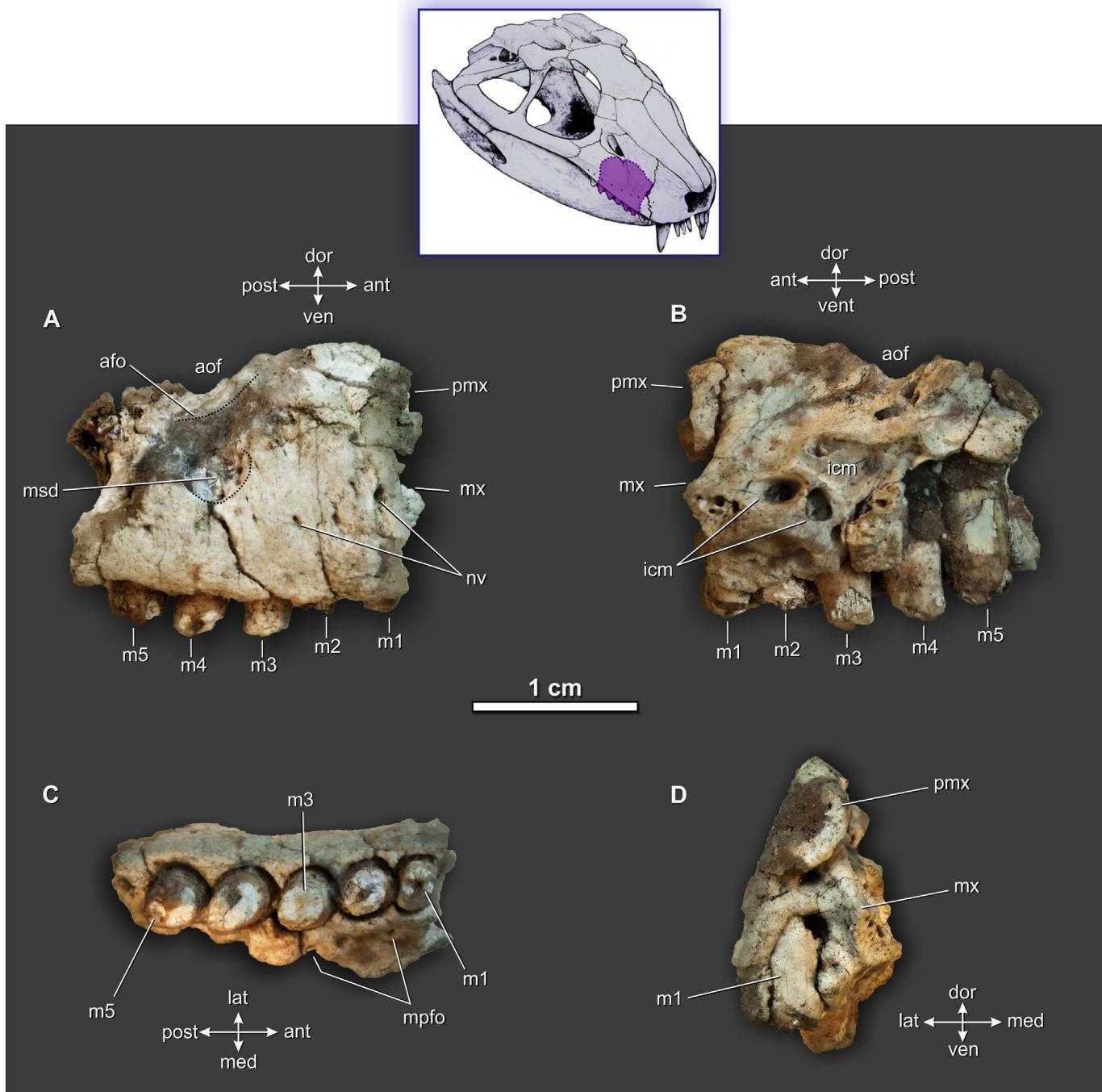


Fig 3. Right maxilla of *Llanosuchus tamaensis* (CRIALR Pv 502) in **A**, lateral; **B**, medial; **C**, ventral; **D**, anterior views. References: **afo**, antorbital fossa; **aof**, antorbital fenestra; **icm**, internal cavity of the maxilla; **m2–m6**, molariforms; **mpfo**, maxillo-palatine foramina; **msd**, maxillary subcircular depression; **mx**, maxilla; **nv**, maxillary neurovascular foramina; **pmx**, premaxilla. Scale bar equals 1 cm.

present in *Notosuchus*, *Mariliasuchus* and *Caipirasuchus stenognathus* (see Andrade and Bertini, 2008; Fiorelli and Calvo, 2008; Pol et al., 2014). The maxillo-palatine fenestra is connected with a passage or internal cavity that extends anterolaterally and ends in a recess located on the medial surface of the maxilla adjacent to the third and fourth maxillary teeth (Figs. 3B and 4B–D). This recess is clearly distinct from the main passage of the nasal cavity. There are other minor accessory and interconnected cavities that would connect with the maxillo-palatine foramina next to the maxillary teeth 3–6 (Fig. 4C). Although these accessory cavities could be

related to the interalveolar recess and maxillary sinuses, future CT analyses on complete skulls of *Notosuchus* are needed to establish the presence of these structures in detail. However, Ösi (2013) suggested that the maxillo-palatine fenestra openings in *Notosuchus* and *Mariliasuchus* (and by extension that of *Llanosuchus*) might have been related to the passage of the vomeronasal organ (Jacobson's organ), an accessory system in the oral cavity with a chemosensory function.

Llanosuchus lacks a rough surface on the palatal surface of the maxilla posterior to the last tooth present in Baurusuchidae (Pol

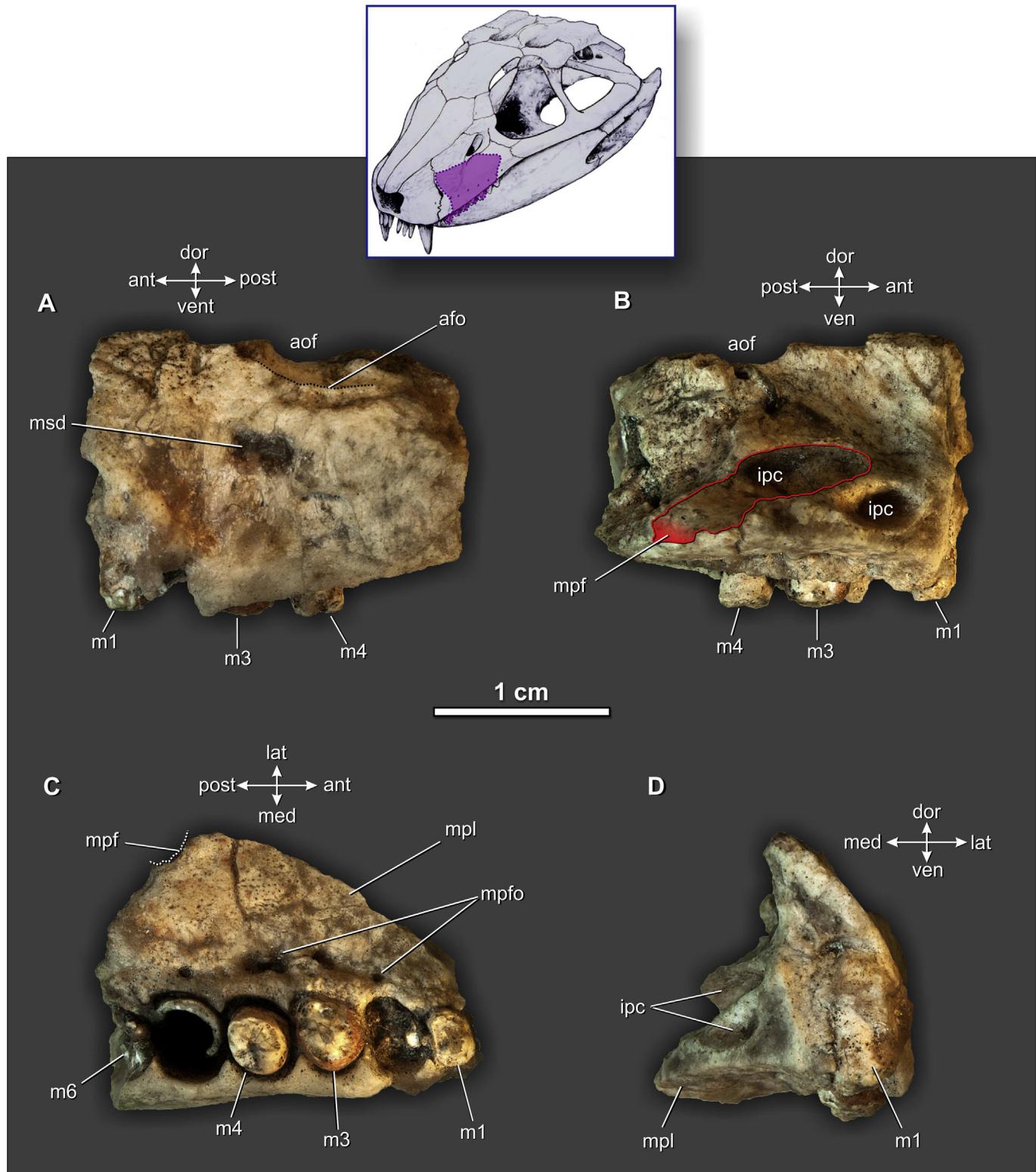


Fig 4. Left maxilla of *Llanosuchus tamaensis* (CRIALR Pv 502) in **A**, lateral; **B**, medial; **C**, ventral; **D**, anterior views. References: **afo**, antorbital fossa; **aof**, antorbital fenestra; **ipm**, internal cavity of the maxilla; **m2-m7**, molariforms; **mpf**, maxillo-palatine fenestra; **mpfo**, maxillo-palatine foramina; **mpl**, maxillo-palatal lamina; **msd**, maxillary subcircular depression. Scale bar equals 1 cm.

and Powell, 2011). However, in *Llanosuchus* there is evidence of evaginated maxillary alveolar edges (Figs. 3C–D and 4C), forming a continuous lamina as in *Notosuchus*, *Comahuuesuchus* and baurusuchids but differing from sphagesaurids (Pol and Gasparini,

2009). Moreover, and contrasting with the condition in peirosaurids (Turner and Buckley, 2008), *Llanosuchus* lacks a prominent depression on the palate near the alveolar margin at the level of sixth or seventh alveolus. The shape and general features of the

teeth of *Llanosuchus* are very similar to those of *Notosuchus* (Fiorelli and Calvo, 2008; Lecuona and Pol, 2008). Six maxillary teeth are partially preserved on both maxillae (Figs. 3 and 4), whereas seven alveoli with teeth are present on the right mandibular ramus (Fig. 5). These maxillary teeth have a single apical cusp; they show no size variation (no enlarged ones) and are implanted deep into the alveoli, which extend almost to the ventral limit of the antorbital fossa. Apparently, the middle and posterior teeth have crowns slightly compressed laterally at their apical ends. On the other hand, the molariforms are not constricted at the base of the crown. As in other notosuchians, the maxillary teeth are implanted in a dental groove (Figs. 3–5) and the width of the tooth root and crown is subequal to each other (Ortega et al., 2000). The first molariform tooth root of *Llanosuchus* is fully implanted in the maxilla and is observed across the premaxillary facet of the maxilla (Lecuona and Pol (2008)) (Fig. 3D). This tooth root clearly displays an angular break that is directed dorsomedially. Although poorly preserved, the teeth apparently have a smooth outer enamel surface and lack horizontal cingula along the buccal and lingual margins at the base of the crown. The posterior teeth are poorly preserved and it cannot be determined whether they have accessory apicobasal keels with cusps or tuberous denticles (such as those in *Mariliاسuchus* and sphagesaurids).

Similar to *Notosuchus*, the molariform teeth of *Llanosuchus* are teardrop-shaped in cross-section, with their main axis oriented obliquely (Fig. 7) with respect to the long axis of the skull (Fiorelli and Calvo, 2008; Lecuona and Pol, 2008). This particular orientation is reflected by the displacement of the distal carina on the maxillary teeth (Fig. 7A) and mesial carina on the mandibular teeth (Fig. 7B). Molariform with this transverse outline are also present in *Notosuchus* and other advanced notosuchians (e.g., *Mariliاسuchus*, *Labidiosuchus*, *Yacarerani*, *Adamantinasuchus*,

Caipirasuchus, *Sphagesaurus*, and *Caryonosuchus*; Fiorelli and Calvo, 2008; Lecuona and Pol, 2008; Iori and Carvalho, 2009; Pol et al., 2014), with the exception of *Morrinhosuchus* (Iori and Carvalho, 2009). However, in *Llanosuchus* and *Notosuchus* the angle formed by the main axis passing through the distal and mesial carina of the first maxillary tooth with respect to the longitudinal axis of the skull is approximately 44° (Fiorelli and Calvo, 2008; Lecuona and Pol, 2008). This angle diminishes in more posterior teeth (Fig. 7), the carinae of the subsequent maxillary ("mt") and mandibular teeth ("dt") steadily decreases from 36 to 12° (mt#2, dt#5: ~36°; mt#3, dt#6: ~30°; mt#4, dt#7: ~23°; mt#5, dt#8: ~18°; and mt#6?, dt#9: ~12°). In other advanced notosuchians, the angles of the carinae – whose main axis is oriented obliquely with respect to the longitudinal axis of the skull – are different from *Llanosuchus* and *Notosuchus*, and may even present intraspecific variations. In *Mariliاسuchus* the carinae are, in general, longitudinally directed with no angularity except for the first maxillary tooth and fifth dentary tooth (see Zaher et al., 2006). Instead, *Caipirasuchus* and *Sphagesaurus* have large angular variations of the carinae on the maxillary teeth, but are clearly different from those of *Llanosuchus* and *Notosuchus*; for instance, *C. paulistanus*: mt1~28°, mt2~30°, mt3~37°, mt4~48°, mt5~52°, mt6~58° (Iori and Carvalho, 2011); *C. montealtensis*: mt1~55°, mt2~48°, mt3~44°, mt4~50°, mt5~55°, mt6>60° (Andrade and Bertini, 2008); *C. stenognathus*: mt1=50°, mt2 and mt3=21°, mt4=30°, mt5=32°, mt6=40° (Pol et al., 2014); *Sphagesaurus*: mt1~45°, mt2~50°, mt3~53°, mt4~55°, mt5~58°, mt6~60° (based on the specimen RCL-100; Pol, 2003). Based on the available data the angle of the carinae on the maxillary teeth seems to decrease posteriorly in *Llanosuchus* and *Notosuchus*, but in *Caipirasuchus* and *Sphagesaurus* this angle seems to increase posteriorly; these variations could reflect differences in their masticatory system and dietary habits, although larger samples of specimens

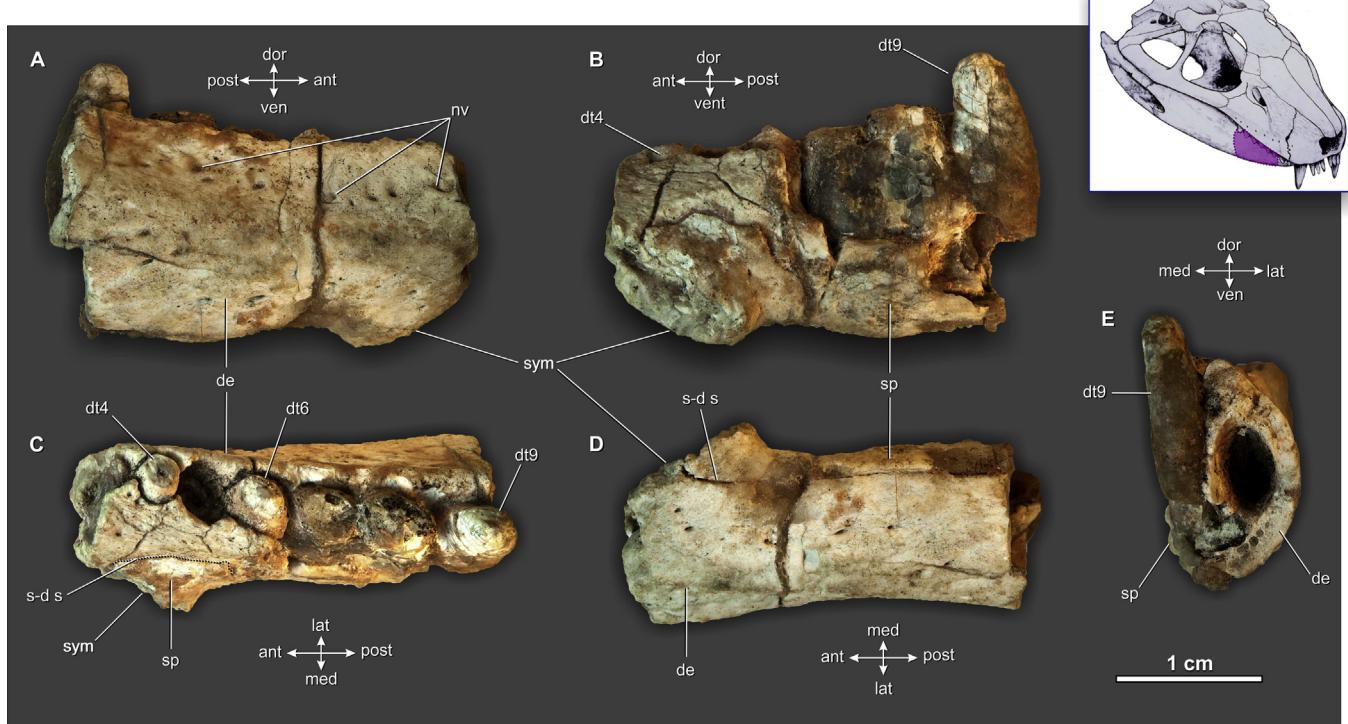


Fig 5. Right mandible fragment of *Llanosuchus tamaensis* (CRIALR Pv 502) in A, lateral; B, medial; C, dorsal; D, ventral; E, posterior views. References: de, dentary; dt4-dt9, dentary teeth (molariforms); nv, maxillary neurovascular foramina; s-d s, splenial-dentary suture; sp, splenial; sym, symphysis. Scale bar equals 1 cm.

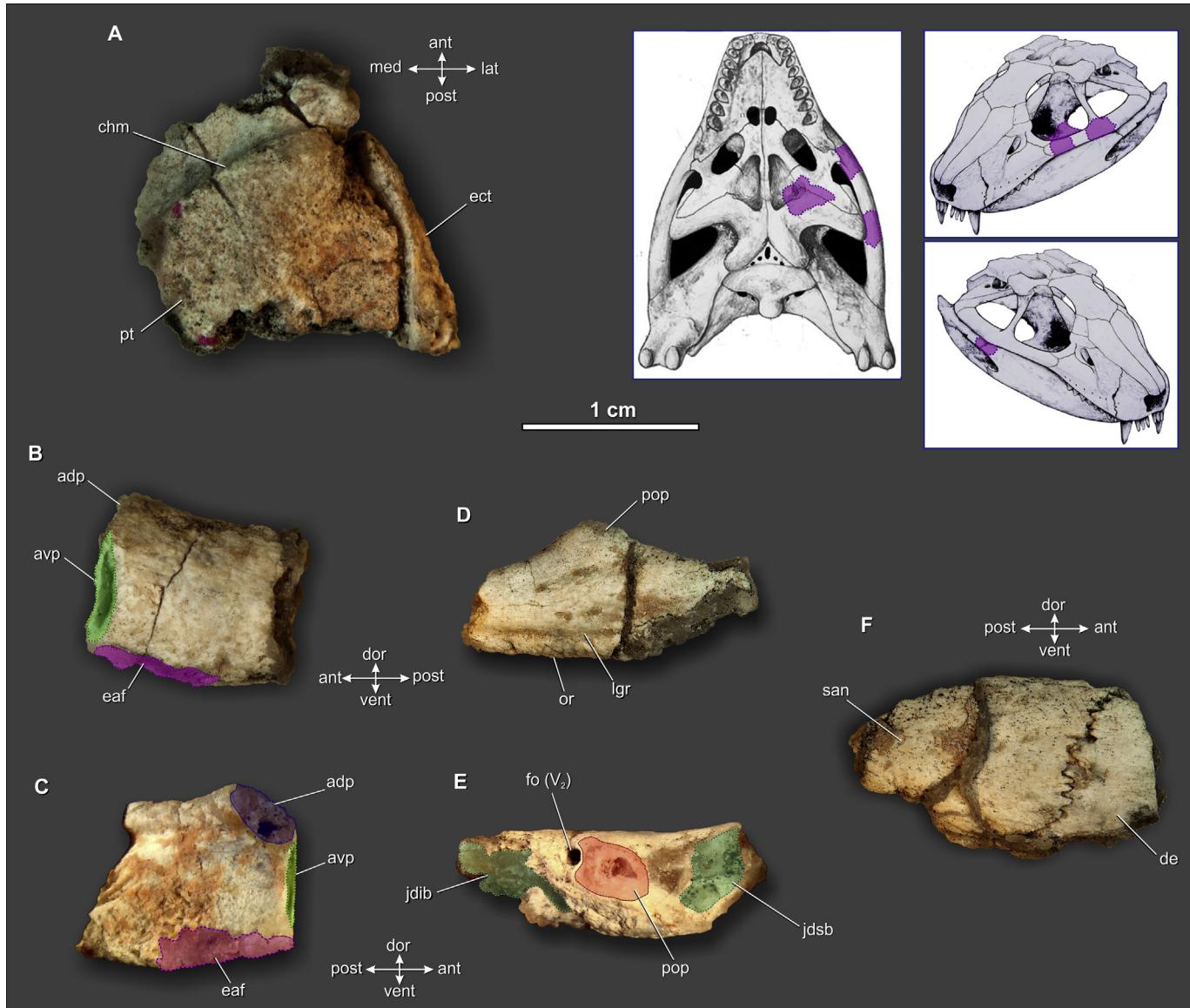


Fig 6. Cranial and mandibular remains of *Llanosuchus tamaensis* (CRIALR Pv 502); **A**, pterygoid and ectopterygoid in ventral view; **B**, anterior fragment of jugal in lateral view; **C**, anterior fragment of jugal in medial view; **D**, posterior fragment of jugal in lateral view; **E**, posterior fragment of jugal in dorsomedial view; **F**, medial fragment of the right mandible in lateral view. References: **adp**, anterodorsal process of the jugal; **avp**, anteroventral process of the jugal; **chm**, choanal posterior margin; **de**, dentary; **eaf**, ectopterygoid articular facet; **ect**, ectopterygoid; **fo** (V_2), foramen (entrance for the maxillary branch of the trigeminal cranial nerve); **lgr**, lateroventral groove; **or**, ornamentation; **pop**, postorbital process of the jugal; **pt**, pterygoid; **san**, surangular. Scale bar equals 1 cm.

from these new taxa are required to test the consistency of these patterns or existence of intraspecific variations (e.g., present among some specimens referred to *Mariliasuchus*).

Large contiguous foramina are located on the palatal branch of the maxilla in *Llanosuchus*, medial to the maxillary teeth 3–6 (Fig. 4C), similar in position although proportionately larger than the palatal foramina of other crocodyliforms. A sagittal torus on the maxillary palatal shelves is absent. The choanae opens on the palate through a deep midline depression, although this depression is not well preserved and the palatal surface of the preserved pterygoid seems to be smooth (Fig. 6A). The preserved margin of the left choana of *Llanosuchus* is very similar to that of *Notosuchus* (Fiorelli, 2005; Fiorelli and Calvo, 2008), which has a broad choanal opening and a medial region of the pterygoid flange that is dorsoventrally thick with some pneumatic spaces. Although the preserved ventral surface of the pterygoid is limited, the base of

the pterygoid flanges appears to be slightly concave without a pterygoid parachoanal fossa (Pol and Powell, 2011). The preserved portion of the left ectopterygoid (Fig. 6A) is fragmentary and laterally articulated with the pterygoid. In general, the ectopterygoid is similar to that of *Notosuchus*. The choanal opening of *Llanosuchus* is delimited posteriorly by an elevated wall (Fig. 6), formed by the pterygoids similar to *Notosuchus* (Fiorelli, 2005; Fiorelli and Calvo, 2008) and other advanced notosuchians such as *Mariliasuchus* and *C. stenognathus* (Zaher et al., 2006; Pol et al., 2014).

Only two fragments of the left jugal have been preserved in *Llanosuchus* (Fig. 6B–F). The anterior fragment is robust with a convex lateral surface (Fig. 6B–C). This portion bears an anterodorsal process with an internal duct, probably to contact the lacrimal, and an anteroventral process which also displays an internal duct, but larger. No large foramina can be observed on the

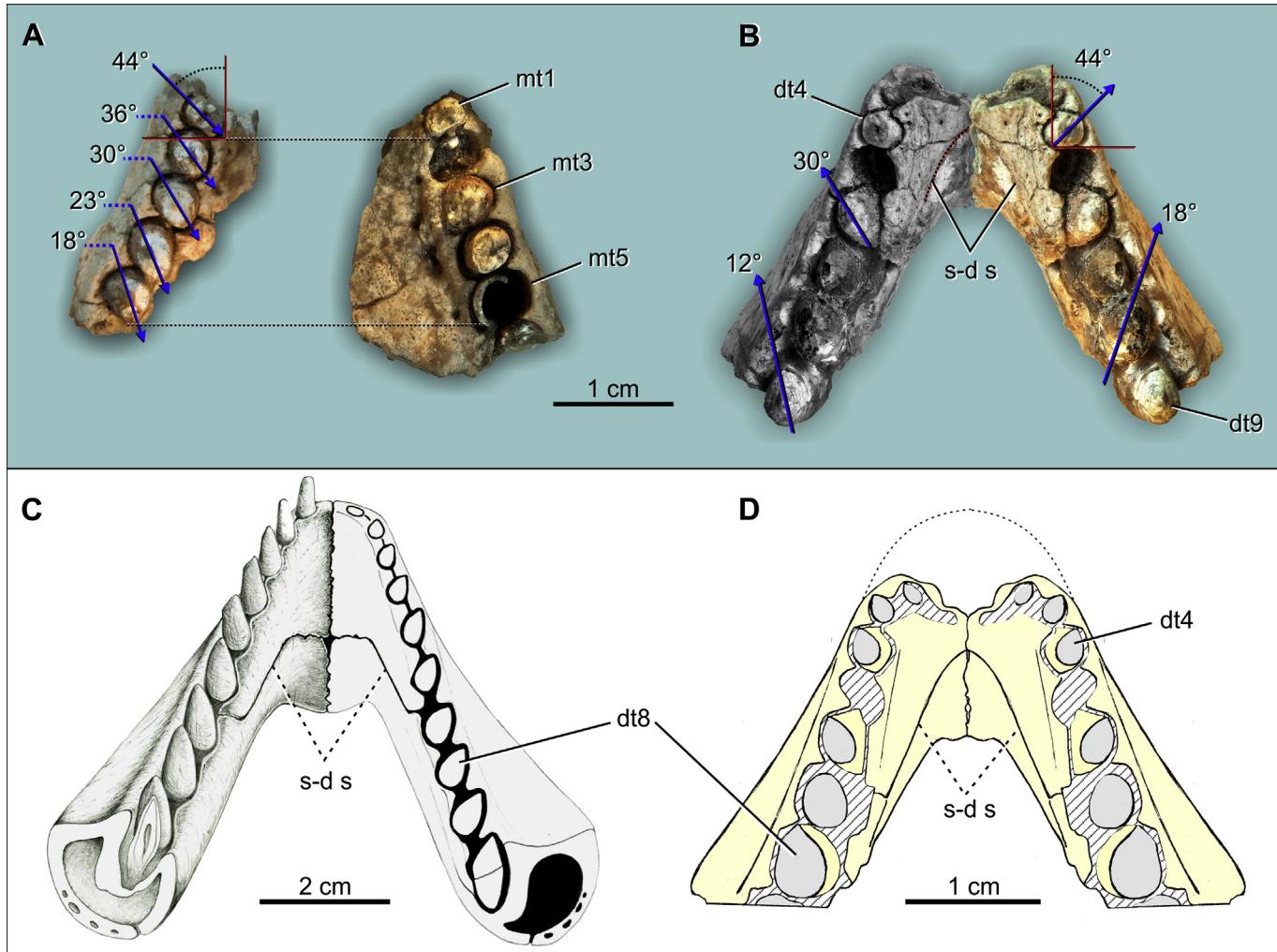


Fig 7. Orientation angles of the distal carina on upper cheek teeth (A) and mesial carina on mandibular teeth (B) of *Llanosuchus tamaensis* (CRIALR Pv 502). A, right and left maxillae in ventral views; B, right mandible in dorsal view; left gray mandible in B is the mirrored image of the right mandible; C, restoration of the mandibles of *Notosuchus terrestris* showing the transversely oriented suture between the splenial and dentary on the dorsal surface of the symphysis (modified from Fiorelli, 2005 and Fiorelli and Calvo, 2008); D, restoration of the mandibles of *Llanosuchus tamaensis* showing the v-shaped anteriorly tapering process of the splenials. References: **dt4-dt9**, dentary teeth; **mt1-mt5**, maxillary teeth; **s-d s**, splenial-dentary suture.

lateral surface of this fragment and it also has an incomplete ventral section that could be the ectopterygoid articular facet. The posterior fragment includes the base of the ascending (postorbital) process (Fig. 6D–E). It is dorsoventrally lower (6.15 mm) than the anterior one (10.1 mm), suggesting an anterior expansion of the jugal; the anterior part is almost twice as broad as the posterior fragment of the jugal. The base of the postorbital process of the jugal preserves an internal jugal duct. Posteromedially to this process, on the infratemporal bar of the jugal, a small foramen represents the entrance for the maxillary branch of the trigeminal nerve (V_2) (Fig. 6E). Lateroventrally, the posterior fragment of the jugal bears a longitudinal groove and ventrally displays some rough ornamentation with fine striations.

The anterior portion of the right mandibular ramus of *Llanosuchus* preserves seven alveoli (3–9) and five partially preserved teeth (Fig. 5). The jaw has the posterior part of symphyseal region well preserved. The dorsal surface of the symphysis is slightly concave and apparently the foramen intermandibularis oralis is absent, being completely enclosed within the splenial, as in *Notosuchus* (Pol et al., 2014). Furthermore, and similar to *Notosuchus* and other advanced notosuchians (e.g., *Marilisuchus*, *Caipirasuchus*, and

Yacarerani), the mandibular ramus of *Llanosuchus* has a posterior peg at the posterior edge of the mandibular symphysis; however, this peg is located on the ventral surface of the symphysis (Fig. 5A–C), a plesiomorphic condition shared only by *Notosuchus* in contrast to the derived condition of sphagesaurids. A posteroventral symphyseal depression is absent as in *Notosuchus* and other advanced notosuchians (see Pol et al., 2014). In lateral view the symphysis of *Llanosuchus* is deep and tapers anteriorly. The ventral surface of the splenial-dentary suture at the symphysis is slightly transverse but tends to be v-shaped (Fig. 5D). This condition is similar to that of other basal notosuchians such as *Malawisuchus* and *Pakasuchus* (Gomani, 1997; O'Connor et al., 2010), as well as in uruguaysuchids (Soto et al., 2011; Pol et al., 2012) and some sebecosuchians (see Montefeltro et al., 2011; Pol and Powell, 2011; Godoy et al., 2014; Kellner et al., 2014; Pol et al., 2014). However, the anterior end of the dentary-splenial suture at the symphysis extends transversely, as in advanced notosuchians such as *Notosuchus* (Fiorelli, 2005), *Comahuesuchus* (Martinelli, 2003), *Mariliusuchus* (Zaher et al., 2006), and sphagesaurids (Novas et al., 2009; Iori et al., 2013; Pol et al., 2014). The splenial-dentary suture on the ventral surface of the mandibular ramus of *Llanosuchus*

is straight posteriorly and would form an angle of up to 58° with its counterpart. This condition differs markedly from that of *Notosuchus* in which the sutures on each mandibular ramus form an angle of approximately 90° (see Fiorelli and Calvo, 2008).

Llanosuchus possesses a v-shaped splenial-dentary suture on the dorsal surface of the symphysis, tapering to a pointed end (the splenials contact each other obliquely) at the level of the fourth tooth (Figs. 5C and 7B, D). This condition differs from that of *Notosuchus* (Fig. 7C) that has a transversely oriented suture between the splenial and dentary (the splenials contacting each other transversely, forming a broad anterior process) on the dorsal surface of the symphysis at the level of the fifth tooth (Fiorelli and Calvo, 2008). This v-shaped anteriorly tapering process of the splenials on the dorsal surface of the mandibular symphysis of *Llanosuchus* (Fig. 7D) is also present in *Morrinhosuchus* (Iori and Carvalho, 2009), *Lorosuchus* (Pol and Powell, 2011), some peirosaurids (e.g., *Pepesuchus*, *Hamadasuchus* and *Montealtosuchus*; Larsson and Sues, 2007; Carvalho et al., 2007; Campos et al., 2011), and also in most neosuchians (e.g., Dyrosauridae, Thalattosuchia, Pholidosauridae, Atoposauridae, Goniopholididae and some eusuchians). As noted above, this condition distinguishes *Llanosuchus* from *Notosuchus* and other notosuchians, such as *Comahuesuchus* and *Caipirasuchus* (Martinelli, 2003; Iori et al., 2013; Pol et al., 2014), the peirosaurid *Gasparinisuchus* (Martinelli et al., 2012), and uruguaysuchids (Pol and Apesteguia, 2005; Sereno and Larsson, 2009; Soto et al., 2011). Thus, the splenials taper to a point on the dorsal surface of the mandibular symphysis (Figs. 5C and 7B, D) at the level of the fourth tooth, which represents an additional autapomorphy of *Llanosuchus*. Despite the incompleteness of the mandibular symphysis, it closely resembles that of *Notosuchus*. Based on the similarity of the mandibles of *Llanosuchus* and *Notosuchus*, the participation of the splenial likely exceeds 20% in ventral view of symphyseal length in *Llanosuchus*. This would match the condition of some notosuchian basal forms, as in *Malawisuchus*, *Pakasuchus*, and uruguaysuchids (Gomani, 1997; Sereno and Larsson, 2009; O'Connor et al., 2010; Soto et al., 2011).

The splenial-dentary suture on the dorsal surface of the mandible of *Llanosuchus* extends posterodorsally from the symphyseal region and reaches the medial alveolar margin of the toothrow between the dentary teeth 6 and 7. This trait is shared with *Notosuchus* and *Morrinhosuchus* (Fiorelli and Calvo, 2008; Iori and Carvalho 2009). Instead, in *Mariliاسuchus* and more derived notosuchians (e.g., Sphagesauridae), the dentary forms the lateral limit and the splenial forms the medial margin (Fig. 5B–C) of the whole molariform toothrow on each mandibular ramus (Zaher et al., 2006; Iori et al., 2013; Pol et al., 2014). Instead, in *Comahuesuchus* and *Simosuchus* the splenial-dentary suture ends much more posteriorly and reaches the ninth and tenth tooth, respectively (Martinelli, 2003; Kley et al., 2010), which is influenced by the unusual shape of the anterior mandibular region.

The left and right lower toothrows are separated from each other by a broad dorsal surface of the symphysis (preserved on the right mandible). This condition is plesiomorphic for notosuchians and present in many ziphosuchians (e.g., *Chimaerasuchus*, *Comahuesuchus*, *Morrinhosuchus*, *Notosuchus*, *Mariliاسuchus*), but differ from that of Sphagesauridae (see Pol et al., 2014). *Llanosuchus* has a compressed and vertically oriented ventrolateral surface of the dentary anterior to the mandibular fenestra (Fig. 5A). The dentary has an unsculptured region below the alveolar margin and its dorsal edge is straight in lateral view and subparallel to the longitudinal axis of skull. The anterior dentary teeth opposite to the premaxilla-maxilla contact are similar in size to the other dentary teeth and are not constricted at the base of the crown (Figs. 5B and E).

The dorsal half of the lateral surface of the dentary (below the alveolar margin) of *Llanosuchus* faces laterodorsally along the mid to posterior region of toothrow, forming a broad alveolar shelf that is strongly inset medially with respect to the ventral part of the lateral surface of the dentary (Fig. 5). This condition is also present in *Malawisuchus*, *Pakasuchus*, and advanced notosuchians (e.g., *Notosuchus*, *Mariliاسuchus*, *Labidiosuchus*, sphagesaurids). However, the alveolar shelf in *Llanosuchus* is less developed than in *Notosuchus*. The size of neurovascular foramina in the mid- to the posterior region of the alveolar edge of the dentary is very small (Fig. 5A), a plesiomorphic condition among notosuchians (also present in *Notosuchus*) that differs from the large foramina present in most sphagesaurids (e.g., *Adamantinasuchus*, *Yacarerani*, and *Caipirasuchus*; Nobre and Carvalho 2006; Novas et al., 2009; Pol et al., 2014). Ventrally, the right splenial is exposed along the mandibular ramus and its medial surface posterior to the symphysis is slightly convex (Fig. 5B–D). Finally, the holotype preserves a fragment of the right dentary and surangular (Fig. 6C), which shows the anterior edge of the mandibular fenestra. This suture is interdigitated and dorsoventrally extensive, similar to that of *Notosuchus*.

5. Phylogenetic relationships

The anatomical information for *Llanosuchus tamaensis* was incorporated in the data set of Leardi et al. (2015b). This data set represents an expanded version of the one used by Pol et al. (2014) and Leardi et al. (2015a), which includes a great number of cranial, mandibular and postcranial characters. Here we incorporate a new character and now, the data matrix consists of 440 characters and 112 taxa (see Supplementary Information). An equally weighted parsimony analysis was conducted using TNT version 1.1 (Goloboff et al., 2008a, 2008b) using a heuristic tree search based on 1000 RAS followed by TBR branch swapping, retaining up to 10 equally parsimonious trees per replication. The resulting most parsimonious trees (MTPs) were subjected to a final round of TBR. Branches were collapsed on the strictest criterion (rule 1 of Coddington and Scharff, 1994). See Supplementary Information for more details on the phylogenetic analyses.

Our analysis recovered 58320 MTPs ($L = 1693$; $CI = 0.311$; $RI = 0.740$) (see Fig. 8). The large amount of trees recovered is caused by the unstable position of several incompletely known taxa: *Coringasuchus*, *Pehuenchesuchus*, *Pabhwehshi*, *Neuquensuchus* and *Microsuchus*. Their inclusion results in different topologies among basal notosuchians, advanced notosuchians and sebecosuchians, and large polytomies at the base of these clades. When the different positions of these taxa are ignored in the MTPs the reduced strict consensus improves significantly, only having minor polytomies in the *Arripesuchus* clade and the advanced notosuchians (*Mariliاسuchus*, *Labidiosuchus* and the Sphagesauridae clade). In general, the results (Fig. 8) are consistent and comparable with previous topologies recovered formerly in other phylogenetic analyses (Pol et al., 2014; Leardi et al., 2015a, 2015b). *Llanosuchus tamaensis* is recovered as a member of the advanced notosuchian clade, being positioned in a polytomy involving also *Notosuchus* and the clade *Labidiosuchus* + *Mariliاسuchus* + Sphagesauridae (Fig. 8). This unresolved position is caused by the inclusion of *Llanosuchus*, as it is depicted either as the sister taxon of *Notosuchus* or as the sister group of the advanced notosuchians more derived than *Morrinhosuchus* and *Notosuchus*. The phylogenetic position of *Llanosuchus* as a notosuchian more derived than *Malawisuchus* + *Pakasuchus* is supported by the presence of a splenial involved in the symphysis forming less than the 50% of the total length of the symphysis (char. 77-1/2; Clark, 1994). *Llanosuchus* shares with other advanced notosuchians the following

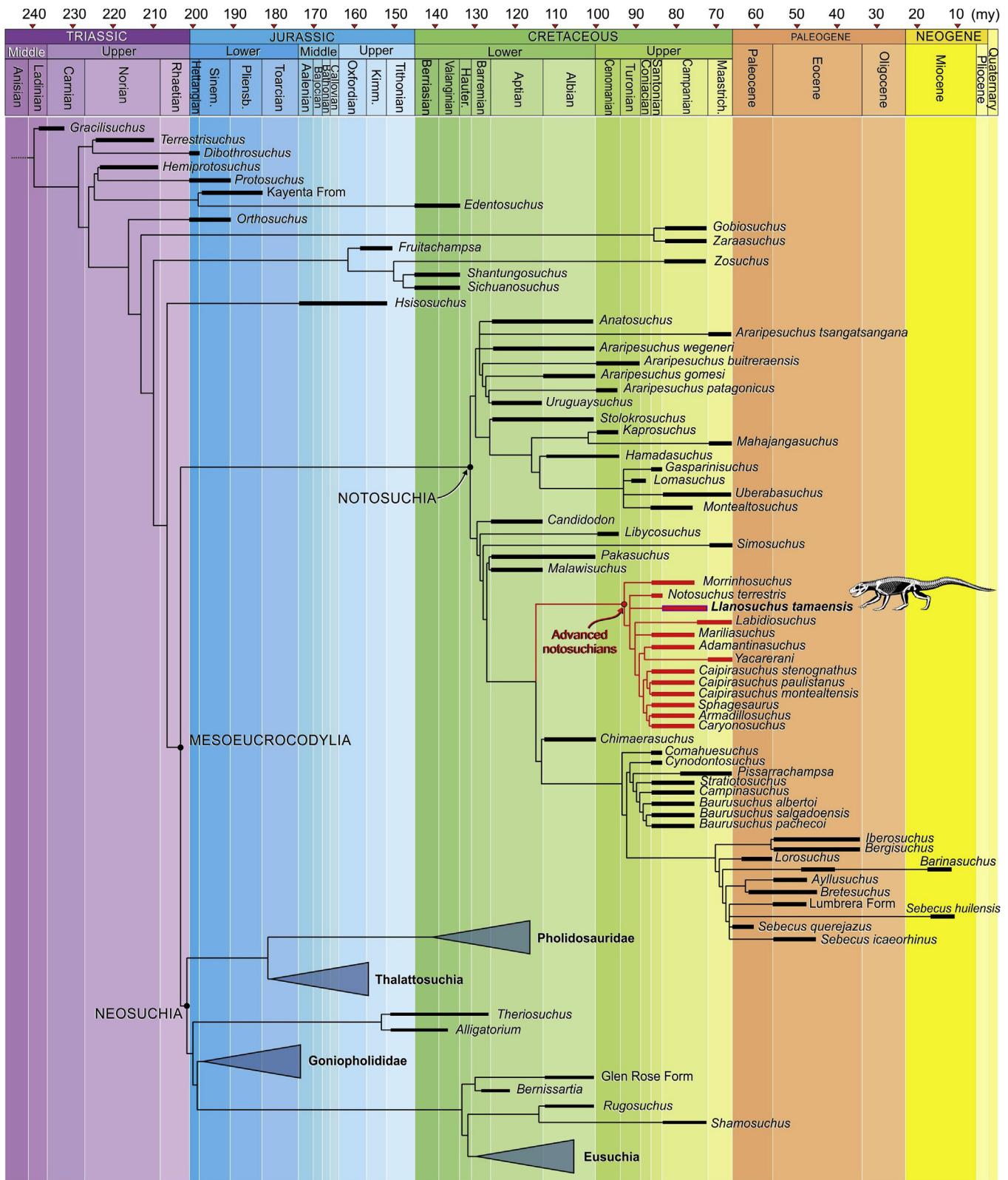


Fig 8. Calibrated phylogenetic relationships of Notosuchia with emphasis on the advanced notosuchian clade (in red) within the context of Crocodyliformes. The reduced strict consensus is shown here after pruning the fragmentary and problematic taxa *Pehuenchesuchus*, *Pabhweishi*, *Coringasuchus*, *Microsuchus* and *Neuquensuchus*. For more information on the phylogenetic analyses see the [Supplementary Information](#). Major clades of neosuchians are collapsed (e.g., Pholidosauridae, Thalattosuchia, Goniopholididae, and Eusuchia) and the age of their oldest member is used for inferring the age of these nodes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

characters: six teeth on the maxilla (char. 108-2; Wu and Sues, 1996; ambiguous in *Llanosuchus* as it has at least six teeth in the maxilla -0/1/2-) and a transitional tooth between the premaxilla and the maxilla (char. 381-1; Andrade and Bertini, 2008). *Llanosuchus* is positioned as an advanced notosuchian more derived than *Morrinhosuchus* based on the presence of obliquely oriented medial and distal carina of the lower posterior teeth (137-1; Pol, 1999). Besides the similarities between *Notosuchus* and *Llanosuchus*, these two taxa are differentiated by two autapomorphies in our phylogenetic analysis. In *Notosuchus* the splenials are expanded at the symphysis in dorsal view, forming a wide and blunt anterior process (440-1; new character), whereas in *Llanosuchus* the splenials taper to a triangular pointed process in this view (440-0; new character). However, this condition is also present in *Uruguaysuchus* and *Comahuesuchus*. On the other hand, *Llanosuchus* has an autapomorphy: the presence of a small posterolateral depression on the maxilla (char. 207-2; modified from Wu et al., 1997), unlike the large depression found in goniopholidids (207-1). A depression in this region of the maxilla is absent in other notosuchians. Finally, the alternative positions of *Llanosuchus* are not supported by any unambiguous synapomorphies, highlighting the incomplete knowledge of the new taxon.

Support values are generally low (see *Supplementary Information*) for most clades of the cladogram. Only the major clades among notosuchians show high support values, such as Mahajangasuchidae, Uruguaysuchidae, Peirosauridae, advanced notosuchians, Sphagesauridae, Sebecosuchia, and Baurusuchidae. In order to test the robustness of our results alternative phylogenetic positions were forced for *Llanosuchus*. To evaluate the different placements of *Llanosuchus* within advanced notosuchians, *Coringasuchus* was excluded a priori of the analysis, since it takes all possible positions in this clade. The phylogenetic hypothesis that places *Llanosuchus* as the sister taxon of Sphagesauridae requires 7 extra steps. However, when the new taxon is forced as the basalmost advanced notosuchian it requires a single extra step. Despite the uncertainty of the phylogenetic affinity of *Llanosuchus* within basal advanced notosuchians, its placement as a member of such a clade is better supported. A position of *Llanosuchus* outside of the advanced notosuchian clade as a derived ziphosuchian more derived than *Pakasuchus* + *Malawisuchus* requires 4 extra steps, whereas placement as the sister group of *Chimaerasuchus* + *Comahuesuchus* + *Sebecosuchia* requires 3 extra steps.

6. Discussion

Llanosuchus tamaensis is represented only by fragmentary cranial material but with important features that allow its recognition as a new notosuchian that radiated in the Early Cretaceous of South America (Pol et al., 2014). *Llanosuchus* is recovered as a member of the Late Cretaceous advanced notosuchian clade, forming a polytomy with *Notosuchus* and *Labidiosuchus* + *Mariliاسuchus* + Sphagesauridae (Fig. 8), a clade supported by the presence of a character previously known only for *Notosuchus*. This clade has low support values, and only a single extra step is required to place the new taxon as the basalmost advanced notosuchian, but 7 extra steps are needed to be considered as the sister group of Sphagesauridae. Thus, the advanced notosuchian affinities of *Llanosuchus* are well supported as several steps are required to remove it from this clade (Fig. 9). Although *Notosuchus* and *Llanosuchus* are very similar, both taxa are differentiated by two autapomorphies in our phylogenetic analysis (see above). In the following section, some paleoecological and paleobiogeographic issues on *Llanosuchus* and the Late Cretaceous South American notosuchians will be discussed.

Based on measurement of the partial remains of *Llanosuchus tamaensis*, it has an estimated skull length up to 9 cm and a total length of 80 cm long. Although *Llanosuchus* is a small-bodied notosuchian (larger individuals of *Notosuchus* have skulls reaching 20 cm in length), the specimen of this new taxon represents an adult or subadult individual based on the number of molariform teeth in the maxillae and in the right mandibular ramus. As in *Llanosuchus*, adult specimens of *Notosuchus* have 6 teeth in each maxilla and 10 teeth in each lower jaw (Fiorelli, 2005; Fiorelli and Calvo, 2008). Smaller and very juvenile specimens assigned to *Notosuchus* (e.g., MUCPv 118, skull length up to 5 cm; Pol and Gasparini, 2007) have only 3 or 4 maxillary teeth. Consequently, the type specimen of *Llanosuchus tamaensis* cannot be regarded as a juvenile of *Notosuchus*.

As noted above, *Llanosuchus* and *Notosuchus* differ on the presence of the splenials expanded at the symphysis in dorsal view, forming a wide and blunt anterior process in *Notosuchus*. The condition of *Llanosuchus* ("v-shaped" anteriorly tapering process of the splenials at the symphysis in dorsal view; Fig. 7B) is not unique among notosuchians and shared with *Morrinhosuchus* (Iori and Carvalho, 2009), *Mariliاسuchus* (Nobre et al., 2008), *Lorusuchus* (Pol and Powell, 2011), some peirosaurids (Carvalho et al., 2007; Larsson and Sues, 2007; Campos et al., 2011) but it clearly differs from that of *Notosuchus*. Furthermore, *Llanosuchus* also has a feature not observed in any other notosuchian: a small subcircular depression on the lateral surface of the maxilla anteroventral to the bulge of the ventral margin of the antorbital fossa (Figs. 3 and 4). To definitely identify this feature as unique for *Llanosuchus*, additional specimens with cranial material must be found.

The presence of *Llanosuchus tamaensis* in Late Cretaceous strata of the Los Llanos Formation of western Gondwana is significant in terms of regional geology and for the age of the unit, considered as Miocene by some authors (e.g., Dávila et al., 2007; Dávila and Lithgow-Bertelloni, 2013, 2014). However, *Llanosuchus* is also the first advanced notosuchian from northwestern Argentina (Fig. 9), a South American endemic group extremely abundant and diverse during the Late Cretaceous (Pol et al., 2014) and extinct at the end of the Cretaceous. The finding of *Llanosuchus* on the Los Llanos Formation supports a Late Cretaceous age for the unit, as the new taxon is well nested within the advanced notosuchians that initially radiated during the Turonian–Santonian (Pol et al., 2014). Notosuchians were terrestrial mesoeucrocodylians with morphological specializations, that allowed them to have a diverse ecology and occupy diverse niches (Fiorelli and Calvo, 2008; Nobre et al., 2008; Kley et al., 2010; Ali and Krause, 2011; Stubbs et al., 2014) and were very common during the Cretaceous (Pol et al., 2014). The advanced notosuchians were an important faunal component in some Late Cretaceous terrestrial ecosystems in South America (Pol et al., 2014; Stubbs et al., 2014). This group possessed great diversity mainly in their craniodental features and dietary habits (Ösi, 2013; Stubbs et al. 2014). Advanced notosuchians include 13 valid taxa from the Late Cretaceous of Brazil, Argentina and Bolivia (see Table 1 and Fig. 9). These advanced notosuchians come from four regions in South America: i) northern Patagonia in Argentina (Bajo de la Carpa Formation); ii) central Bolivia (Cajones Formation); iii) southern Brazil (Adamantina and Marília Formations); and iv) northwestern Argentina (Los Llanos Formation). As noted by Pol et al. (2014), more than half of the diversity of these advanced notosuchians comes from the Adamantina Formation (Fig. 9). However, *Llanosuchus* represents an advanced notosuchian in a new basin outside of the Neuquén and Bauru basins.

The paleobiogeographic and stratigraphic distribution of advanced notosuchians, and the addition of *Llanosuchus*, is particularly interesting. The geographic location of *Llanosuchus* is midway between other Late Cretaceous regions with known

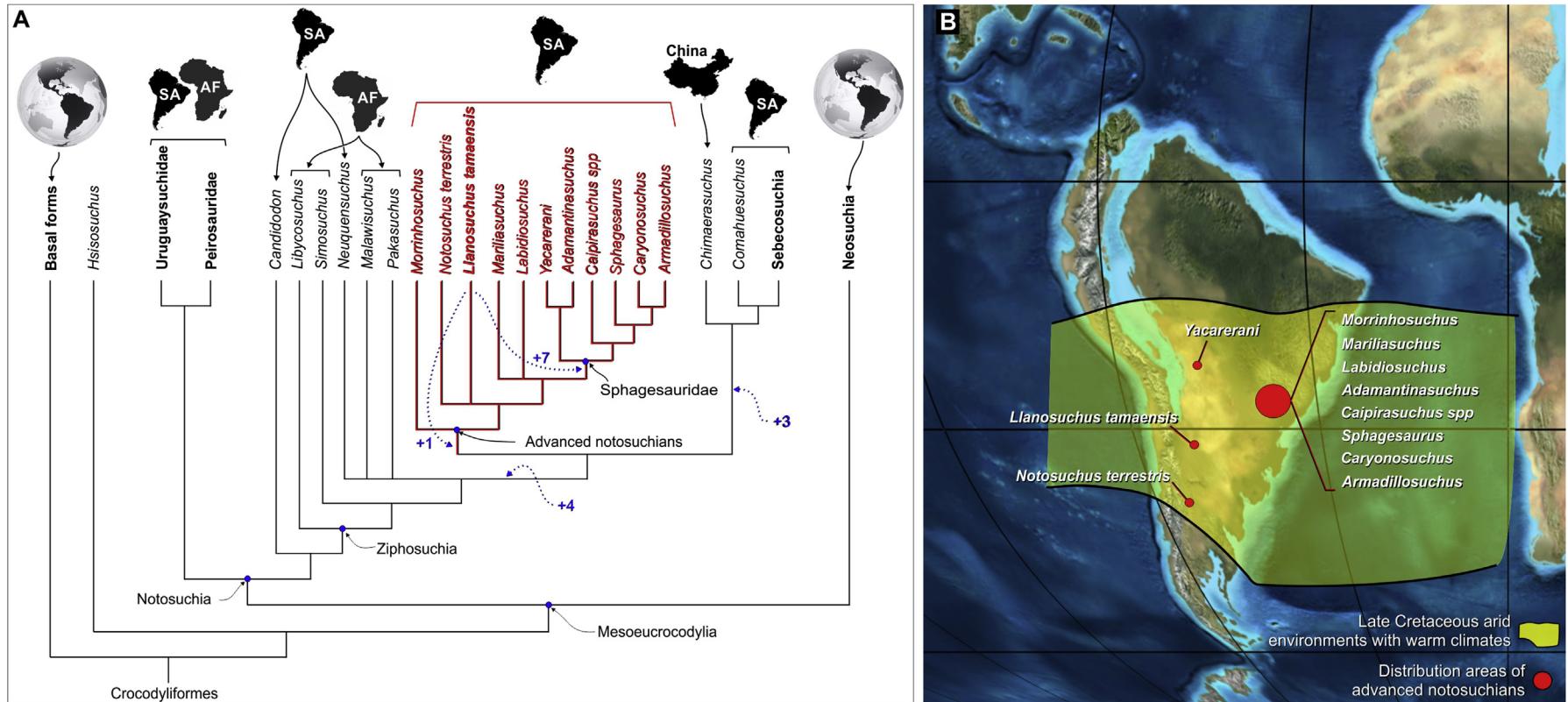


Fig 9. A, Phylogenetic relationships of Notosuchia and their land mass provenances showing the South American endemism of advanced notosuchians (in red). In addition, the blue dotted arrows indicate the extra steps when *Llanosuchus tamaensis* is forced as the sister group of Sphagesauridae (+7; which is highly suboptimal), as the basalmost advanced notosuchian (+1), as a derived ziphosuchian more derived than *Pakasuchus* + *Malawisuchus* (+4) or as the sister group of *Chimaerasuchus* + *Comahuesuchus* + *Sebecosuchia* (+3). B, Paleogeographic map of South America during the Late Cretaceous with the distribution of the advanced notosuchians; Late Cretaceous paleogeographic map provided by Dr. Ron Blakey and paleoclimatic reconstruction based on [Scotese \(2005\)](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

List of advanced notosuchian taxa, provenances, geological units, ages and their references.

"Advanced Notosuchian" taxa	Country – State	Unit – Formation	Stage	Reference
<i>Morrinhosuchus luziae</i>	Monte Alto, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Iori and Carvalho, 2009
<i>Llanosuchus tamaensis</i>	Tama, La Rioja, Argentina	Los Llanos Formation	Campanian?	This study
<i>Notosuchus terrestris</i>	Neuquén–Río Negro, Argentina	Bajo de la Carpa Formation	Santonian	Woodward, 1896; Gasparini, 1971
<i>Mariliasuchus amarali</i>	Marília, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Carvalho and Bertini, 1999
<i>Labidiosuchus amicum</i>	Peirópolis, Minas Gerais State, Brazil	Marilia Formation	Upper Campanian–Maastrichtian?	Kellner et al., 2011b
<i>Yacarerani boliviensis</i>	Santa Cruz de la Sierra, Bolivia	Cajones Formation	Maastrichtian?	Novas et al., 2009
<i>Adamantinasuchus navae</i>	Marília, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Nobre and Carvalho, 2006
<i>Caipirasuchus montealtensis</i>	Monte Alto, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Andrade and Bertini, 2008
<i>Caipirasuchus paulistanus</i>	Monte Alto, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Iori and Carvalho, 2011
<i>Caipirasuchus stenognathus</i>	General Salgado, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Pol et al., 2014
<i>Sphagesaurus huenei</i>	São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Price, 1950; Pol, 2003
<i>Caryonosuchus pricei</i>	Pte. Prudente, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Kellner et al., 2011a
<i>Armadillosuchus arrudai</i>	General Salgado, São Paulo State, Brazil	Adamantina Formation	Santonian–Campanian?	Marinho and Carvalho, 2009

advanced notosuchians (Patagonia, Bolivia and Brazil; Fig. 9B). However, there are others important Upper Cretaceous formations in South America without notosuchian remains (see Novas, 2009). *Llanosuchus* and *Notosuchus* show homologous craniodental features, but also lived in similar climatic and ecological regions: the Bajo de la Carpa and Los Llanos formations were dominated by eolian sedimentation in a markedly seasonal to semi-arid climate (Sánchez et al., 2006; Fiorelli, 2010; Basilici et al., 2014; see Supplementary Information). According to Basilici et al. (2014), the medium annual precipitation during the cumulative paleosols development of the Los Llanos Formation in the Tama region ranged from 230 mm/y to 450 mm/y. The paleoenvironment where *Llanosuchus* lived was arid and pedogenesis kept pace with eolian sedimentation and the deposits were quickly incorporated into the soils. The result was the formation of a succession of accretionary (or cumulative) soils (Basilici et al., 2014). In this regard, Carvalho et al. (2010) suggested that the Gondwanan distribution of Noto-suchia during the Cretaceous was determined mostly by climate, which was dry and characterized by a marked seasonality (Fig. 9B). This fits perfectly with the paleoenvironmental characteristics of the units where the advanced notosuchians are distributed in Brazil and Argentina: warm Cretaceous climate in semi-arid environments dominated by eolian deposition (Sánchez et al., 2006; Basilici et al., 2009; Basilici and Dal'Bó, 2010; Carvalho et al., 2010; Dal'Bó et al., 2010; Fiorelli, 2010; Garrido, 2010; Basilici et al., 2014). According to Carvalho et al. (2010), the aridity and seasonal warm climate prevailing during the Late Cretaceous of Gondwana in the localities with advanced notosuchians may explain the development of some ecological strategies by the members of this group and their dominance and high diversity in some units (e.g., Bajo de la Carpa and Adamantina Formations) and their absence in others. The exploration of Cretaceous units deposited in semi-arid paleoenvironments could be the key to future finds of advanced notosuchians. Finally, this illustrates the notable hyperdiversity of notosuchians in the Late Cretaceous of South America with at least 24 species of Notosuchia in the time span Santonian–Maastrichtian. Another remarkable case of high notosuchians diversity is evidenced during the Cretaceous in Africa and Madagascar (Sereno and Larsson, 2009; Krause et al., 2010), as well during the late Cenozoic in South America with the high crocodylian diversity (Scheyer et al., 2013; Salas-Gismondi et al., 2015).

7. Conclusions

Llanosuchus tamaensis from the Upper Cretaceous of La Rioja Province, northwestern Argentina, represents a new species of the

advanced notosuchian clade. *Llanosuchus* shared several derived features with other advanced notosuchians and is positioned as an advanced notosuchian more derived than *Morrinhosuchus* based on the presence of obliquely oriented medial and distal carinae on the lower molariform teeth. Despite the fragmentary condition of the holotype, *Llanosuchus* is remarkably similar to *Notosuchus*; both taxa are differentiated by two autapomorphies: the form of the splenials at the symphysis and the presence in *Llanosuchus* of a small posterolateral depression on the maxilla.

The diversity of advanced notosuchians in the Late Cretaceous of South America may be explained by both intrinsic paleobiological features and paleoenvironmental factors. The presence of a new small-bodied mammal-like crocodyliform in the Cretaceous of western Gondwana halfway between the known South American notosuchian species (Brazil, Patagonia and Bolivia), has interesting geologic and biogeographic implications. The presence of *Llanosuchus tamaensis* in the Los Llanos Formation, along with a series of recent paleontological discoveries – chiefly sauropod, theropod, and ornithopod dinosaurs –, provided crucial evidence to redefine it as Late Cretaceous. Furthermore, the discovery of *Llanosuchus* adds another case of an advanced notosuchian in a region characterized by warm paleoclimates and semi-arid paleoenvironment. These features are important factors to understand the hyperdiversity of notosuchians in the Late Cretaceous of Gondwana, and would have great impact in their ecological strategies and evolutionary history.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2015.12.003>.