The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2011, **163**, S173–S198. With 16 figures

A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the middle Cretaceous of Uruguay and its phylogenetic relationships

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Received 15 June 2009; revised 24 March 2010; accepted for publication 26 October 2010

Uruguaysuchus is a small mesoeucrocodylian known from several partial skeletons and skulls from the Guichón Formation (middle Cretaceous, Uruguay). Several authors have pointed out derived similarities of this taxon with different basal notosuchian genera, highlighting its importance for mesoeucrocodylian phylogeny and biogeography. However, the holotype is only partially prepared and has not been available for study for many years. Thus, phylogenetic studies have included this form based on the original description, thereby resulting in a large amount of missing data in the character scorings of this taxon. Here, we describe a new specimen from the type locality consisting of a partial skull, lower jaw and cervical vertebrae which can be referred to *U. aznarezi*. The new specimen allows for the recognition and scoring of several characters previously unknown for this taxon, thus providing a more extensive diagnosis, as well as new information for understanding its phylogenetic relationships. These characters are congruent with the morphology present in basal notosuchians. The relationships of *Uruguaysuchus* are tested through a cladistic analysis using a recently published data set including the new information. The phylogenetic results differ from previous analyses, recovering this taxon as the sister group of the *Araripesuchus* clade. *U. terrai* is considered a juvenile individual of *U. aznarezi*.

doi: 10.1111/j.1096-3642.2011.00717.x

ADDITIONAL KEYWORDS: anatomy – Cretaceous – phylogeny – Notosuchia – Uruguay.

INTRODUCTION

In 1932, several partial skulls and skeletons belonging to at least seven individuals of small, terrestrial crocodyliforms were discovered during the drilling of a water well in the town of Guichón, Paysandú province, Uruguay (see Fig. 1). The agronomist Jorge Aznárez sent the abundant remains to the Argentinean palaeontologist Lucas Kraglievich (1886–1932), who unfortunately died before he was able to study them. Kraglievich's wife sent them to another Argentinean palaeontologist, Carlos Rusconi (1898–1969), who published a detailed description (Rusconi, 1933), and recognized a new genus, *Uruguaysuchus*, and two new species, *U. aznarezi* and *U. terrai*. Since then, *Uruguaysuchus* has played a key role in the recognition of the infraorder Notosuchia (Gasparini, 1971), which is the most diverse group of Crocodyliformes from the Cretaceous of Gondwana and is characterized by the presence of heterodont dentition with a remarkable disparity in the tooth

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Figure 1. A, map of Uruguay illustrating exposed sequences of the Guichón Formation (black arrow = town of Guichón). B, location of Guichón, from where FC-DPV 2320 comes (it is also the type locality of *Uruguaysuchus*), about 90 km east of Paysandú (Paysandú province, north-west Uruguay).

anatomy among its members. Moreover, *Uruguaysuchus* is still the best-represented Mesozoic vertebrate from Uruguay.

Unfortunately, the holotype of *Uruguaysuchus aznarezi*, a *c.* 1.2-m-long articulated adult individual (including a complete skull, mandible, right forelimb, 18 vertebrae, both ilia and partial right hindlimb, as well as a few associated osteoderms), is only partially prepared. More importantly, the type material is housed at a private collection (Colección Aznárez, Bella Vista, Maldonado province, Uruguay) and has not been available for study for many years. Unfortunately, all five paratypes are currently lost. The holotype of the second species described by Rusconi, *U. terrai*, is also housed in the Colección Aznárez. Although it has been heavily damaged during its transportation (as already noted by Rusconi, 1933), a photograph of the original specimen (a complete mandible and skull in articulation) does exist.

The first detailed study on the affinities of *Uruguaysuchus* was conducted by Gasparini (1971), after performing a first-hand study of the original material. Gasparini (1971) noted similarities between this taxon and *Araripesuchus gomesii* (Price, 1959) and clustered these two taxa in the family Uruguaysuchidae. Recent cladistic studies have included this form based on the published information (Rusconi, 1933), albeit with an abundance of missing character data (e.g. Buckley *et al*., 2000; Ortega *et al*., 2000). These studies have retrieved *Uruguaysuchus* in alternative positions, closely allied with other basal notosuchians such as *Simosuchus* (Buckley *et al*., 2000; Turner, 2006), *Candidodon* (Andrade & Bertini, 2008; Fiorelli & Calvo, 2008), *Notosuchus* (Jouve *et al*., 2006), or as the most basal member of Ziphosuchia (i.e. the clade including all notosuchians except *Araripesuchus*; Pol, 2003; Gasparini, Pol & Spalletti, 2006; Turner & Buckley, 2008). As noted by Gasparini *et al*. (1998), *Uruguaysuchus* can be considered as an 'enigma in the evolutionary history of crocodiles'.

The new specimen of *U. aznarezi* described herein was found in the fossil vertebrate collection of the Facultad de Ciencias in Montevideo (Uruguay), and is probably the same specimen briefly mentioned but not described nor figured by Lambert (1940). It comes from the same locality that yielded the previously known *Uruguaysuchus* specimens. These remains include a partial skull, a lower jaw and three cervical vertebrae and allow for the recognition of several characters previously unknown for this taxon that shed light on the phylogenetic relationships of *Uruguaysuchus*.

Institutional abbreviations: CA, Colección Aznárez (Bella Vista, Uruguay); FC-DPV, Colección de Vertebrados Fósiles, Facultad de Ciencias (Montevideo, Uruguay); MPCA, Museo Paleontológico Carlos Ameghino (Cipolletti, Argentina); MPMAB, Museo Paleontológico Municipal Alejandro Berro (Mercedes, Uruguay); MUNHINA, Museo Nacional de Historia Natural y Antropología (Montevideo, Uruguay).

GEOLOGICAL SETTING

The Guichón Formation (Bossi, 1966) crops out in Paysandú, Río Negro and Salto provinces, western Uruguay (Fig. 1). According to Goso & Perea (2004), it comprises mainly pink-greyish to reddish sandstones, which contain moderate to well-sorted, subrounded, fine to medium-sized grains in a pelitic matrix. These sandstones (which compositionally are feldspathic wackes) are either massive or may instead exhibit parallel lamination, cross-lamination and graded bedding. These lithologies were deposited in south-west-trending alluvial–fluvial systems comprising low-sinuosity channels traversing through sandy plains. Subordinate to the already mentioned sandstones are conglomeratic and pelitic lithologies, interpreted as channel-fill and overbank deposits, respectively. It is inferred that the Guichón

Formation was deposited in warm, semi-arid climatic conditions (Goso, 1999; Goso & Perea, 2004).

The Guichón Formation unconformably overlies flood basalts of the Arapey Formation (radiometrically dated to 132 Ma – Hauterivian; Féraud *et al*., 1999), and is in turn unconformably overlain by sandstones, conglomerates and pelites of the Mercedes Formation (Campanian–Maastrichtian; Daners & Guerstein, 2004; Goso & Perea, 2004). Both the Arapey and the Mercedes Formations were formally defined by Bossi (1966). Although Bossi (1966) also defined the Asencio Formation, it must be noted that most authors have partly or totally included the Asencio Formation within the Mercedes Formation (Ford & Gancio, 1988; Goso, 1999; Bossi & Ferrando, 2001; Goso & Perea, 2004; see discussion in Martínez & Veroslavsky, 2004). The Guichón and Mercedes Formations are included in the Paysandú Group (Bossi & Navarro, 1991).

Deposition of the Paysandú Group began under endorrheic conditions after extrusion of the Neocomian flood basalts (an event regionally known as the Serra Geral magmatism), which in Uruguay extends over 25 000 km^2, with a maximum thickness of 220 m. This sedimentary scenario continued in the Argentinean Mesopotamia, where the unit depocentre is located. In particular, the Guichón Formation can be partly correlated with the Argentinean Puerto Yeruá Formation (Goso, 1999; Goso & Perea, 2004). Traditionally, the Paysandú Group has been considered to represent the youngest deposits of the Norte Basin, although other authors consider that given its peculiarities the recognition of a separate basin is justified: the Litoral del Río Uruguay Basin, or Litoral Basin (Goso, 1999; Goso & Perea, 2004).

AGE OF THE GUICHÓN FORMATION

In addition to the *Uruguaysuchus* material (see Rusconi, 1933), the Guichón Formation has yielded a few dinosaurian teeth described by Huene (1934) that are currently lost, including a single theropod tooth (perhaps the same that was tentatively identified as coming from a sebecosuchian by Mones, 1997) and two teeth with ornithischian affinities.

The age of this unit is not well established. It is only certain that it is younger than Hauterivian and older than Campanian. Palaeontological evidence was previously insufficient or incorrectly interpreted. According to Huene (1934) the theropod tooth was very similar to one described by Lambe (1902) as occurring closely associated to ornithomimid bones in Late Cretaceous deposits from Canada. Given that the edentulous nature of the ornithomimids was then unknown, Huene (1934) mistakenly referred the tooth from Guichón to the family Ornithomimidae. This was the main argument upon which the Guichón Formation was considered of Senonian age in the following decades. Bonaparte (1978) considered that the two ornithischian teeth belonged to the Iguanodontidae, which in his interpretation supported the same age. Soto & Cambiaso (2006) reviewed both Huene's and Bonaparte's early determinations, and concluded that the purported ornithomimid and iguanodontid material should be better regarded as belonging to indeterminate theropods and basal iguanodontians, respectively. This reinterpretation eliminated the evidence supporting a Late Cretaceous age for the Guichón Formation. Although the phylogenetic position of this taxon is not well established, most authors have retrieved it in a basal position within Notosuchia. In South America, these forms (e.g. *Candidodon*, *Araripesuchus gomesii*, *A. patagonicus*, *A. buitreraensis*) are usually recorded from the middle Cretaceous (Aptian–Cenomanian). In more recent Cretaceous deposits (e.g. Campanian–Maastrichtian) these forms are absent and the notosuchian fauna comprises derived notosuchians (e.g. *Notosuchus*, *Sphagesaurus*, *Comahuesuchus*, *Mariliasuchus* and baurusuchids). In other regions of Gondwana, however, basal notosuchians seem to have survived toward the end of the Cretaceous (e.g. *Simosuchus* and *A. tsangatsangana* from Madagascar).

On the other hand, the geological evidence, such as the discordance with the overlying Mercedes Formation (Campanian–Maastrichtian; Daners & Guerstein, 2004; Goso & Perea, 2004) and the facies similarity with the Migues Formation (Albian; Campos *et al*., 1997) from the southern Santa Lucía Basin, has prompted some authors (Goso, Perea & Perinotto, 1999; Goso & Perea, 2004) to suggest an Early Cretaceous age for this unit. It should also be noted that the putatively correlated Puerto Yeruá Formation (Argentina) is also difficult to constrain beyond a Cretaceous age (De Valais, Apesteguía & Udrizar Sauthier, 2003).

SYSTEMATIC PALAEONTOLOGY

CROCODYLIFORMES HAY, 1930

MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983

NOTOSUCHIA GASPARINI, 1971

URUGUAYSUCHIDAE GASPARINI, 1971

Type genus: Uruguaysuchus Rusconi, 1933.

Diagnosis: The family Uruguaysuchidae is supported by two unambiguous synapomorphies: surangular forming approximately one-third of the glenoid fossa and dorsal surface of mandibular symphysis strongly concave and narrow, trough shaped. See discussion in the section on 'Phylogenetic relationships' below.

Comments: Although it is still premature to give a phylogenetic definition of the family Uruguaysuchidae (as the clade is only weakly supported), it should be noted that the only existing phylogenetic definition (that of Carvalho, Ribeiro & Avilla, 2004) is incomplete. A node-based (employing both *Uruguaysuchus aznarezi* and *Araripesuchus gomesii* as internal specifiers) or stem-based (using also *Notosuchus terrestris* as the external specifier) phylogenetic definition is equally possible. However, it should also be noted that if eventually *Uruguaysuchus* turns out to be closer to Ziphosuchia (instead of being the sister taxon of *Araripesuchus*), a node-based Uruguaysuchidae would be redundant with Notosuchia, and a stem-based Uruguaysuchidae would include a paraphyletic array of basal notosuchians.

URUGUAYSUCHUS RUSCONI, 1933

Type species: Uruguaysuchus aznarezi Rusconi, 1933.

Revised diagnosis: Uruguaysuchus can be diagnosed by the presence of the following unique combination of characters (autapomorphies marked with an asterisk): heterodont dentition (maxilla: 1–2 incisiviform teeth, 1 caniniform tooth and 9–10 post-caniniform teeth; dentary: 6–7 incisiviform teeth, 10–11 'post-caniniform' teeth); hypertrophied 2nd or (in juveniles) 3rd maxillary tooth; post-caniniform spatulated teeth showing strong buccolingual compression, subcircular in shape (in buccal or lingual view), with a pointed central cusp and minute denticles in a single row along the mesial and distal margins*; strong constriction at the base of the crown and marked apicobasal groove along the lingual surface of the root; choanal septum completely divides the opening; posterior region of septum with subcircular cross-section and anterior region T-shaped in cross-section* (broad expansion at the ventral surface of the choana); ventral surface of choanal septum bearing a longitudinal groove; acute anterior tip of the choanal septum that wedges between the palatines; basisphenoid and basioccipital not exposed in ventral view of the skull (given that the extensive posterior region of the pterygoid flanges projects caudally)*; pterygoids fused posterior to the choanal opening, but towards the posterior ends the two flanges meet, forming a narrow sulcus*; posterior border of the choanal opening formed by an elevated rim that projects more ventrally than the palatal surface of the pterygoid flanges*; lateral surface of the quadrate pierced by a dorsally located preotic siphoneal opening, partially exceeding the dorsal margin of the otic aperture*.

URUGUAYSUCHUS AZNAREZI RUSCONI, 1933

Synonymy: Uruguaysuchus terrai Rusconi, 1933.

Diagnosis: Same as for genus, by monotypy.

Holotype: CA, unnumbered.

Referred material: FC-DPV 2320, partial skull (Figs 2–8), mandible (Figs 9–11), atlas intercentrum (Fig. 13), and two cervical vertebrae and a cervical rib (Fig. 14). Other materials referred to *U. aznarezi* not described herein, presumably from the same locality, include MPMAB 2881 (two post-caniniform teeth, one osteoderm and a partial humerus) and MUNHINA 451 (two fragmentary vertebrae).

Locality and horizon: Guichón, Paysandú province, Uruguay. Guichón Formation (middle Cretaceous; see above for discussion of possible age).

SKULL

GENERAL FEATURES

The skull is incompletely preserved, lacking all the elements of the dorsal surface of the rostrum and skull table (Fig. 2). Only part of the lateral surface of the rostrum and temporal elements has been preserved, but the palate and base of the braincase are virtually complete. Only the base of a large antorbital fenestra is present on the right side of the skull, but the palatal openings are completely preserved. The suborbital fenestrae are elongated and ovoid, occupying over 20% of the total skull length. The choanal opening is also long and ovoid, having a narrower anterior end than posterior end.

PREMAXILLA

Both premaxillae are preserved (Fig. 2A), although the left element is best preserved. The lateral surface is ventrally smooth and slightly ornamented with small pits on the posterodorsal region (Fig. 3). The left premaxilla preserves the lateral margins of the external nares (Fig. 3). As indicated by the vertical orientation of this margin, the external nares faced anteriorly, as in most non-neosuchian crocodyliforms. Below the margin of the narial opening, the premaxilla bears a small perinarial depression that fails to reach the alveolar margin of the premaxilla. The posteroventral margin of the premaxilla is tightly sutured to the maxilla, as in most notosuchians (including *Araripesuchus* spp.; e.g. Pol & Apesteguía,

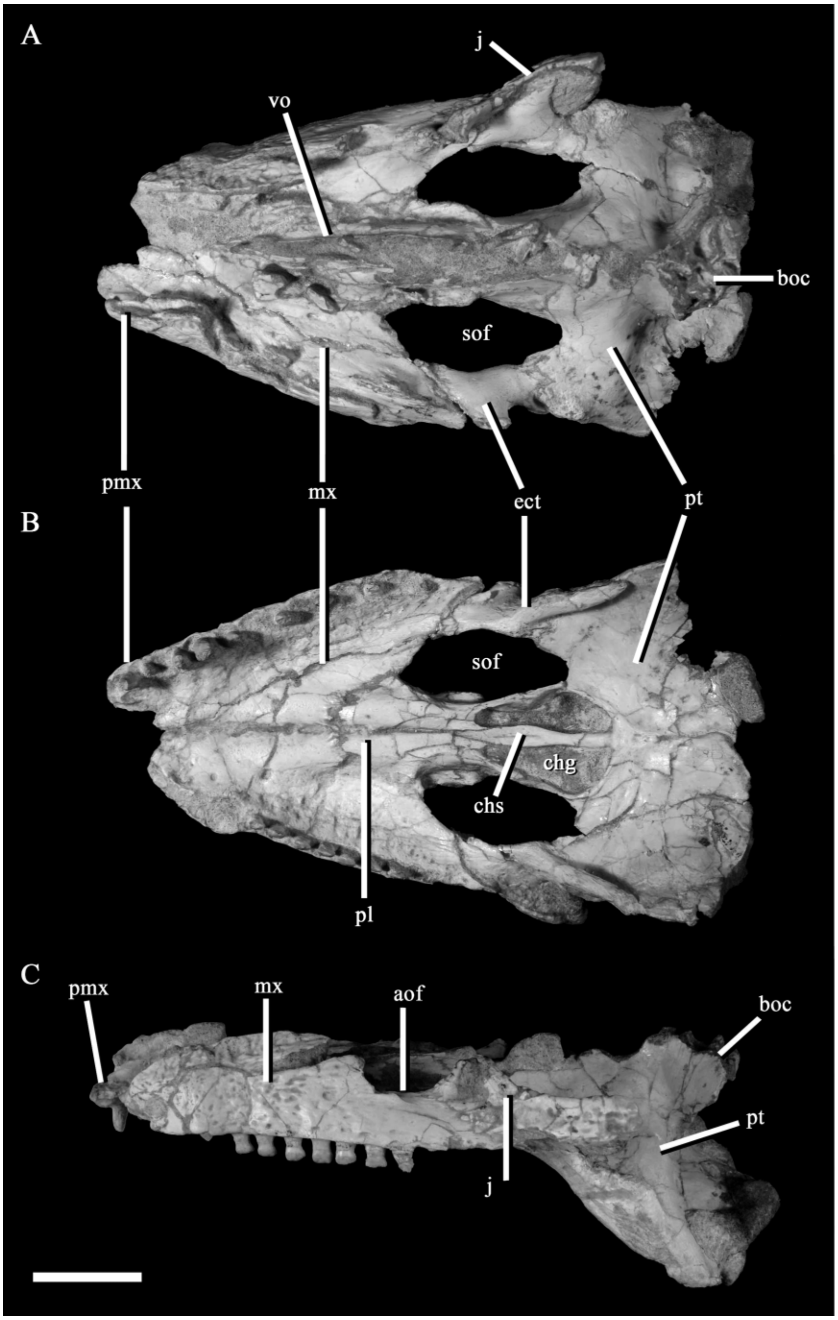

Figure 2. FC-DPV 2320. Skull. A, dorsal view. B, ventral view. C, right lateral view (inverted). Scale bar = 1 cm.

2005), except for *Malawisuchus* and *Chimaerasuchus* (Wu & Sues, 1996; Gomani, 1997), which have a small notch at the ventral contact of the premaxilla–maxilla. A large neurovascular foramen is present at the premaxilla–maxilla suture, just above the alveolar margin, a feature also present in most notosuchians (including *Araripesuchus* spp.). The premaxilla–maxilla suture runs vertically along its ventral half and is directed posterodorsally above the large neurovascular foramen, forming the ventral margin of the posterodorsal process of the premaxilla. This process is well developed, as in most mesoeucrocodylians. The palatal surface of the premaxilla is not complete, but the premaxilla–maxilla suture extends anteromedially from the alveolar margin and bears a small depression medial to the last premaxillary alveolous. All premaxillary alveoli are confluent with one another, lacking complete interalveolar septa.

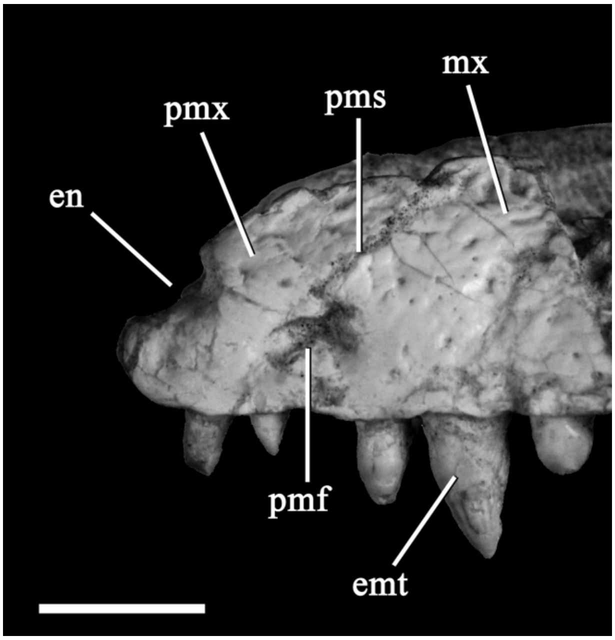

Figure 3. FC-DPV 2320, anterior end of rostrum in left lateral view. Scale bar = 2 cm.

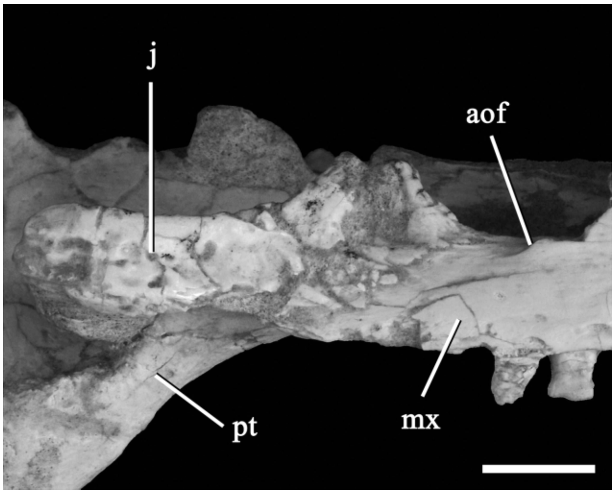

Figure 4. FC-DPV 2320, detail of right jugal and lacrimal in lateral view. Scale bar = 2 cm.

MAXILLA

The maxillae are incomplete but the right element has most of its lateral surface preserved and the palatal processes of both maxillae are completely preserved. The lateral surface of the maxilla is vertically oriented so that the rostrum was probably oreinirostral (as with the rostrum of the type specimen described by Rusconi, 1933). The lateral surface of the maxilla bears an ornamentation pattern composed of small subcircular pits well spaced from each other (Figs 2, 3). This type of ornamentation is present in most crocodyliforms, but distinguishes *Uruguaysuchus* (and *Araripesuchus* and *Libycosuchus*; Ortega *et al.*, 2000) from derived notosuchians (including baurusuchids) that exhibit a vermiform ornamentation pattern composed by elongated grooves and ridges. The pits are distributed along the entire lateral surface of the maxilla, except for the posterior region of the lateral surface of the maxilla (below the antorbital fenestra; Fig. 4). This pattern of ornamentation is also similar to *Araripesuchus* but different from derived notosuchians (*Notosuchus*, *Mariliasuchus*, *Sphagesaurus*) that have a well-defined smooth region above the alveolar margin. A series of small neurovascular foramina is dorsoventrally aligned and located above the alveolar margin on the lateral surface of the maxilla. At the posterior end of the lateral surface of the maxillae, part of the ventral margin of the external antorbital fenestra is preserved (Figs 2, 4). Although this opening is not complete, the ventral margin indicates the opening was significantly larger than in most notosuchians (except for the basal forms of these clade, such as *Simosuchus* or *A. gomesii*). The maxilla forms a shallow fossa along the anteroventral margin of the antorbital opening. This differs from the condition of *Araripesuchus* spp. (*A. gomesii*, *A. patagonicus*, *A. tsangatsangana*; Pol & Apesteguía, 2005; Turner, 2006) and *Simosuchus* (Buckley *et al.*, 2000), in which the maxilla does not form an antorbital fossa at the anteroventral margin of the antorbital fenestra, but resembles the morphology of *Notosuchus terrestris*.

The palatal processes of the maxillae are broad, laminar, and are sutured to one another and to the palatines, forming the extensive secondary palate characteristic of mesoeucrocodylians (Fig. 2). The posteromedial region of the palatal branches is slightly bulged anterior to their contact with the anterior process of the palatines, at the point where the nasopharyngheal ducts open anteriorly on the dorsal surface of the palatal branches of the maxilla. Medial to the alveoli, a series of large neurovascular foramina is present. The maxilla forms the anterolateral margin of the suborbital fenestra and is sutured to the ectopterygoid at the anteroposterior midpoint of this opening. The maxillary alveoli are all confluent to each other, lacking interalveolar septa. However, the alveoli are delimited by slightly developed bony projections that extend from the buccal and lingual sides. The bony projections of the enlarged anterior alveolous are the most developed, nearly delimiting this alveolous from adjacent alveoli. The alveolar groove ends anterior to the orbital margin, with the posteriormost two alveoli located at the level of the anterior margin of the suborbital fenestra. In this region, the palatal branch of the maxilla is broad and separates the posterior alveoli from the margin of the suborbital fenestra.

LACRIMAL

Only the base of the right lacrimal has been preserved. It is sutured anteroventrally to the posterior end of the maxilla, and posteroventrally to the anterior process of the jugal. Its ventral end is mediolaterally restricted and anteroposteriorly expanded, and bears a depressed area on the lateral surface that probably represents the caudal end of the antorbital fossa (Fig. 4). The ventral expansion of the lacrimal separates the jugal from the anterior margin of the antorbital fossa, as in all crocodyliforms, except for *Simosuchus* and metriorhynchids.

JUGAL

Only the anterior region of the suborbital branch of the jugal has been preserved (Fig. 4). This region of the jugal is dorsoventrally low and reaches the level of the anterior margin of the orbit, but does not seem to surpass this point. This resembles the condition of some notosuchians (e.g. *Malawisuchus*, *Mariliasuchus*; Gomani, 1997; Andrade & Bertini, 2008), although it contrasts with the anteriorly projected jugal of peirosaurids (e.g. *Lomasuchus*, *Montealtosuchus*, *Mahajangasuchus*; Turner & Buckley, 2008) and advanced notosuchians (*Sphagesaurus* and the sebecosuchians *Baurusuchus*, *Iberosuchus* and *Sebecus*). The lateral surface of the jugal (Fig. 4) is ornamented with small subcircular pits and has a shallow concavity at the anteroventral margin of the orbit, as in *A. patagonicus*.

VOMERS

Both vomers have been partially preserved on the dorsal surface of the palate. They are thin and laminar bones, which are anteroposteriorly elongated, extending approximately 30% of the skull length (Fig. 2A). They dorsally overlap the anteromedial process of the palatines and posteromedial region of the palatal branches of the maxillae, thereby forming a roof over the rostral end of the nasopharyngeal duct.

PALATINES

Both palatines are well preserved and exposed in ventral view (Fig. 2B). The palatines are completely sutured to each other, forming an extensive secondary palate, as in most mesoeucrocodylians. Being completely sutured to each other and with the left and right maxillae, *Uruguaysuchus* lacks the anterior palatal fenestra present in some basal crocodyliforms (e.g. Fruita Form, *Zosuchus*; Pol & Norell, 2004) and in some advanced notosuchians (*Notosuchus*, *Mariliasuchus*; e.g. Andrade & Bertini, 2008). The anterior process of the palatines largely exceeds the anterior margin of the suborbital fenestra, and wedges between the palatal branches of the maxilla (Fig. 2B), as in *A. gomesii* and other basal mesoeucrocodylians. The lateral margin of this process converges anteriorly and the anterior tip is transversally oriented, so that the entire anterior process of the palatines resembles a truncated triangle. The maxilla–palatine suture ends at the anterior tip of the ovoid suborbital fenestra. From this point, the palatines narrow posteriorly, creating a narrow palatine bar that forms the floor of the nasopharyngeal duct.

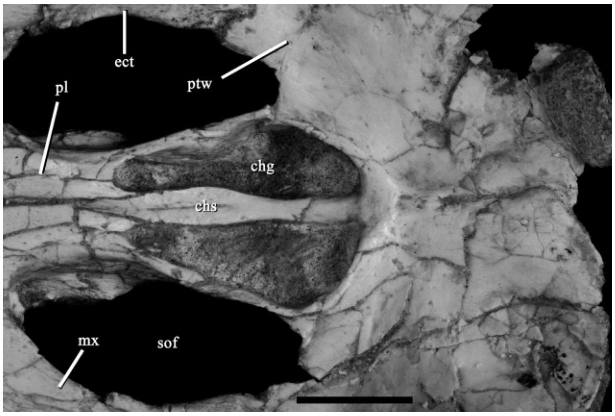

Figure 5. FC-DPV 2320, detail of choanal region. Scale bar = 2 cm.

At the anteroposterior midpoint of the suborbital fenestra the palatines form the anterior margin of the choanal opening, forming a mesosuchian type of palate (Fig. 5). The palatines slightly diverge posteriorly, forming the anterior half of the lateral margins of the internal choana, as in most basal mesoeucrocodylians. Given the posterolateral divergence of the palatines along the choanal margins, the internal choana of *Uruguaysuchus* broadens posteriorly (Fig. 5), a condition that contrasts with that of most basal notosuchians, which have subparallel choanal margins (e.g. *Araripesuchus* spp., *Malawisuchus*, *Candidodon*, *Simosuchus*; Gomani, 1997; Buckley *et al*., 2000; Pol & Apesteguía, 2005). The posterolateral ends of the palatines are firmly sutured to the pterygoids. This morphology is the plesiomorphic condition of basal mesoeucrocodylians and basal notosuchians (e.g. *Araripesuchus* spp., *Simosuchus*), but it differs from the morphology of advanced notosuchians (e.g. *Notosuchus*, *Comahuesuchus*, *Mariliasuchus*, baurusuchids), which have rod-like palatine processes that project posterolaterally and contact the flanges of the pterygoids (and the ectopterygoids). The anterior margin of the choanal opening is rounded, and the palatines at this point are separated by a thin acute anterior tip of the pterygoid choanal septum (Fig. 5), resembling the condition of *A. patagonicus* (Ortega *et al.*, 2000).

PTERYGOIDS

The pterygoids (Figs 2A, B, 5, 6A) are completely preserved and are exposed in dorsal and ventral views. The anteromedial region bears a deep choanal groove that is closed posteriorly, delimiting the margins of the choanal opening. The posterior border of the choanal opening is rounded and mediolaterally broad, so that the entire choanal opening is ovoid (Fig. 5). The posterior choanal margin is formed by an elevated rim that projects more ventrally than the palatal surface of the pterygoid flanges (Fig. 5). This elevated rim contrasts with the condition of most notosuchians, except for *Anatosuchus*. In the latter taxon, however, the choanal posterior border reaches the caudal margin of the pterygoid flanges whereas in *Uruguaysuchus* the choana extends only along the anterior third of the pterygoid flanges. At the midline, the posterior choanal rim projects caudally, forming an elevated sagittal ridge that reaches the narrow pterygoideal notch located at the caudal end of the pterygoids (see below). A similar sagittal ridge is also

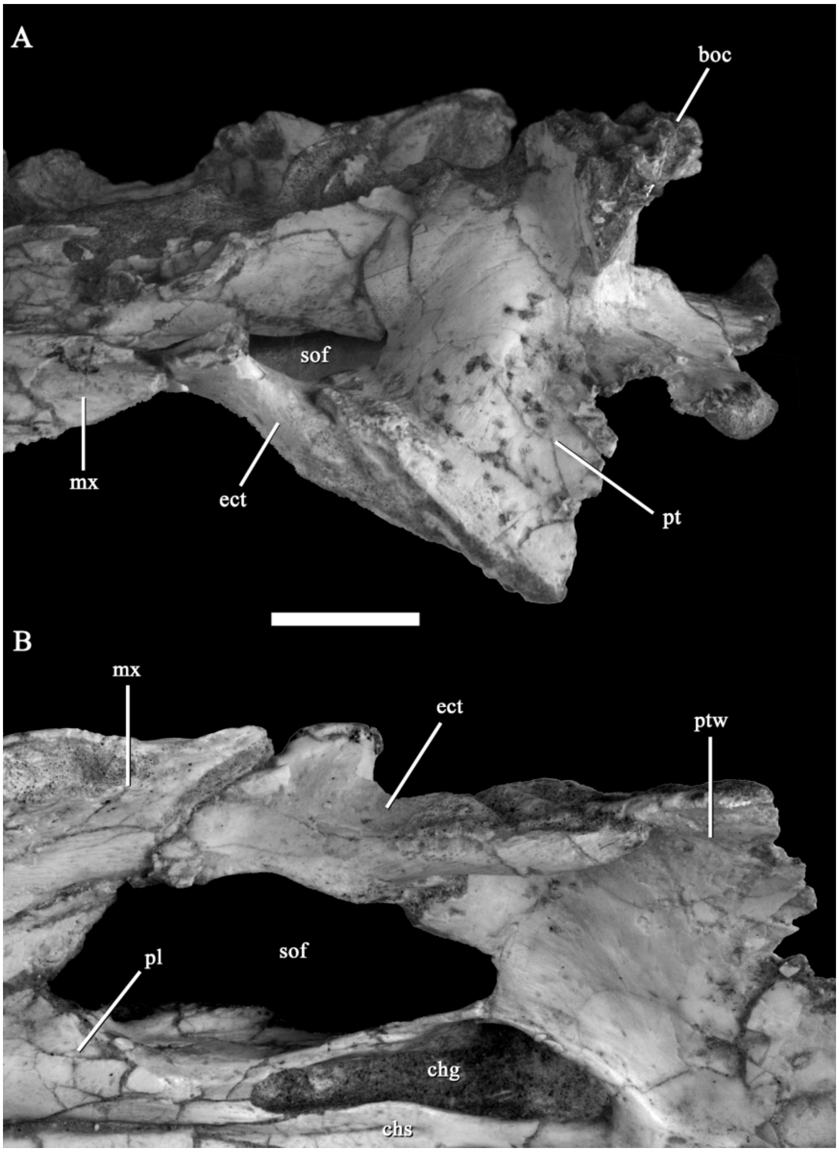

Figure 6. FC-DPV 2320. A, left pterygoid and ectopterygoid in laterodorsal view. B, detail of right ectopterygoid in ventral view. Scale bar = 2 cm.

present posterior to the choana in *A. gomesii* and *A. buitreraensis*, but not in *A. patagonicus* (Ortega *et al*., 2000; Pol & Apesteguía, 2005).

Within the internal nares, the pterygoid has a well-developed choanal septum that completely divides the choanal groove. A similar septum is present in *Araripesuchus* spp. and some other basal mesoeucrocodylians (e.g. *Mahajangasuchus*, *Simosuchus*; Buckley *et al*., 2000; Turner & Buckley, 2008), but in more advanced notosuchians the septum is much less developed and fails to completely divide the choanal opening (e.g. *Notosuchus*, *Mariliasuchus*, *Malawisuchus*; Gomani, 1997; Andrade & Bertini, 2008). The choanal septum is relatively narrow and subcylindrical in cross-section along its posterior half, but it has an expanded ventral surface along its anterior half (Fig. 5). The ventral surface of the septum in this region bears an incipiently developed longitudinal groove. The anterior tip of the septum tapers rapidly and forms the acute anterior process that wedges between the palatines at the anterior margin of the choanae (Fig. 5). The choanal septum of *Uruguaysuchus* bears derived features only found in *Simosuchus* and some species of *Araripesuchus*. The presence of a T-shaped choanal septum (with a broad expansion at the ventral surface of the choana) is only found in *Simosuchus* and in the South American species of *Araripesuchus* (*A. buitreraensis*, *A. patagonicus*, and *A. gomesii*; Pol & Apesteguía, 2005). Furthermore, the presence of a longitudinal groove is also only found in those taxa, although in *Simosuchus* this groove is much broader (forming a shallow concave surface) and is more developed anteriorly to the choanal rostral margin. Finally, the acute anterior tip of this elongated septum that wedges between the palatines is only known to exist in *A. patagonicus* and *Simosuchus*. None of these characters is found in more derived notosuchians or outside Notosuchia, although it must be noted that *Mahajangasuchus* also has a ventrally broad choanal septum (Turner & Buckley, 2008).

The pterygoid flanges are broad and laminar, and are slightly curved ventrally along their lateral extension (Fig. 6). Thus, the ventral surface of the pterygoid flanges forms a shallow concavity in the palate posterior and posterolateral to the choanal opening. The anterior margin of the pterygoids forms the posterior margin of the suborbital fenestra as in most mesoeucrocodylians except for advanced notosuchians (e.g. *Notosuchus*, *Mariliasuchus*, *Comahuesuchus*, *Sphagesaurus*, baurusuchids). Given the lateral expansion of the pterygoid flanges, the posterior margin of the suborbital fenestra is narrow and concave (Fig. 2). The ventral surface of the pterygoid flanges is smooth (Fig. 6), as in most mesoeucrocodylians, and lacks the distinct transversal groove present in *A. buitreraensis* (Pol & Apesteguía, 2005). The lateral margins of the flanges are only slightly thickened and are sutured to the posterior process of the ectopterygoid (Fig. 6). Both flanges meet at the midline of the palate and form an extensive surface of the pterygoids posterior to the choanal opening (Fig. 5). This posterior region of the pterygoid flanges is remarkably extensive, and projects caudally beyond the level of the basisphenoid and basioccipital (Fig. 6A). Thus, these two elements are not exposed in ventral view of the skull. This condition is unique among basal mesoeucrocodylians, in which the pterygoid flanges are much less extensive posteriorly; hence, the basisphenoid is well exposed on the ventral surface of the skull. The pterygoids are fused posterior to the choanal opening but towards the posterior ends the two flanges meet, forming a narrow sulcus (Fig. 5). This is also a unique character of *Uruguaysuchus*, as in this region most basal mesoeucrocodylians (including all notosuchians) have a pterygoid notch through which the basisphenoid is visible in ventral view of the skull.

ECTOPTERYGOID

Both ectopterygoids have been completely preserved (Fig. 6) and they show the plesiomorphic condition present in most mesoeucrocodylians (including basal notosuchians) forming only the posterior half of the lateral margin of the suborbital fenestra. The anterolateral end of the ectopterygoid has well-developed anterior and posterior processes that suture extensively to the posterior branch of the maxilla (Fig. 6B). The anterior process is well separated from the posterior region of the toothrow by a broad posterior region of the maxillary palatal branch. The ectopterygoid is twisted along its medial extension and its rod-like posterior process projects posteriorly along the lateral edge of the pterygoid flanges. The caudal tip of this posterior process ends well before the caudal margin of the pterygoid flanges (Fig. 6). All these characters are congruent with the morphology found in basal notosuchians (e.g. *Araripesuchus*, *Malawisuchus*, *Anatosuchus*) and other basal mesoeucrocodylians (e.g. peirosaurids) but differ markedly from the derived condition of the ectopterygoid of derived notosuchians (*Notosuchus*, *Mariliasuchus*, *Sphagesaurus*, *Comahuesuchus*, baurusuchids), in which this bone extends over the ventral surface of the pterygoid flanges and (in some cases) contact the posterolateral end of the palatines.

BASISPHENOID

The basisphenoid is completely preserved except for its dorsolateral processes. Due to the extensive posterior projection of the pterygoid flanges, the basisphenoid is not exposed on a ventral view of the skull. This contrasts with the generalized condition of non-eusuchian crocodyliforms in which the basisphenoid is broadly exposed on the ventral surface of the skull. However, a poorly exposed basisphenoid is also present in some basal mesoeucrocodylians (e.g. *Anatosuchus*, *Lomasuchus*), in which this bone is also hidden by the pterygoid flanges. The basisphenoid is therefore visible in posterior view of the skull and is located dorsally and anteriorly to the caudal end of the pterygoid flanges (Fig. 6A), above the pterygoid sulcus.

As in most mesoeucrocodylians, the basisphenoid is crescentic to triangular and its lateral margins converge ventrally along the sutures with the ascending quadrate process of the pterygoids. The dorsal margin is transversely oriented and firmly sutured to the ventral margin of the basioccipital. The central region of the basisphenoid is deeply depressed and bears a rounded pit located at the dorsoventral midpoint of this bone. This pit extends ventrally toward the ventral tip of the basisphenoid located just above the pterygoid sulcus. The central depression is bounded by two ridges that extend parallel to the lateral margins of the basisphenoid (medial to the basisphenoid–pterygoid suture). These ridges are slightly laterally concave and converge anteriorly narrowing the ventral end of the central depression of the basisphenoid. Similar ridges are present in some notosuchians (e.g. *Notosuchus* MACN-RN 1045) and some basal crocodyliforms (e.g. *Sichuanosuchus*, *Zosuchus*; Pol & Norell, 2004). The basisphenoid–basioccipital contact is notched at the midline, where a small foramen intertympanicum is located. As the dorsolateral processes of the basisphenoid are not preserved in FC-DPV 2320, lateral eustachian foramina are also not preserved.

BASIOCCIPITAL

Only the ventral region of the basioccipital is preserved in FC-DPV 2320. The ventral surface of this bone is vertically oriented and faces posteriorly, instead of facing posteroventrally as in most notosuchians. The central region of the basioccipital bears a sharp longitudinal keel that extends ventrally down to the opening of the foramen intertympanicum. The presence of this keel is a widespread feature among crocodyliforms and is present in most basal mesoeucrocodylians (e.g. peirosaurids, *Sebecus*, *Araripesuchus*, *Anatosuchus*, *Mariliasuchus*) but is absent in others, including *Simosuchus* and *Sphagesaurus*.

QUADRATE

Only the anterodorsal otic region of the quadrate is preserved in FC-DPV 2320 (Fig. 7). The region includes the anterior and dorsal margins of the otic aperture. This margin is only slightly concave anteriorly and suggests the presence of a relatively large and dorsoventrally elongated otic aperture, as in *A. buitreraensis* and *A. gomesii* (Pol & Apesteguía, 2005). Anterodorsally from the otic aperture, the lateral surface of the quadrate is pierced by a single and relatively large preotic siphoneal opening (anterior foramen aërum *sensu* Iordansky, 1973). A similar opening is also present in most basal mesoeucrocodylians (nosotuchians, peirosaurids), but in *U. aznarezi* this opening seems to be more dorsally located, partially exceeding the dorsal margin of the otic aperture (Fig. 7).

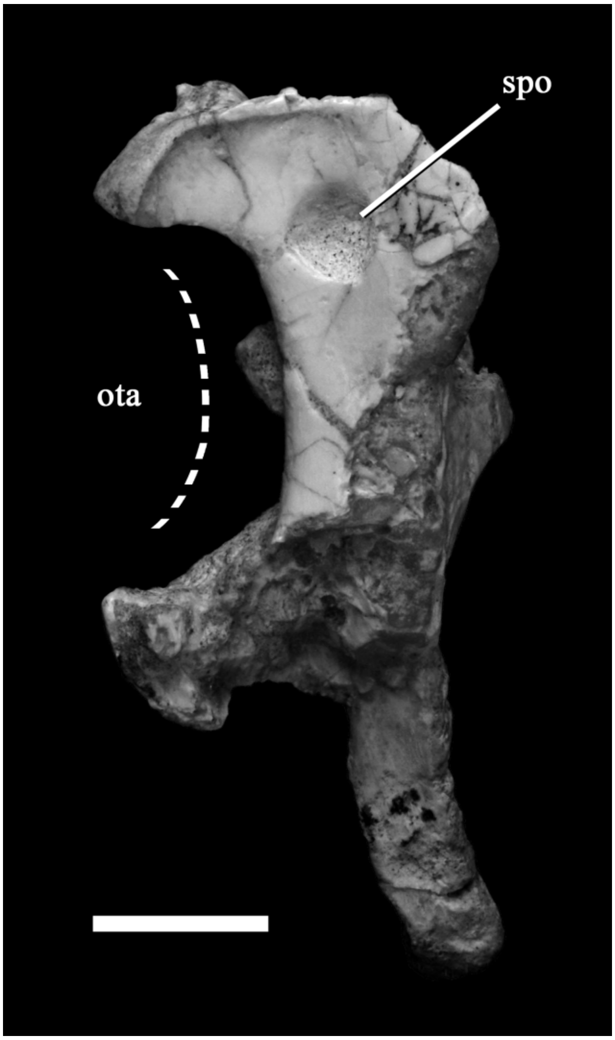

Figure 7. FC-DPV 2320, otic region of right quadrate in lateral view. Scale bar = 2 cm.

PALPEBRAL

Only the right anterior palpebral has been preserved in disarticulation from the rest of the skull. This bone

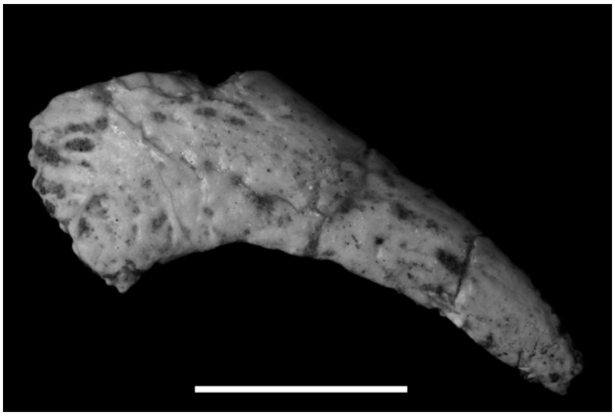

Figure 8. FC-DPV 2320, right anterior palpebral in dorsal view. Scale bar = 2 cm.

is curved and elongated (Fig. 8), having a narrow posterior projection. The morphology of this palpebral resembles that of *A. gomesii* but contrasts with the broad anterior palpebral of *A. buitreraensis* (Pol & Apesteguía, 2005). The dorsal surface of the palpebral is ornamented with small and well-spaced circular pits (Fig. 8).

LOWER JAW

General features

The mandible is well preserved, having a complete right ramus (Fig. 9). The mandibular rami are straight and converge anteriorly forming a V-shaped lower jaw in dorsal and ventral views. The lower jaw is characterized by a shallow and relatively long symphysis that extends along the level of the first ten mandibular teeth. The lower jaw also has a remarkably large external mandibular fenestra that is ovoid, with its major axis oriented longitudinally. The fenestra is enclosed by the dentary, surangular, and angular, increasing in height posteriorly and occupying more than two-thirds of the dorsoventral extent of the mandibular ramus (Fig. 9C).

Dentary

The dentary extends along more than half the mandibular ramus and increases its dorsoventral height posteriorly. The ornamentation is restricted to the ventral surface of the dentaries along the symphyseal region, as in most notosuchians. The lateral surface of the dentaries is mostly smooth, but bears a few small pits close to its ventral margin (Fig. 9). The dentaries are slightly disarticulated from each other in the symphyseal region, but the suture would have formed the anterior two-thirds of the symphyseal length. In ventral view the symphyseal region tapers anteriorly, ending in a pointed tip; the anterior ends of the dentaries are not completely preserved.

The dorsal surface of the symphysis broadens posteriorly and is flat along the anterior half, although it forms a slightly developed concavity towards the contact with the splenials (Figs 9A, 10B), as in *Araripesuchus* (see below). The anterior end of the mandibular symphysis is remarkably shallow in lateral view and progressively deepens posteriorly (Fig. 10A). The alveolar margin is horizontally directed and is slightly convex in lateral view. The ventral margin is straight and directed posteroventrally.

The lateral surface of the dentaries is flat and vertical at the symphyseal region, and bears a series of relatively large neurovascular foramina that are dorsoventrally aligned and parallel to the alveolar margin. Posterior to the symphysis, the lateral surface of the dentary is divided by a longitudinal ridge that separates this surface into two distinct regions (Fig. 10A). Ventral to this ridge the dentary is flat, smooth and vertically oriented, instead of being low and convex as in neosuchian crocodyliforms. This flat surface extends posteriorly, forming the anterior and anterodorsal margins of the external mandibular fenestra. The dentary does not seem to extend ventrally to the external mandibular fenestra, as in most notosuchians, although this region is not perfectly preserved. Dorsal to the longitudinal ridge, the lateral surface of the dentary is medially inset, separating the alveolar margin of posterior mandibular teeth from the lateral surface of the dentaries (Fig. 10A). This condition is also found in most notosuchians, including basal forms (*Simosuchus*, *Libycosuchus*, *A. patagonicus*, *A. buitreraensis*, *A. wegeneri*), but is absent in *A. gomesii* and in *A. tsangatsangana* (Turner, 2006).

The dentary of *Uruguaysuchus* lacks discrete alveoli. Instead the entire lower toothrow is set in an extensive alveolar groove. Although the distribution of this character within Notosuchia needs to be explored further, the presence of a continuous alveolar groove in the lower toothrow seems to be present both in *Uruguaysuchus* and in *Simosuchus*, whereas in derived notosuchians (e.g. *Notosuchus*, *Mariliasuchus*, *Sphagesaurus*; Pol, 2003; Andrade & Bertini, 2008) the anterior lower teeth are set in discrete alveoli. The condition of most species of *Araripesuchus* is currently unknown, but anterior discrete alveoli are present in *A. tsangatsangana* (Turner, 2006), and a fragmentary specimen referred to *Araripesuchus* (MPCA-PV 236; see Pol & Apesteguía, 2005) has all but the anteriormost tooth set in a continuous alveolar groove.

Along the symphyseal region the dentary has small bony projections that partially delimit the anterior

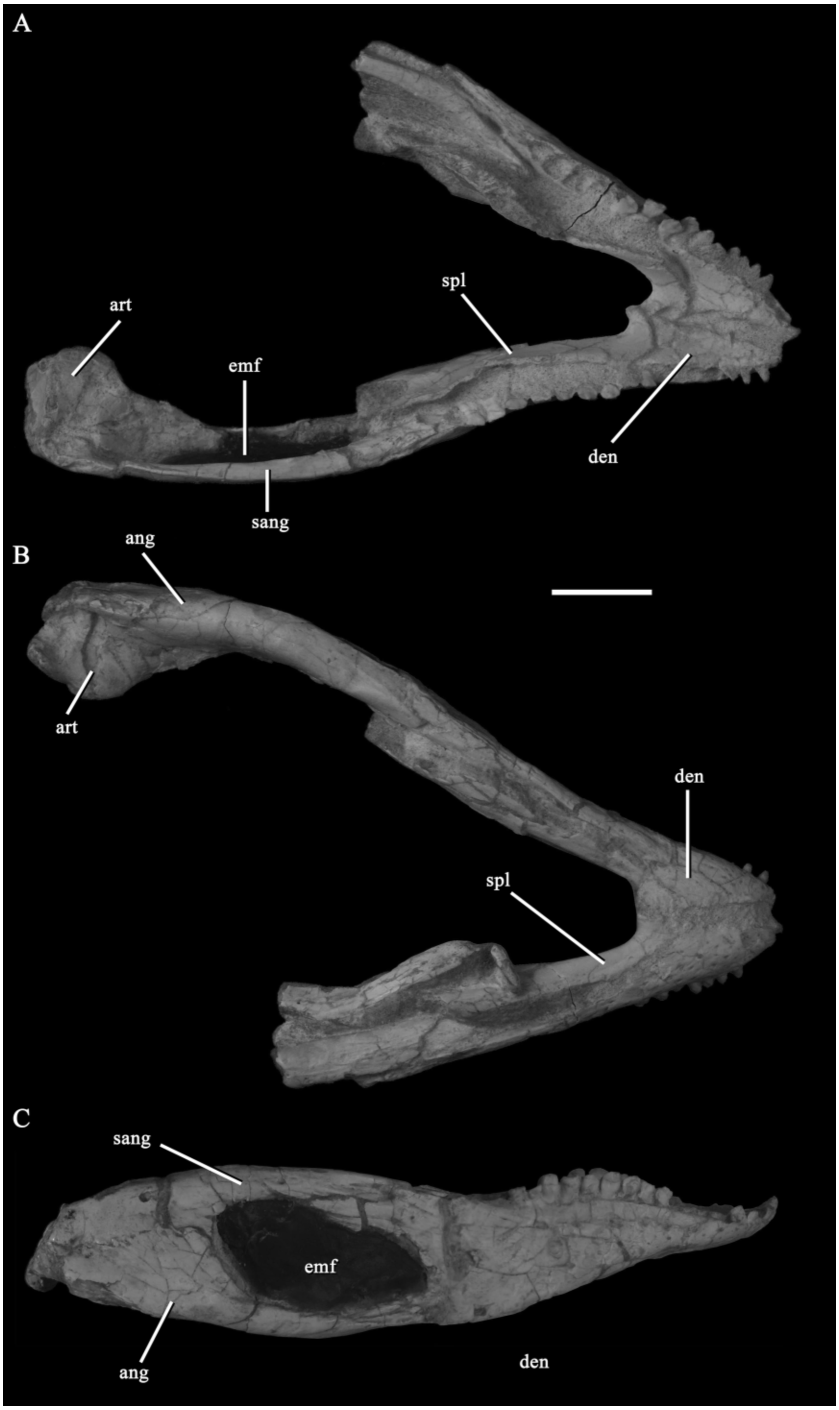

Figure 9. FC-DPV 2320, mandible. A, dorsal view. B, ventral view. C, lateral view. Scale bar = 1 cm.

alveoli. Post-symphyseal teeth are set in a broad, continuous alveolar groove. In this region the dentary forms the buccal margin and the base of the alveoli (Figs 9A, 10B). Posterior to this region the alveolar groove is closed lingually by the extensive vertical wall of the splenial (see below).

Splenial

The splenials are broadly exposed in ventral view. They form part of the mandibular symphysis and cover the anterior half of the mandibular rami of the lower jaw. The anterior ends of the splenials are sutured to each other forming the posterior third of

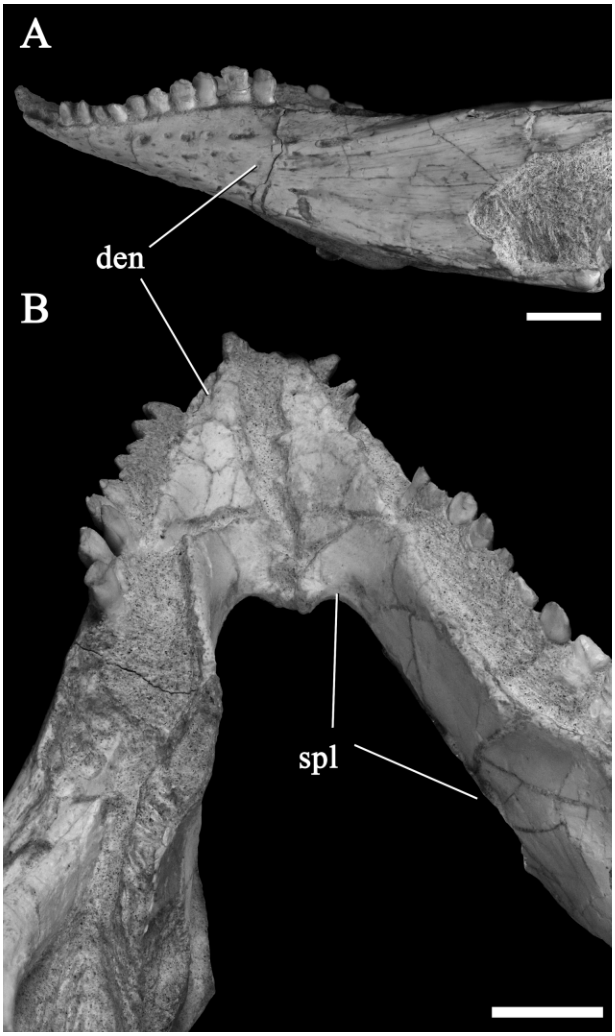

Figure 10. FC-DPV 2320, symphyseal region of lower jaw. A, left lateral view. B, posterodorsal view. Scale bar = 2 cm.

the mandibular symphysis, as in most basal mesoeucrocodylians (Fig. 9).

The ventral surface of the splenial symphyseal region is smooth. The lateral margins are sutured to the dentaries and converge anteriorly forming a V-shaped suture. The posterior margin of the splenial symphyseal suture forms a pointed posterior peg (Fig. 10B), a derived feature present in most notosuchians, except for *A. gomesii*. Two small foramina for the anterior exit of the mandibular branch of the trigeminal nerve are located just lateral to the posterior splenial peg (Fig. 10B), as in *Simosuchus* and the South American species of *Araripesuchus*, but in constrast to the condition of *A. tsangatsangana* (Turner, 2006) and derived notosuchians (*Notosuchus*, *Comahuesuchus*). The dorsal surface of the splenial symphyseal region forms an anteriorly rounded suture with the dentaries, but seems to lack the anterior pointed process present in some species of *Araripesuchus* (MPCA-PV 236; see Pol & Apesteguía, 2005). However, this region is incompletely preserved and the presence of such a process cannot be ruled out at the moment. Towards the posterior region of the symphysis the splenials expand dorsally forming a vertical lamina that covers the medial surface of the dentaries up to the lingual margin of the alveoli. Therefore, the dorsal surface of the symphysis is concave and trough shaped along its posterior half and tapers and flattens anteriorly, lacking an anteriorly elevated ridge of the anteriormost dentary alveoli. This derived morphology resembles the condition of some specimens of *Araripesuchus* (e.g. *A. gomesii*, MPCA-PV 236).

Posterior to the symphyseal region the splenial is an extensive lamina that covers the entire medial surface of the mandibular ramus. The medial surface is flat to slightly concave and lacks the posterior openings for the mandibular branch of the trigeminal nerve that is present in more derived crocodyliforms.

The dorsal margin of the splenials forms the lingual margin of the alveolar groove and along the posterior region of the toothrow it is slightly expanded mediolaterally, as in *Araripesuchus* sp. (MPCA-PV 236). The posterior margin of the splenials is deeply concave and forms the rostral margin of the internal mandibular fenestra (Fig. 9A). The ventral margin of the splenials is deflected laterally so that these bones form part of the ventral surface of the mandibular ramus too, as in all basal mesoeucrocodylians.

ANGULAR

The angular is anteriorly low and greatly increases its dorsoventral depth posterior to the external mandibular fenestra. The angular completely lacks ornamentation on its lateral, ventral, and medial surfaces. The anterior tip of the angular contacts the dentary and on the medial surface the anterior end of the angular contacts the posteroventral margin of the splenial, below the internal mandibular fenestra. The angular forms the entire ventral margin of the external mandibular fenestra and along this region the ventral surface of the angular is transversely convex and its dorsal surface is markedly concave (Fig. 9A, B). Thus, below the mandibular opening the angular is elongated and trough shaped, as in most basal mesoeucrocodylians.

The angular expands dorsally along the posterior margin of the external mandibular fenestra, forming the ventral half of the post margin of this opening. At this point, the angular forms the ventral two-thirds of the lateral surface of the mandibular ramus and is sutured to the surangular through a longitudinally oriented suture (Fig. 11A). The posterior end of the

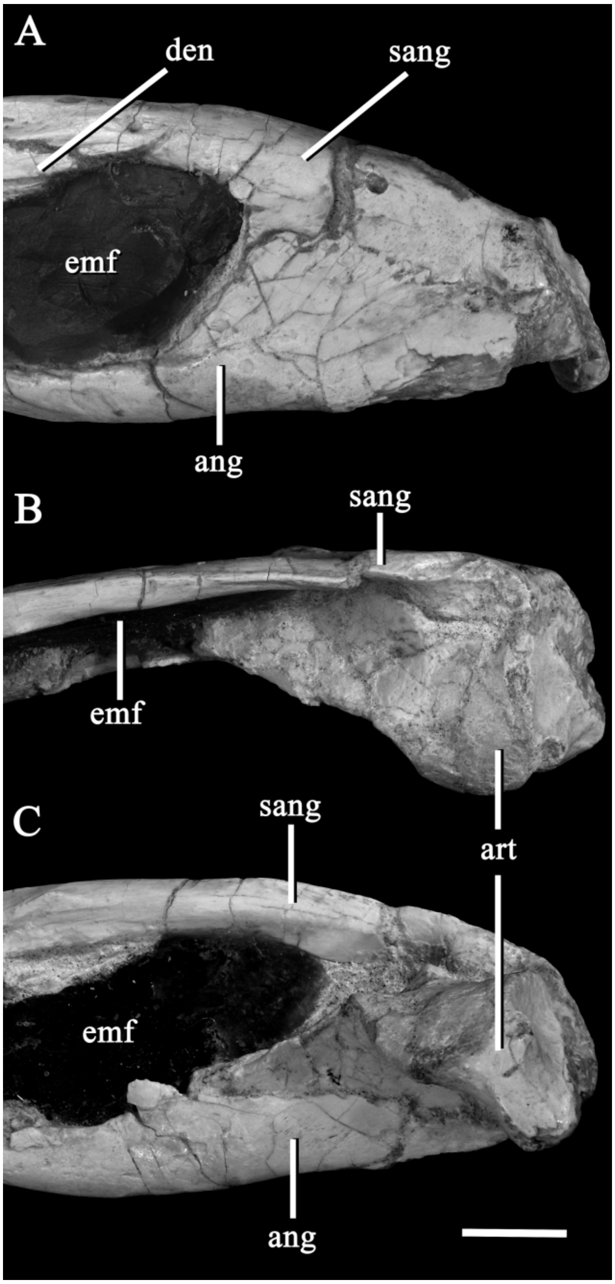

Figure 11. FC-DPV 2320, articular region of lower jaw. A, lateral view (inverted). B, dorsal view. C, medial view. Scale bar = 2 cm.

angular reaches the caudal end of the mandibular ramus, overlapping laterally the articular, including the retroarticular process (Fig. 11A). Along this region the angular also covers ventrally and medially the ventral surface of the articular bone (Fig. 11C). In this same region the ventral surface of the angular narrows markedly, forming a slightly developed ridge that underlies the articular (Fig. 9B). This ridge may be the attachment site of the muscle pterygoideus posterior, and therefore this muscle would not extend onto the lateral surface of the mandibular ramus. This resembles the morphology of some derived notosuchians (e.g. *Notosuchus*, *Mariliasuchus*) but contrasts with the ridge that delimits this insertion on the lateral surface of the angular of other notosuchians (e.g. *A. gomesii*, *A. tsangatsangana*, *Libycosuchus*, baurusuchids).

In lateral view, the ventral margin of the angular is slightly upturned posterior to the external mandibular fenestra, so the entire mandibular ramus is slightly convex in this view (Fig. 9C). The dorsal deflection of the posterior region of the angular of *Uruguaysuchus* is more developed than in *A. gomesii* and *A. patagonicus*, but not as much as in *A. tsangatsangana* (Turner, 2006) or *Libycosuchus*. In this feature, the angular of *Uruguaysuchus* resembles the condition of *Simosuchus* and more derived notosuchians (e.g. *Mariliasuchus*).

SURANGULAR

The surangular is a relatively low and elongated bone that forms the posterior half of the dorsal margin of the mandibular ramus and is completely devoid of ornamentation (Fig. 9C). The anterior tip of the surangular is a mediolaterally restricted lamina that wedges between the dorsal surface of the dentary and the splenial, reaching the posteriormost dentary alveolous (Fig. 9A). The surangular becomes gradually exposed on the lateral surface of the mandibular ramus at the level of the external mandibular fenestra.

The surangular–dentary suture extends posteriorly on the lateral surface of the mandible from the alveolar margin, reaching the dorsal margin of the external mandibular fenestra at the anteroposterior midpoint of this opening. Posterior to this point the surangular forms the dorsal margin of the external mandibular fenestra (Fig. 9C). Along this region, the surangular is relatively low given the remarkably large external mandibular fenestra. The dorsal margin of the surangular is straight above this opening (Fig. 9C), as in most basal mesoeucrocodylians (including *Araripesuchus*, *Libycosuchus*, and *Mariliasuchus*). *Simosuchus* and several derived notosuchians (including baurusuchids) instead have a markedly convex dorsal edge of the surangular along this region. Posterior to the external mandibular fenestra, the dorsal margin of the surangular deflects ventrally towards the ventrally located glenoid facet (Fig. 9C). This ventral deflection is also present in *Simosuchus* and more derived notosuchians, but is absent in *Libycosuchus* and *Araripesuchus*. Along this deflected surface the dorsal margin of the surangular bears a sharp longitudinal crest that is progressively more developed towards the articular region (Fig. 11B).

The lateral surface of the posterior region of the surangular completely covers the lateral surface of the articular, including the retroarticular process (Fig. 11). Lateral to the surangular–articular contact, the surangular bears a well-developed concave facet that merges with the glenoid surface of the articular. This facet presumably formed an articular facet for the quadratojugal (Fig. 11B). This accessory articulation is present in several basal mesoeucrocodylians (see Phylogenetic Relationships). However, *Simosuchus* and derived notosuchians (e.g. *Notosuchus*, *Mariliasuchus*, *Sphagesaurus*, *Baurusuchus*) lack this accessory articulation. The accessory glenoid facet of the surangular faces dorsomedially and is delimited laterally by the sharp longitudinal crest that is located on the dorsal surface of the surangular. Therefore, this facet is completely hidden in lateral view (Fig. 11). The mediolateral extension of the glenoid facet of the surangular is approximately one-quarter the breadth of the glenoid facet of the articular.

ARTICULAR

The articular of *Uruguaysuchus* possesses some derived features only present in notosuchian crocodyliforms. The glenoid surface of the articular is slightly elongated anteroposteriorly and lacks a distinct longitudinal ridge (Fig. 11B, C), as in most notosuchians (including *Araripesuchus*). Elongation of the glenoid facet is moderate, with its maximum anteroposterior extension being approximately 75% the maximum mediolateral extension. This proportion resembles that of *Araripesuchus*, but contrasts with the extremely elongated facet of some derived notosuchians (e.g. *Notosuchus*). The elongation of the facet is more developed in the medial facet than in the lateral facet. The dorsal surface of the glenoid facet is relatively flat and the facet for the lateral condyle of the quadrate faces dorsally, whereas the facet for the quadrate medial condyle faces dorsomedially (Fig. 11B, C). Therefore, the medial condyle of the quadrate seems to have been more ventrally projected than the lateral condyle, as in most notosuchian crocodyliforms. Similar to the derived condition in all notosuchians, the glenoid facet of the articular of *Uruguaysuchus* lacks a posterior buttress (Fig. 11C). Other crocodyliforms have a dorsally projected posterior buttress that limits the posterior displacement of the quadrate during occlusion.

Anterior to the glenoid facet, the articular projects an anteroventrally directed process that tapers anteriorly. The lateral margin of this process is longitudinally oriented and the medial margin is obliquely oriented so that this process is triangular shaped in dorsal view (Fig. 11B).

The retroarticular process is remarkably short in comparison with that of most notosuchian crocodyliforms, with the exception of *Simosuchus*. This process projects posteroventrally from the caudal margin of the glenoid facet. The posterior surface of the retroarticular process is divided into two distinct regions. The lateral region, which occupies most of the retroarticular process, faces posteriorly, and extends from the lateral margin to the midpoint of the medial glenoid facet of the articular (Fig. 11B). At this point the retroarticular has a posteriorly directed peg located dorsally on the retroarticular process, close to the posterior margin of the glenoid facet (Fig. 11B, C). This peg does not extend ventrally along the retroarticular process and thus fails to separate completely the lateral and medial regions of the retroarticular process. A similar feature is only present in *Simosuchus* among notosuchian crocodyliforms. The medial region of the retroarticular process is much shorter than the lateral region and extends at the level of the medial half of the inner glenoid facet of the articular (Fig. 11C). This region is deflected medially, facing posteromedially.

The morphology of the retroarticular process of *Uruguaysuchus* differs from that of most notosuchians, which have a much more developed medial flange that is paddle shaped with a broad concave surface that faces posteromedially and is more posteriorly projected. The retroarticular process of *Uruguaysuchus* is short even in comparison with that of *Simosuchus*, which has a relatively short and posteroventrally projected retroarticular process.

DENTITION

The specimen of *Uruguaysuchus* described here has several important features preserved in its dentition, although none of the toothrows is completely preserved. FC-DPV 2320 has preserved three premaxillary alveoli (Fig. 1B), although the presence of an additional tooth socket is highly probable given that the anterior tip of the premaxilla has not been preserved. This is congruent with the four premaxillary alveoli described by Rusconi (1933) for this taxon and the generalized condition of four premaxillary teeth found in basal mesoeucrocodylians (including most notosuchians except for *Sphagesaurus*, *Chimaerasuchus*, and baurusuchids). All the premaxillary teeth (and premaxillary alveoli) are relatively small (Figs 2B, 3) and therefore *Uruguaysuchus* lacks an enlarged premaxillary caniniform, a feature present in all notosuchians (e.g. *Libycosuchus*, *Candidodon*, *Mariliasuchus*, *Notosuchus*; Andrade & Bertini, 2008) except for *Araripesuchus* and *Simosuchus* (Buckley *et al*., 2000).

The right maxilla bears 12 alveoli but due to incomplete preservation it is not clear if the left maxilla had 12 or 13 teeth (Fig. 1B). Thus, the entire upper toothrow would be composed by 16–17 teeth, a number that matches the toothcount of the lower dentition (17) (Fig. 8A). It must be noted that Rusconi (1933), based on the holotype of *U. aznarezi*, reported 13 teeth in the upper tooth row and 12 in the lower one; the lack of preparation of this specimen allows us to suppose that more teeth (or at least the alveoli) would have been present in the holotype. The maxillary tooth count of *Uruguaysuchus* is relatively high in comparison with most notosuchians that have seven or fewer maxillary teeth (e.g. *Candidodon*, *Malawisuchus*, *Notosuchus*, *Mariliasuchus*, *Comahuesuchus*, *Sphagesaurus*, baurusuchids). However, basal notosuchians such as *Araripesuchus*, *Libycosuchus*, and *Simosuchus* (Buckley *et al*., 2000; Pol & Apesteguía, 2005) have higher tooth counts as in *Uruguaysuchus*, resembling the generalized condition of basal mesoeucrocodylians.

The tooth morphology of *Uruguaysuchus* bears several autapomorphic characters that distinguish this taxon from all other known crocodyliforms. The dental series has a high degree of heterodonty, showing three main morphological types: incisiviform, caniniform, and post-caniniform teeth.

Incisiviforms are present in the anterior region of both the upper and the lower toothrows. In the upper toothrow this tooth type is present through the second maxillary position (Fig. 2). In the lower dentition, this morphology seems to be present in the first six or seven positions (Fig. 10A). Incisiviforms are small and conical teeth that are slightly recurved lingually (Figs 3, 10A). An isolated incisiviform shows that the crown is slightly inflated at its base but the crown-root is only slightly constricted (Fig. 12C). The enamel surface of this tooth is mostly smooth although a faintly developed wrinkling pattern can be observed at high magnification by scanning electron microscopy (Fig. 12D). The distal margin of this tooth bears a well-developed keel that extends from the tooth apex down to the bulbous region of the base of the crown (failing to reach the crown-root limit). This keel is slightly sinuous but lacks true denticles (non ziphodont *sensu* Prasad & de Lapparent de Broin, 2002; Fig. 12D).

The caniniform is a conical tooth that is approximately twice as large as the other teeth (Fig. 3) and is exclusively present in the upper toothrow, occupying in FC-DPV 2320 (as in *U. terrai* and a juvenile specimen of *U. aznarezi*, but differing from the holotype of *U. aznarezi*) the third maxillary alveolous (Fig. 12B). An enlarged maxillary caniniform located in the second or third maxillary alveolous is also present in several basal notosuchians (e.g. *Araripesuchus*, *Anatosuchus*, *Malawisuchus*; Gomani, 1997; Pol & Apesteguía, 2005) but is absent in more derived notosuchians (e.g. *Notosuchus*, *Mariliasuchus*, *Sphagesaurus*; Pol, 2003; Andrade & Bertini, 2008). The caniniform of *Uruguaysuchus*, however, differs from that of other notosuchians in the presence of four thick apicobasal carinae. The base of the crown of the caniniform tooth is bulbous and a more developed constriction is present between the crown and the root in comparison with that of the incisiviform teeth.

The post-caniniform teeth are located in the upper and lower toothrows. In the maxilla these elements are present from the fourth to the 12th (or 13th) position, and in the lower toothrow these elements are present posteriorly to the seventh alveoli. The post-caniniform teeth of *Uruguaysuchus* have several autapomorphic features. The crown of these teeth is markedly flattened buccolingually and has a circular outline when viewed in lateral view (Fig. 12A). The rounded profile of the tooth crown is basally limited by an extremely well-developed constriction between the crown and the root (Fig. 12), resembling the condition of *Simosuchus*. The crown of these teeth is characterized by the presence of a central apical cusp that has a variable degree of development along the toothrow (Fig. 12E, G). Two slightly developed grooves extend apicobasally on the lingual and buccal surfaces of the crown, diverging basally from the mesial and distal limits of the central cusp. The central cusp and its associated grooves are more developed in some of the post-caniniform teeth (Fig. 12E) than in others (Fig. 12G, H). In some teeth, the buccal or lingual surface of the crown bears additional apicobasal grooves located between the two major grooves mentioned above (Fig. 12G). Mesial and distal from this central cusp, the margins of the crown bear denticles that vary in their number, development, and extension along the tooth margins in different post-caniniform teeth.

Some teeth have either seven or eight denticles located on the distal and mesial margins of the crown that are well separated from the central cusp and that extend basally down to the midpoint of the crown, approximately at the level of the maximum mesiodistal expansion of the crown (Fig. 12E). However, in those post-caniniform teeth in which the central cusp is not as developed, there are only four mesial and distal denticles that are smaller, closely spaced between each other, and located closer to the central cusp (Fig. 12G, H). Furthermore, in these teeth, the mesial and distal denticles are restricted to the apical region of the crown, being well separated from the maximum point of mesiodistal extension of the crown (Fig. 12G). Therefore, in these teeth the central cusp and the denticles form a subhorizontally oriented occlusal margin (Fig. 12G, H).

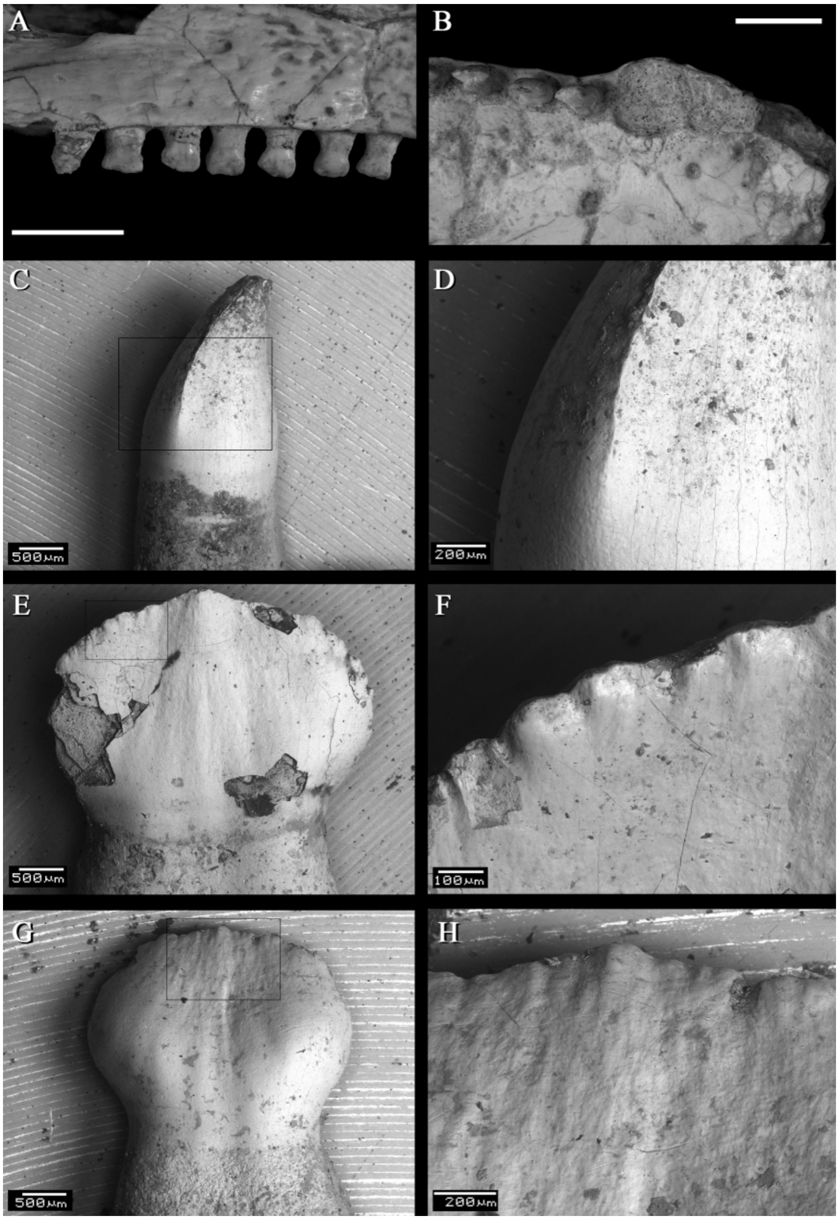

Figure 12. FC-DPV 2320, A, posterior maxillary teeth in lateral view. B, detail of anterior maxillary alveoli in occlusal view. C, anterior incisiviform tooth. D, detail of distal carina in anterior incisiviform tooth (see box in C). E, cheek tooth. F, detail of marginal denticles of tooth shown in E. G, posterior cheek teeth. H, apical denticle of tooth shown in Fig. 11H.

The shape of the mesial and distal denticles is also interesting in terms of their similarity with those of other crocodyliforms. These denticles are well separated from each other by interdenticular slits created by a constriction of the enamel and dentine and therefore cannot be described as pseudoziphodont in which the 'denticles' are exclusively formed by enamel ridges and foldings (*sensu* Prasad & de Lapparent de Broin, 2002). Each denticle is buccolingually broad and tuberous in overall shape. This denticular morphology resembles that of *Mariliasuchus* (Andrade & Bertini, 2008) and *Notosuchus* (Lecuona & Pol, 2008) but contrasts with the buccolingually flattened denticles present in other ziphodont crocodyliforms (e.g. *Sebecus*, *Dakosaurus*; Legasa, Buscalioni & Gasparini, 1994; Pol & Gasparini, 2009). However, the denticles of *Uruguaysuchus* bear also a sharp cutting edge that extends along the mesial or distal edge of the crown (Fig. 12F). Interestingly, this sharp ridge extends over the interdenticular slits in addition to being present over each of the denticles (Fig. 12F). The presence of this sharp carina distinguishes the

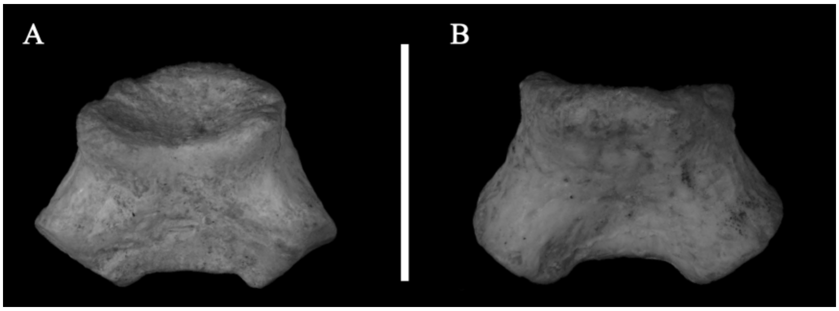

Figure 13. FC-DPV 2320, atlas intercentrum. A, dorsal view. B, ventral view. Scale bar = 1 cm.

teeth of *Uruguaysuchus* from those of the derived notosuchians (e.g. *Notosuchus*, *Mariliasuchus*), in which the denticles are completely rounded and lack a sharp cutting edge. A similar sharp edge is, in turn, present in most crocodyliforms with ziphodont dentition (e.g. *Sebecus*, *Dakosaurus*). Thus, the denticles of *Uruguaysuchus* bear a unique combination of characters that can be interpreted as intermediate between the generalized ziphodont dentition and the condition of derived notosuchians (termed ziphomorph for *Mariliasuchus* by Andrade & Bertini, 2008).

The presence of denticulated tooth margins has also been reported for *Araripesuchus wegeneri* and is also present in the posterior lower teeth of *A. gomesii* (AMNH 24450). Its presence, however, cannot be confidently determined (or rejected) in *A. patagonicus* or *A. buitreraensis*. The unusual crown morphology of *Simosuchus* has also been compared with that of *Uruguaysuchus* (Buckley *et al*., 2000). The superficial similarities of post-caniniform teeth of *Uruguaysuchus* with distal teeth of *Simosuchus* led Soto (2005) to propose that the diet of the former genus included plant material (besides other animals), as postulated for *Simosuchus* by Buckley *et al*. (2000). However, the dentition of the Malagasy taxon is highly modified, as it has multicusped teeth in the entire toothrow and most crowns (except those of posteriormost teeth) have three triads of cusps separated by extremely deep notches rather than the central cusp and denticulated mesial and distal margins that characterize post-caniniform teeth of *Uruguaysuchus*.

CERVICAL VERTEBRAE

The atlantal intercentrum, two articulated anterior cervical vertebrae, and several cervical ribs are the only postcranial remains associated with this specimen. The intercentrum is broader than long, with a large anterior articular facet for the occipital condyle and two posterior articular facets for the atlantal ribs (Fig. 13). The posterior rib facets project posterolaterally forming an angle of 45° with each other (Fig. 13). The central region between the articular processes of the atlas intercentrum is extremely short and broad, and has a broad concavity on both its dorsal and its ventral surfaces.

The anterior cervical vertebrae are probably the third and fourth elements of the cervical series (Fig. 14). The neural spines of these vertebrae are lost, although the preserved dorsal surface of the neural arches suggests their spine was anteroposteriorly short and located mostly over the posterior half of the dorsal surface of the neural arches. The neural arches are anteroposteriorly short and dorsoventrally high in comparison with those of neosuchian crocodyliforms but resemble the condition of *Notosuchus* (Pol, 2005). The prezygapophyses are short and dorsally recurved, so that their distal end is projected dorsally rather than anterodorsally (Fig. 14A), also resembling the condition of *Notosuchus* (Pol, 2005). The postzygapophyses are incompletely preserved and it cannot be determined if they had a suprapostzygapophyseal lamina connecting them to the neural spine. Anterior to the articular facet of the postzygapophyses, an anteroventrally oriented ridge extends on the dorsal region of the lateral surface of the neural arch, being more developed in the third cervical vertebra. The articular surfaces of the zygapophyses form an angle of approximately 45° with the sagittal plane. The diapophyses are robust and directed ventrolaterally (Fig. 14C). Their articular facets are ovoid with the major axis oriented anteroposteriorly. A deep depression is present below the diapophyses and above the parapophyses, extending over both the neural arch and the vertebral centrum. The cervical centra are low and long, being approximately twice as long as high. The parapophyses are located at the anterior margin of the centrum and are laterally projected (Fig. 14A, C). A thin longitudinal ridge extends posteriorly to the parapophyses along the vertebral centrum, delimiting ventrally the concave surface located between the parapophysis and the diapophysis. Below this ridge the centrum is also markedly concave and its ventral surface bears a

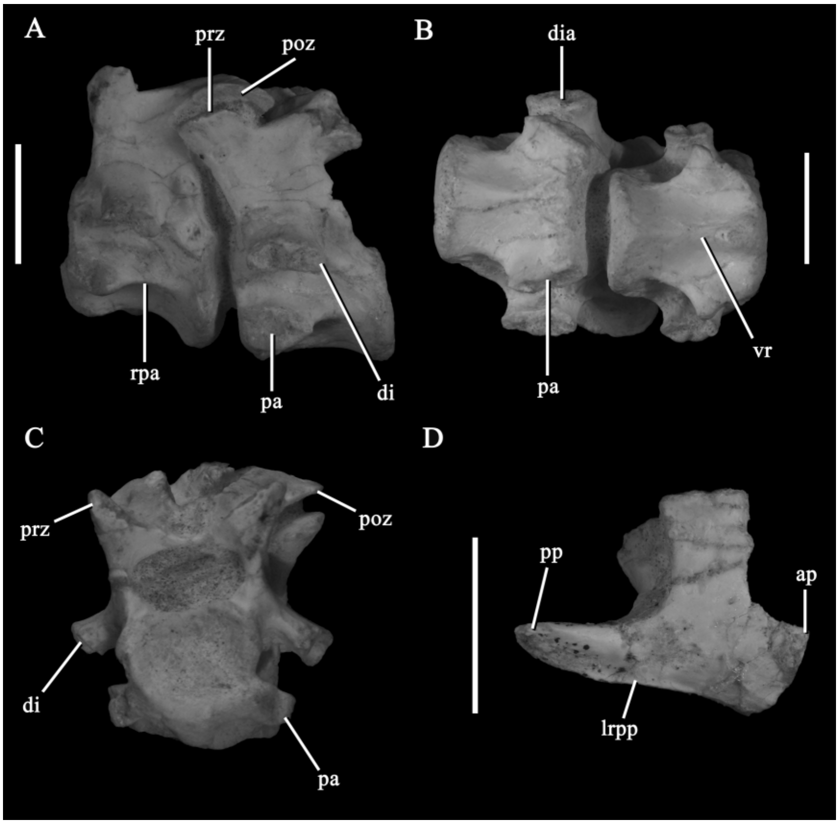

Figure 14. FC-DPV 2320, anterior cervical vertebrae. A, left lateral view. B, ventral view. C, anterior view. D, anterior cervical rib in lateral view. Scale bar = 1 cm.

longitudinal ridge that delimits the ventral extension of the concavity (Fig. 14B). The anterior end of this ridge is ventrally projected forming a moderately developed hypapophysis (Fig. 14A, B). The articular surfaces of the centrum are subcircular in outline and concave, and the neural canal above them is mediolaterally wider than dorsoventrally high (Fig. 14C).

The preserved cervical ribs (Fig. 14D) have a short and dorsoventrally high anterior process that laterally overlaps the posterior process of the preceding vertebra. Posteriorly, the rib has an elongated and low posterior process. The lateral surface of the posterior process bears a longitudinal keel and lacks the posterodorsally directed accessory process present in *A. tsangatsangana* and *Mahajangasuchus* (Turner, 2006).

PHYLOGENETIC RELATIONSHIPS

Rusconi (1933) originally placed the genus *Uruguaysuchus* in the family Notosuchidae, but later Gasparini (1971) defined Uruguaysuchidae to cluster *Uruguaysuchus* with *Araripesuchus*, as a family of the infraorder Notosuchia. As noted above, after these studies several authors noted derived similarities of *Uruguaysuchus* either with notosuchians (Pol, 2003) or with *Araripesuchus* and neosuchians (Ortega *et al*., 2000). Recent cladistic studies retrieved this taxon as alternatively allied with several notosuchians, such as *Notosuchus*, *Candidodon*, and *Simosuchus* (e.g. Buckley *et al*., 2000; Pol & Apesteguía, 2005; Jouve *et al*., 2006; Andrade & Bertini, 2008). However, as noted above, these authors based their inferences on the information available from the literature given that the specimens were not available for study, which resulted in a large number of missing entries (or even erroneous scorings) for *Uruguaysuchus* in phylogenetic datasets.

The specimen described herein provides new information for more rigorously testing the phylogenetic affinities of *Uruguaysuchus*. This new information was used to complete the character scorings of *Uruguaysuchus* in a recently published dataset (Pol & Gasparini, 2009) comprising 257 characters scored across 59 taxa. In this previous study *Uruguaysuchus* had 57% of the cells scored with missing entries. The new specimen provided information to score an additional 59 characters that were previously unknown or uncertain for this taxon, reducing the amount of missing entries to 33% (see Supplementary

Information, Appendices S1–4, for the full character list, data matrix, and complete list of unambiguous synapomorphies).

The updated data matrix was analysed in TNT (Goloboff, Farris & Nixon, 2008) using equally weighted parsimony analysis. A heuristic tree search was performed conducting 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding ten trees per replicate). The analysis yielded two most-parsimonious trees (MPTs) of 859 steps (CI = 0.365, RI = 0.710) that were found in 74% of the replicates. The strict consensus of the MPTs (Fig. 15) places *Uruguaysuchus* within Notosuchia as the sister taxon to the clade *Araripesuchus*. This result contrasts with more recent cladistic analyses (including that of Pol & Gasparini, 2009) that depicted *Uruguaysuchus* closer to more derived notosuchians. The clade of *Uruguaysuchus* and *Araripesuchus* forms a monophyletic Uruguaysuchidae, as originally conceived by Gasparini (1971). In our analysis Uruguaysuchidae is diagnosed by two unambiguous synapomorphies: surangular forming approximately one-third of the glenoid fossa (character 156.1) and dorsal surface of mandibular symphysis strongly concave and narrow, trough shaped (character 189.1). The latter character is so far only recorded in *Uruguaysuchus* (see Fig. 10B), *A. gomesii* (DGM 423-R), and in one specimen referred to *Araripesuchus* from the Cenomanian of Patagonia (MPCA-PV 236; see Pol & Apesteguía, 2005). All other basal mesoeucrocodylians lack this derived feature. The former synapomorphic feature is known in *A. gomesii* (AMNH 24450) and *Uruguaysuchus* (Fig. 11B) but the condition of other species of *Araripesuchus* is not known. A surangular participation in the mandibular glenoid facet, however, has also been reported to be present in some basal mesoeucrocodylians not included in this analysis (e.g. *Hamadasuchus*, *Montealtosuchus*, *Mahajangasuchus*, *Sebecus*) as well as in other groups of crocodyliforms (e.g. *Protosuchus*, dyrosaurids). This feature has evolved several times in Crocodyliformes and may have a broader distribution among basal mesoeucrocodylians than in the optimization obtained in our analysis. Further studies expanding the taxonomic sampling of basal mesoeucrocodylians are needed to assess a more thorough understanding on the evolution of this character. Finally, although this position is the most parsimonious explanation of the available data, the sister-group relationship of *Araripesuchus* with *Uruguaysuchus* is poorly supported; trees with one extra step depict the latter taxon as more closely related to ziphosuchians than to *Araripesuchus* (as in some of the previous phylogenetic studies; Pol, 2003; Gasparini *et al*., 2006; Turner & Buckley, 2008; Pol & Gasparini, 2009). Further data on *Uruguaysuchus*, such as a re-study of the more complete type specimen, will undoubtedly help to resolve this issue.

Despite these uncertainties, the notosuchian affinities of *Uruguaysuchus* are strongly supported by the available data (constrained analysis forcing this taxon to be placed outside Notosuchia requires at least 11 extra steps). Even when *Uruguaysuchus* and *Araripesuchus* are both forced to be placed outside Notosuchia (i.e. more closely related to peirosaurids and neosuchians), the most parsimonious topologies are six steps longer than in the unconstrained analysis.

Furthermore, the available information on *Uruguaysuchus* strongly supports a basal position for this taxon within Notosuchia. Constrained analyses forcing *Uruguaysuchus* to be more derived than *Simosuchus* (or even closely related to this taxon as suggested by Buckley *et al*., 2000) requires between six and ten extra steps, implying more extra steps as more derived positions are forced in the constrained searches. In summary, based on the current information *Uruguaysuchus* can be safely depicted as one of the most basal notosuchians, either as the sister group of *Araripesuchus* (as in the MPTs obtained here) or possibly as a basal taxon of the clade formed by *Lybicosuchus* and more derived forms (Ziphosuchia *sensu* Ortega *et al*., 2000; see Fig. 15).

STATUS OF *URUGUAYSUCHUS TERRAI*

As already stated, Rusconi (1933) recognized a second species of *Uruguaysuchus*, *U. terrai*, based mainly on differences in the tooth count in the upper tooth row. Both Soto (2005) and Andrade & Bertini (2005) independently questioned the taxonomic validity of maintaining the distinction of *U. terrai* from *U. aznarezi*. *U. terrai* apparently possesses four maxillary teeth more than *U. aznarezi*: two incisiviforms, one caniniform, and ten post-caniniforms versus one incisiviform, one caniniform and seven post-caniniforms, respectively (Fig. 16). However, as already stated, it must be noted that the lack of preparation of the holotype of *U. aznarezi* does not allow an assessment of the total number of post-caniniform teeth (i.e. whether there are teeth beyond the ninth maxillary position).

Moreover, the maxilla of Rusconi's specimen no. 4 (Fig. 16), a juvenile *U. aznarezi* according to this author, exhibits two incisiforms and one caniniform (being the third maxillary tooth), the same condition as in *U. terrai*. Curiously, Rusconi (1933) did not explicitly mention this relevant point. Interestingly,

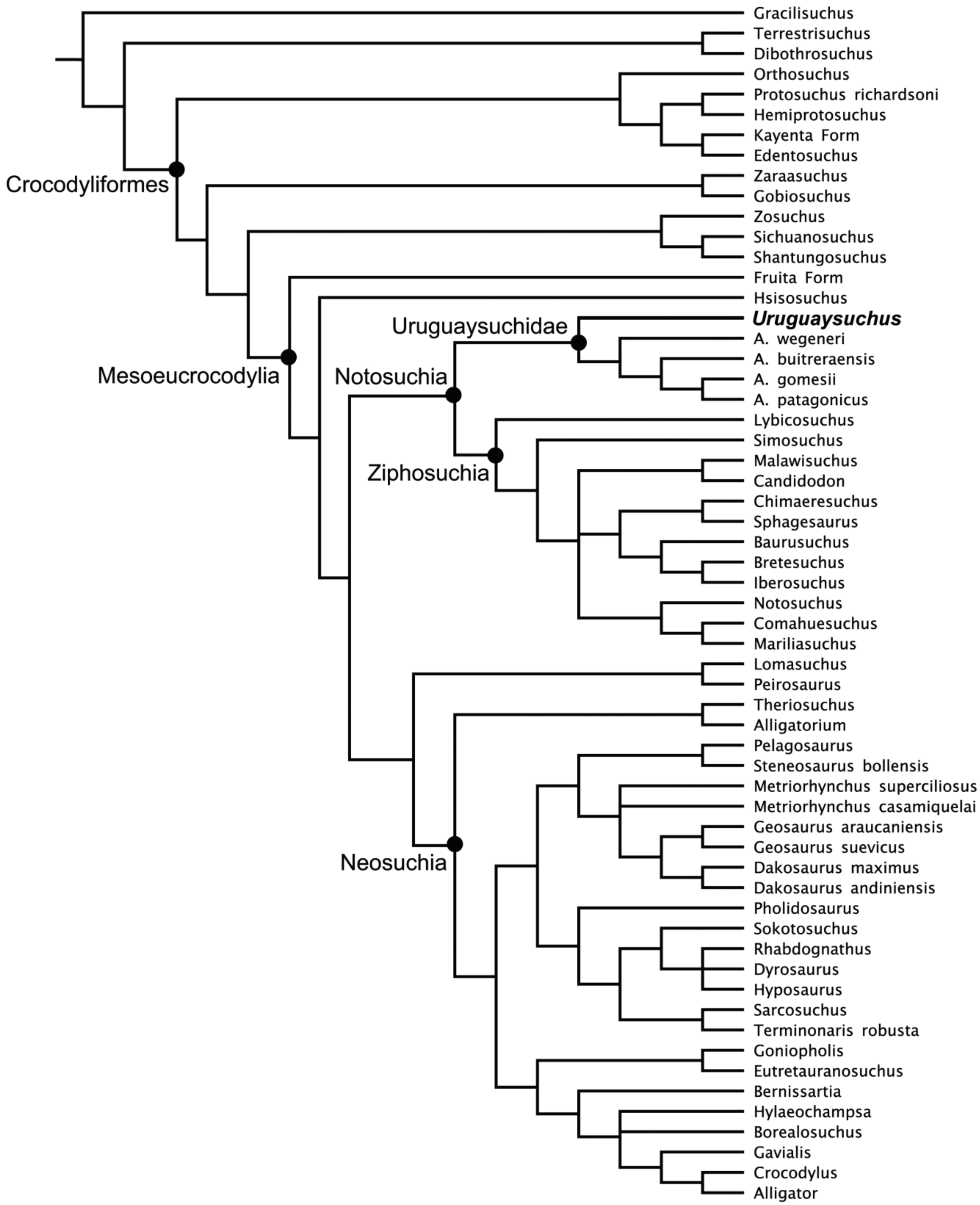

Figure 15. Strict consensus of the two MPTs found in the phylogenetic analysis, based on the dataset published by Pol & Gasparini (2009). The new information provided by FC-DPV 2320 allowed us to recover *Uruguaysuchus* as the sister taxon of the *Araripesuchus* clade.

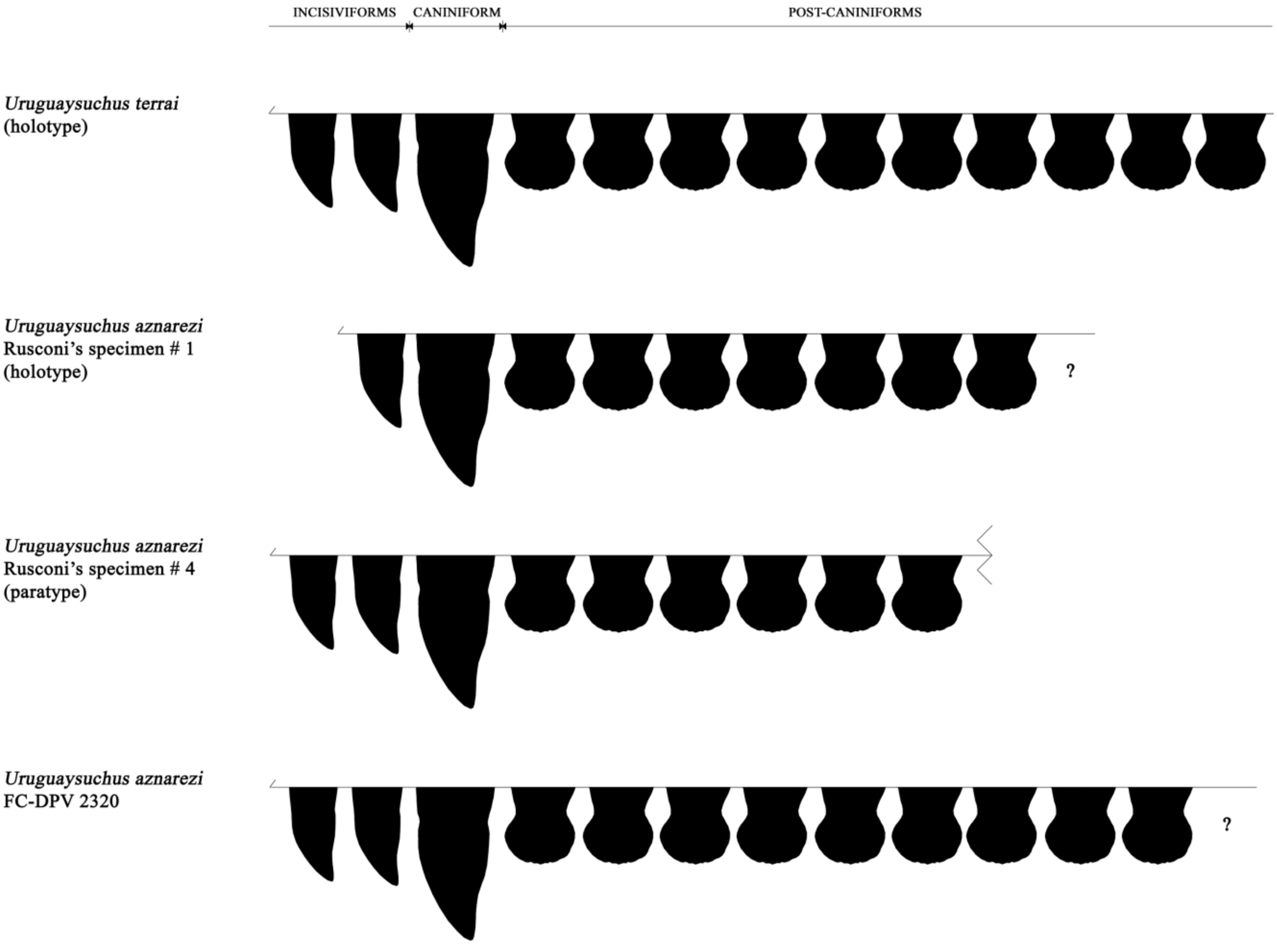

Figure 16. Schematic diagram (not intended to reflect the real size or shape differences among teeth) depicting maxillary teeth in *U. terrai* and three specimens of *U. aznarezi* (the holotype being probably the only adult individual) drawn at the same size. Based on descriptions and drawings provided by Rusconi (1933) in all cases except for FC-DPV 2320. Question marks indicate the possibility of an additional tooth.

his fig. 20 illustrates seven post-caniniform alveoli although only six are implied in the text.

Furthermore, several measurements of *U. terrai* are consistently smaller than those of the only adult individual of *U. aznarezi* (holotype), approaching those of juveniles of *U. aznarezi*.

As proposed by Soto (2005), minor differences in the dental formulae can be explained by intraspecific variation in tooth count, which is rather common among crocodyliforms, either fossil or extant (C. Brochu, com. pers., 2008). In particular, if it is true that *U. terrai*, *U. aznarezi* no. 4 and FC-DPV 2320 represent juvenile individuals, it may be necessary to invoke ontogenetic loss of tooth positions to explain the fact that the adult individual of *U. aznarezi* (holotype) has only one incisiviform maxillary tooth instead of two. Such a phenomenon has already been recorded in several crocodylian species (e.g. *Crocodylus cataphractus*, *C. porosus*, *C. siamensis*, and *Tomistoma schlegelii*; Mook, 1921; Wermuth, 1953; Iordansky, 1973) as well as in the tyrannosaurid theropods *Tyrannosaurus rex* and *Albertosaurus libratus* (Carr, 1999).

On the other hand, the hypothesis that *U. aznarezi* could bear more post-caniniform teeth than recognized by Rusconi (1933) received support when FC-DPV 2320 was prepared. Indeed, the specimen described herein (Fig. 16) showed the presence of at least 12 maxillary teeth (two incisiviforms, one caniniform, and at least nine post-caniniforms), reducing the apparent gap between the tooth count of *U. aznarezi* and *U. terrai*.

In conclusion, given that no real differences in the maxillary dentition exist, we regard *U. terrai* as a juvenile individual of *U. aznarezi*. Thus, as proposed by Soto (2005) and Andrade & Bertini (2005), *U.*

terrai must be considered a junior synonym of the latter taxon.

CONCLUSIONS

Uruguaysuchus from the middle Cretaceous of Uruguay has been shown to be a relevant taxon for mesoeucrocodylian phylogeny and biogeography (e.g. Buckley *et al*., 2000).

The new specimen described herein allows the recognition of several characters previously unknown for this taxon, thereby providing new insight for understanding its phylogenetic relationships.

According to the phylogenetic analysis presented herein, *Uruguaysuchus* is a basal notosuchian. Features such as a completely septated choanal opening, a well-developed anterior and posterior process on the ectopterygoid lateral end, a dentary failing to extend beneath external mandibular fenestra, the presence of a maxillary dental groove (absence of interalveolar septa), a slightly elongated glenoid facet that lacks a posterior ridge, and participation of the surangular in the glenoid facet conform a unique combination of characters present in basal notosuchians (e.g. *Araripesuchus*, *Simosuchus*), being part of the evidence that led us to postulate a similar position for *Uruguaysuchus*.

Moreover, *Uruguaysuchus* is closely related to *Araripesuchus*, both genera being recovered as sister taxa in the phylogenetic analysis, although it must be noted that this relationship is poorly supported. A similar result was also obtained by Turner & Buckley (2008) in one of the runs of the phylogenetic analysis they performed.

Overall, taking into account the plesiomorphic characters of *Uruguaysuchus* and the absence of basal notosuchians after the Cenomanian in different basins of South America (e.g. Neuquén and Bauru Basins), a middle Cretaceous age for the Guichón Formation seems a plausible hypothesis given the available evidence. Recently discovered remains of sauropod dinosaurs could shed more light on this topic (Perea *et al*., 2006; M. Soto & D. Perea, unpubl. data).

U. terrai probably represents a juvenile individual of *U. aznarezi*, and must be considered a junior synonym of the latter taxon. Minor differences in the dental formulae can be probably explained invoking intraspecific variation in tooth count.

The specimens from Guichón thus represent a monospecific assemblage. As suggested by Rusconi (1933), given that the individuals were concentrated in a small 2-m^2 surface, and that they included articulated material (notably the holotype of *U. aznarezi*, but also some of the paratypes and FC-DPV 2320), they were probably buried due to the collapse of the walls of a burrow. The shovel-shaped snout would assist in excavating burrows, as suggested for *Malawisuchus* and *Simosuchus* (Gomani, 1997; Buckley *et al*., 2000), although in the absence of characters clearly correlated with burrowing this remains highly speculative.

Notosuchian crocodyliforms included carnivorous (e.g. sebecosuchians), omnivorous (e.g. *Mariliasuchus*), and presumably herbivorous (e.g. *Chimaerasuchus*, *Simosuchus*) forms. *Uruguaysuchus* probably had an omnivorous diet, given the disparate morphology between incisiviform and post-caniniform teeth.

Uruguaysuchus is a heterodont notosuchian, with incisiviform premaxillary, mesial dentary, and mesial maxillary teeth. The second (in adults) or third (in juveniles) maxillary tooth is an hypertrofied caniniform.

The post-caniniform, spatulate lateral teeth are highly apomorphic: they are strongly buccolingually compressed and subcircular in shape (in buccal or lingual view), with a pointed central cusp and minute denticles in a single row along the mesial and distal margins.

This particular morphology adds to the increasing variety of dentition and feeding styles currently recognized among notosuchian crocodyliforms (e.g. Pol, 2003).

Although less enigmatic than a decade ago, the basal notosuchian *Uruguaysuchus* is still raising questions: new and more challenging ones. We will be probably close to answer at least some of them provided that the holotype is properly prepared in the near future.

ACKNOWLEDGEMENTS

We are deeply indebted to Laura Reiner (MEF, Trelew), who skilfully and carefully prepared the new *Uruguaysuchus* specimen. SEM images were possible thanks to Aluar Aluminio Argentino SAIC and the valuable help of Mr Jaime Groizard. Marco B. de Andrade provided bibliographic references. M.S. dedicates this paper to all the people from Guichón, especially J. C. Ualde and A. Suanes. Review of an earlier draft by Patrick O'Connor greatly contributed to improve this manuscript.

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APPENDIX

ANATOMICAL ABBREVIATIONS

aft	anterior foramen for mandibular branch of trigeminal nerve
ang	angular
aof	antorbital fossa
ap	anterior process
art	articular
boc	basioccipital
bsp	basisphenoid
chg	choanal groove
chs	choanal septum
den	dentary
di	diapophysis
ect	ectopterygoid
emf	external mandibular fenestra
emt	enlarged maxillary tooth
j	jugal
lac	lacrimal
lrpp	longitudinal ridge on lateroventral surface of posterior process
mgf	medial glenoid facet of articular
mx	maxila
ota	otic aperture
pa	parapophysis
pdr	posterior dentary ridge
pl	palatine
pmf	foramen in the premaxilla–maxilla suture
pms	premaxilla–maxilla suture
pmx	premaxila
poz	postzygapophysis
pp	posterior process
prz	prezygapophysis
psp	posterior splenial peg
pt	pterigoid
ptw	pterigoid wing
rap	peg of retroarticular process
rart	retroarticular process
rpa	ridge posterior to parapophysis
sang	surangular
sgf	surangular glenoid facet
sof	suborbital fenestra
spl	splenial
spo	siphoneal opening
vr	ventral ridge

SUPPORTING INFORMATION

Additional Supporting information may be found in the online version of this article:

Appendix S1. Character list corresponding to data matrix used in phylogenetic analysis.
Appendix S2. Data matrix used in the phylogenetic analysis.
Appendix S3. List of unambiguous synapomorphies.
Appendix S4. Fossil taxa used in phylogenetic analysis.