

New cranial remains of the bizarre notosuchid *Comahuesuchus brachybuccalis* (Archosauria, Crocodyliformes) from the Late Cretaceous of Río Negro Province (Argentina)

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Abstract. New cranial remains of *Comahuesuchus brachybuccalis* Bonaparte from the Late Cretaceous Bajo La Carpa Formation of Río Negro Province (Argentina) are described. *Comahuesuchus brachybuccalis* differs from all other crocodyliforms in having the association of the following derived features: extremely short, wide and circular snout; five anterior small teeth in the maxilla except the third hypertrophied caniniform; eleven teeth in the dentary with the anterior ones procumbent; all lower teeth small and circular in cross section except the tenth hypertrophied caniniform; dorsally opened paracanine fossa in the posterior maxillary region; contact among the ectopterygoid, pterygoid and palatine in the ventral region of the pterygoid wing; lachrymal with a long and thin process projecting laterally; and anterior portion of the dentary low and transversely broad, with an anteroposterior elongated symphysis extending at the level of the ninth tooth. The phylogenetic analysis nests *C. brachybuccalis* within the notosuchian clade, also represented by *Malawisuchus mwakasyungutiensis* and *Chimaerasuchus paradoxus* from the Early Cretaceous of Africa and China, and *Notosuchus terrestris* and *Sphagesaurus huenei* from the Late Cretaceous of South America. This group is diagnosed by having the external surface of the premaxilla and maxilla with two plane of exposure, one facing laterally (almost vertical) and the other dorsolaterally (almost horizontal); the dentary extending beneath the mandibular fenestra; a reduced number of maxillary teeth; and the articular facet for the quadrate condyle almost twice as long as wide lacking a posterior transversely ridge (uncertain in *Comahuesuchus* and *Sphagesaurus*).

Resumen. NUEVOS RESTOS CRANEANOS DEL BIZARRO NOTOSUCHIDO *COMAHUESUCHUS BRACHYBUCCALIS* (ARCHOSAURIA, CROCODYLIFORMES) DEL CRETÁCICO TARDÍO DE LA PROVINCIA DE RÍO NEGRO (ARGENTINA). Se describen nuevos restos craneanos de *Comahuesuchus brachybuccalis* Bonaparte del Cretácico Tardío de la Formación Bajo La Carpa de la Provincia de Río Negro (Argentina). *C. brachybuccalis* difiere de todos los otros crocodyliformes por tener la asociación de los siguientes caracteres derivados: hocico extremadamente corto, ancho y de contorno circular; cinco dientes maxilares pequeños, excepto el tercer caniniforme hipertrofiado; once dientes en el dentario, con los anteriores procumbentes; dientes inferiores pequeños y circulares en sección transversal, excepto el décimo caniniforme hipertrofiado; fosa paracarina abierta dorsalmente en la región posterior del maxilar; contacto entre ectopterigoides, pterigoides y palatino en la región ventral del ala del pterigoides; lacrimal con un largo y delgado proceso proyectado lateralmente; y porción anterior del dentario baja y transversalmente ancha, con sínfisis mandibular elongada anteroposteriormente entendiéndose hasta la altura del noveno diente. El análisis filogenético ubica a *C. brachybuccalis* dentro del clado de los notosuchios, representado por *Malawisuchus mwakasyungutiensis* and *Chimaerasuchus paradoxus* del Cretácico Temprano de África y China, y *Notosuchus terrestris* y *Sphagesaurus huenei* del Cretácico Tardío de América del Sur. Este clado está diagnosticado por tener la superficie externa del premaxilar y maxilar con dos planos de exposición, la región lateroventral casi vertical y la dorsolateral casi horizontal; el dentario entendiéndose por debajo de la fenestra mandibular; un número reducido de dientes maxilares; y la faceta articular para el cuadrado casi el doble de larga que ancha, sin la cresta transversal posterior (incierto en *Comahuesuchus* y *Sphagesaurus*).

Key words. Crocodyliformes. Notosuchids. *Comahuesuchus brachybuccalis*. Cretaceous. Río Negro Province.

Palabras clave. Crocodyliformes. Notosuchidos. *Comahuesuchus brachybuccalis*. Cretácico. Provincia de Río Negro.

Introduction

During the Cretaceous there was a great diversity of adaptive types of basal mesoeucrocodyliforms (see Clark, 1994) that developed bizarre features in the skull, the lower jaws and especially in the dentition distinguishing them from the stereotypical crocodylian morphology. Many of these taxa were recovered from Gondwanan regions and possible relationships among them were previously established (e.g.

Wu and Sues, 1996; Gomani, 1997; Buckley *et al.*, 2000; Pol, 1999, in press). They include *Notosuchus terrestris* (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991a) and *Comahuesuchus brachybuccalis* (Bonaparte, 1991a; Martinelli, 2000) both from the Late Cretaceous of Argentina; *Sphagesaurus huenei* (Price, 1950; Pol, in press), *Candidodon itapecuruense* (Carvalho, 1994) and *Mariliasuchus amarali* (Carvalho and Bertini, 1999) from the Cretaceous of Brazil; *Malawisuchus mwakasyungutiensis* (Clark *et al.*, 1989; Gomani, 1997) from the Early Cretaceous of Malawi; *Chimaerasuchus paradoxus* (Wu *et al.*, 1995) from the Early Cretaceous of China, and *Simosuchus clarki*

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(Buckley *et al.*, 2000) from the Late Cretaceous of Madagascar.

Notosuchus has a mammal-like snout and antero-posterior jaw movement (Gasparini, 1971; Bonaparte, 1991a), as in *Malawisuchus*, *Chimaerasuchus* and *Sphagesaurus* (Clark *et al.*, 1989; Gomani, 1997; Wu *et al.*, 1995; Wu and Sues, 1996; Pol, in press). *Malawisuchus* and *Candidodon* have some teeth with a central cusp and a lingual cingulum bearing small cusps resembling a molariform (Clark *et al.*, 1989; Gomani, 1997; Carvalho, 1994). *Sphagesaurus* has the upper and lower cheek teeth arranged as reverse triangles, and the lower jaws are also capable of lateral and posterior movements (Pol, in press). *Chimaerasuchus* has cheek teeth with numerous cusps aligned in three parallel rows that decrease in size posteriorly, resembling the postcanine teeth of tritylodontid synapsids (Wu *et al.*, 1995). *Simosuchus* possesses a short and blunt snout, with upper and lower teeth with numerous cusps arranged in a single longitudinal row (Buckley *et al.*, 2000).

Fieldwork during 1989 carried out by staff of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", led by Dr. J. F. Bonaparte, near Chacra La Isla-Paso Córdova, Río Negro Province, Argentina (figure 1) results in the discovery of a new specimen of the notosuchian *Comahuesuchus brachybuccalis* Bonaparte, 1991a. It comes from Bajo La Carpa Formation (Neuquén Group), assigned to the Santonian (Legarreta and Gulisano, 1989; Bonaparte, 1991a; Hugo and Leanza, 2001). This small crocodyliform shows notable features in the anterior region of the skull, with a very short, wide and circular snout, together with a peculiar structure in the lower jaws.

The aim of this paper is to describe this new remains and to discuss the phylogenetic relationships

of *Comahuesuchus* among basal mesoeucrocodylian crocodyliforms.

From Bajo de la Carpa Formation were also recovered abundant remains of the basal snake *Dinilysia patagonica* Woodward, the theropod dinosaurs *Velocisaurus unicus* Bonaparte and *Alvarezsaurus calvoi* Bonaparte, the birds *Patagopteryx deferrariisi* Alvarenga and Bonaparte and *Neuquenornis volans* Chiappe and Calvo, and the crocodyliforms *Notosuchus terrestris* Woodward and *Cynodontosuchus rothi* Woodward.

Abbreviations. Institutional abbreviations used in this paper are as follow: MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (N: Colección Neuquén, RN: Colección Río Negro) (Buenos Aires, Argentina); MLP: Museo de La Plata (La Plata, Argentina); MOZ: Museo "Profesor-Dr. Juan A. Olsacher" (Zapala, Argentina); MUCPv: Museo de Ciencias Naturales de la Universidad Nacional del Comahue (Neuquén, Argentina); PVL: Instituto Miguel Lillo (Tucumán, Argentina); RCL: Museo de Ciencias Naturales Pontificia Universidade Católica de Minas Gerais (Minas Gerais, Brazil).

Materials. For comparison purposes were studied the following specimens: *Comahuesuchus brachybuccalis*: MACN-N 30 and 31; *Hemiprotosuchus leali*: PVL 3829; *Notosuchus terrestris*: MACN-RN 1037, 1038, 1039, 1040, 1041, 1045, 1046, MACN-N 22, 23, 24 MLP 64-IV-16-1, 64-IV-16-2, 64-IV-16-3, 64-IV-16-5, 64-IV-16-7, 64-IV-16-11 and 64-IV-16-11; and *Sphagesaurus huenei*: RCL-100. Other anatomical information was taken from the literature.

Systematic paleontology

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Benton and Clark, 1988
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
COMAHUESUCHIDAE Bonaparte, 1991a

Diagnosis. As for species.

Comahuesuchus Bonaparte, 1991a

Type species. *Comahuesuchus brachybuccalis* Bonaparte, 1991a.

Holotype. MUCPv 202: partial skull with articulated incomplete lower jaws (Bonaparte, 1991a).

Referred material. MACN-N 30: incomplete rostrum and anterior region of the lower jaws; MACN-N 31: incomplete rostrum and anterior region of the lower jaws; P 6131 MOZ: partial skull with articulated incomplete lower jaws.

Locality, horizon and age. MUCPv 202, MACN-N 30, MACN-N 31 are from the northern region of the

Figure 1. Location map of Paso Córdova locality, Río Negro Province, Argentina. The arrow indicates the outcrop where the new specimen of *Comahuesuchus brachybuccalis* (P 6131 MOZ) was discovered / Mapa de ubicación de la localidad Paso Córdova, Provincia de Río Negro, Argentina. La flecha indica el afloramiento donde fue encontrado el nuevo espécimen de *Comahuesuchus brachybuccalis* (P 6131 MOZ).

Neuquén city, Neuquén Province; P 6131 MOZ is from Chacra La Isla–Paso Córdoba locality, Río Negro Province. Bajo La Carpa Formation, Río Colorado Subgroup (Ramos, 1981), Neuquén Group; Santonian (Legarreta and Gulisano, 1989; Bonaparte, 1991a; Hugo and Leanza, 2001).

Diagnosis. *Comahuesuchus brachybuccalis* differs from all other crocodyliforms in having the association of the following features: 1) snout extremely short, very wide with circular outline in dorsal aspect; 2) five anterior small teeth in the maxilla except the third hypertrophied caniniform; 3) eleven teeth in the dentary with the anterior ones procumbent; all small and circular in cross section except the tenth transversely narrow hypertrophied caniniform; 4) dorsally opened paracanine fossa in the posterior maxillary region; 5) very wide and short secondary palate; 6) contact among the ectopterygoid, pterygoid and palatine in the ventral region of the wing of the pterygoid; 7) lachrymal with a long and thin process projecting laterally; 8) anterior portion of the dentary low and transversely broad, with an anteroposterior elongated symphysis extending at the level of the ninth tooth. With the exception of character 5 all the above mentioned features are autapomorphic for this species.

Description and comparisons

Skull (Figure 2)

The new skull of *Comahuesuchus brachybuccalis* (P 6131 MOZ) is about 25% larger than the holotype (Bonaparte, 1991a) and it is slightly dorsoventrally flattened. The skull is almost rectangular in shape in dorsal aspect, with an extremely short, wide, and circular snout. The external nares are forward projected and the large orbits are laterally oriented.

Premaxilla. The lateral contact between premaxilla and maxilla is nearly vertical ventrolaterally, and becomes more horizontal dorsomedially. On the alveolar border of the premaxilla–maxilla suture there is a small notch. The external nares are confluent and open anteriorly with a curved lateral border. In the dorsal aspect, two vascular foramina larger than those of the maxilla are located laterally to the external nares, near the alveolar edge of the premaxilla. The premaxilla has an unusual notch placed lateroventrally from the dorsal edge of the nares, and above it the bone is ornamented with anteroposterior or shallow furrows (figure 2A). This notch is present in some specimens of *Notosuchus*, in *Chimaerasuchus*, and in *Sphagesaurus*. In this specimen (P 6131 MOZ), the dorsal process of the premaxilla is more developed than in the holotype and has a sharper angle. Also, the sutures with nasal and maxilla are wider (figure 2A). In ventral aspect, the contact with the

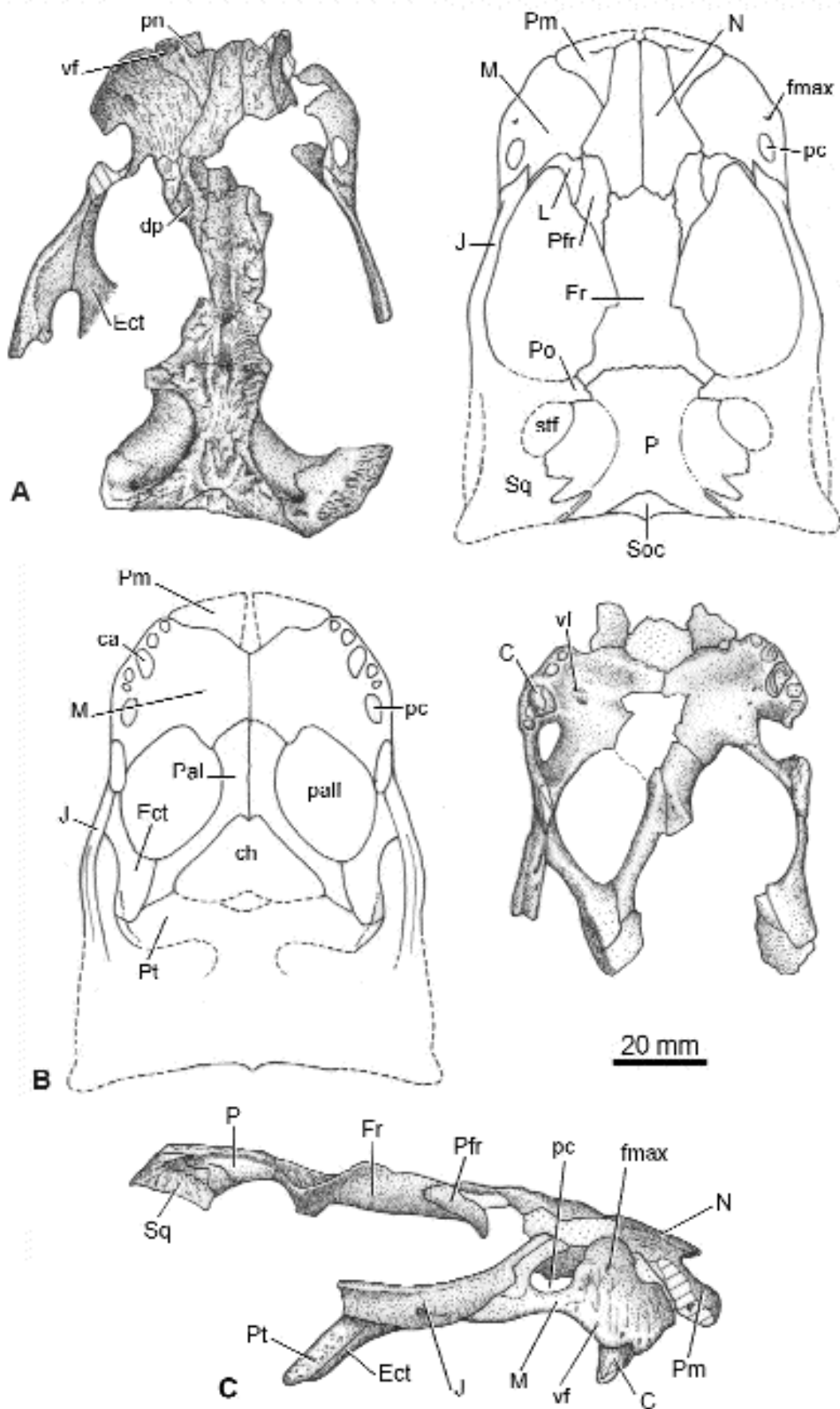
maxilla is overlapping, not sutured. The contact between both premaxillae is not preserved. In MACN–N 31 there is a large oval-shaped incisive foramen and the premaxillae contact medially behind this foramen.

Maxilla. In lateral view, the maxilla is a high, short and anteriorly convex bone with a marked alveolar process for the hypertrophied caniniform tooth. The maxilla has two planes of exposure, one faces laterally (almost vertical) bearing numerous vascular foramina and without ornamentation, and the other faces dorsolaterally (almost horizontal) bearing slight furrows. Behind the caniniform tooth the alveolar border curves up (figure 2C), instead of being straight as in *Notosuchus*, *Malawisuchus*, *Sphagesaurus* and *Chimaerasuchus*. A posterior process located below the jugal produces a long contact between both elements similar to *Malawisuchus* (Gomani, 1997), *Simosuchus* (Buckley *et al.*, 2000), and *Anatosuchus minor* (Serenio *et al.*, 2003). In *Notosuchus* and *Sphagesaurus* this process is less developed (Gasparini, 1971; Bonaparte 1991a; Pol, in press).

The dorsally opened paracanine fossa (figure 2) is located in the posterior region of the maxilla behind the maxillary teeth and in front of an edentulous area that is evident in ventral view (figure 2B). The ventral opening of this fossa is a little more than twice the anteroposterior diameter of the dorsal opening. In its anterior wall, the fossa bears a vascular foramen. The inner wall is dorsoventrally extensive and convex. The maxillary process that separates the paracanine fossa from the palatine fenestra is strong, uniting the maxillary jugal process with the palatine region of the maxilla and forming a small floor in the anterolateral orbital region. The presence of a paracanine fossa is considered an autapomorphy of *Comahuesuchus*. In basal mesoeucrocodylians, a paracanine fossa is only reported in baurusuchids (e.g. *Baurosuchus pachecoi*; Price, 1945) and peirosaurid (e.g. *Lomasuchus palpebrosus*; Gasparini *et al.*, 1991) but it is located in the anterior region of the maxilla, near or on the suture with the premaxilla, and it is laterally open. In other mesoeucrocodylians, such as sebecids (e.g. *Sebecus icaeorhinus*; Simpson, 1937; Colbert, 1946), there is a depression on the lateral surface of the premaxilla–maxilla for a lower tooth.

In the lateral aspect, anterior to the paracanine fossa there is a large foramen probably for the maxillary branch of the trigeminal nerve. This foramen is located on the suture between the maxilla and premaxilla in *Notosuchus* (MACN RN–1040), *Sphagesaurus* (Pol, in press) and *Simosuchus* (Buckley *et al.*, 2000).

The maxillary contact with the nasal is shorter than in *Notosuchus* due to the shortness of both elements. In both *Malawisuchus* and *Simosuchus* this contact is even more reduced.



The maxilla is excluded from the anterior orbital border (figure 2A) by a thin long lateroventral process of the lachrymal. This is well preserved in MACN-N 31. In *Protosuchus* (Colbert and Mook, 1951), *Notosuchus* (differing from that figured by Bonaparte, 1991a: 33), *Chimaerasuchus*, *Sphagesaurus*, *Simosuchus* and *Araripesuchus* the maxilla does not contribute to the orbital border, while in *Malawisuchus* it does. The antorbital fenestra is absent such as in *Chimaerasuchus*, *Baurusuchus* (Price, 1945) and sebecid (e.g. Colbert, 1946; Gasparini, 1972).

In ventral view, the maxillae meet along the middle line of the palate as in most mesoeucrocodylians, but differing from *Simosuchus*. The maxillae are transversely wide, anteroposteriorly short and the surface is mainly concave. Numerous vascular foramina of different sizes are observed. The contact with the palatine forms a slight ridge oblique to the sagittal plane. The maxilla-palatine fenestra observed in *Notosuchus* is absent in *Comahuesuchus* as in *Malawisuchus*, *Sphagesaurus*, *Simosuchus*, *Chimaerasuchus*, *Araripesuchus*, and *Anatosuchus*. The maxilla forms the anteromedial and anterolateral edge of the palatine fenestra (figure 2B), this being oval in shape and proportionally larger than in *Notosuchus* and *Malawisuchus*. The maxillary contact with ectopterygoid is reduced. In ventral view it is axially oriented while in dorsal view it is transversely oriented. In ventral view, the lateral border of the maxilla can be divided into three morphological regions: the anterior part bearing the five alveoli, the middle region forming a thin wall around the paracanine fossa and the posterior part that is a thick, enlarged edentulous area with small and shallow pits (better preserved of the left side) (figure 2B). This thickened region is also observed in MACN-N 31.

Nasal. The nasal is almost as long as the frontal. It gets wider posteriorly until the contact with the prefrontal, where it becomes narrower to contact the frontal in an oblique suture (figure 2A). As in *Notosuchus*, *Malawisuchus*, *Chimaerasuchus*, *Sphagesaurus*, and *Anatosuchus*, the nasal forms the dorsal edge of the nares, and the anterior edge is posteriorly located to the level of the anterior border of the premaxilla. Posterodorsally there is a shallow depression on the nasal, that in MACN-N 31 is relatively deeper. The nasal does not contact the lachrymal (figure 2A). The lack of contact between lachrymal and nasal is also shared with *Chimaerasuchus*.

Lachrymal. In dorsal view, the long axis of the lachrymal is anteroposteriorly oriented contacting with the prefrontal and the maxilla but not with the nasal (figure 2A). In MACN-N 31 and MUCPv 202

(Bonaparte, 1991a) the lachrymal is well preserved showing a long and narrow process projecting laterally which contacts the jugal and excludes the maxilla from the orbital edge (figure 2A).

Prefrontal. In dorsal view, the prefrontal is elongated and narrow, as in *Malawisuchus*, *Chimaerasuchus* and *Simosuchus*. This differs from *Notosuchus* in which the prefrontal is wide and short (Gasparini, 1971; Bonaparte, 1991a). The prefrontal has a wide medial contact with the frontal, like in *Notosuchus*, *Malawisuchus*, and *Simosuchus*. The contact with the nasal is also extensive (figure 2A), similar to *Notosuchus* and *Simosuchus*. In the holotype (Bonaparte, 1991a), the contact between prefrontal and frontal is shorter. There is a short contact between prefrontal and maxilla (figure 2A) as in *Chimaerasuchus*, but it is absent in *Protosuchus haughtoni* (Gow, 2000; in *P. richardsoni* this contact was figured by Colbert and Mook, 1951), *Notosuchus*, *Malawisuchus*, *Simosuchus* and *Araripesuchus* (in some specimens this contact is present; Turner, personal communication). Dorsally, a slight ridge separates two distinct surfaces, one ornamented with furrows, and the other without ornamentation. This area is for the support of the palpebral bone.

Frontal. The frontal is a long, dorsally concave bone. It is narrow anteriorly and it contacts the nasal anteriorly and the prefrontal laterally. It widens posteriorly and contacts the parietal transversely and the postorbital laterally. In *Notosuchus*, the frontal is relatively shorter and wider (Gasparini, 1971; Bonaparte, 1991a). The frontal is excluded from the margin of the supratemporal fenestra.

In the holotype, both frontals are not fused, probably reflecting its juvenile ontogenetic stage. In the P 6131 MOZ, the frontals are strongly fused. Furthermore, it is densely ornamented with grooves and ridges on its dorsal surface, instead of circular pits as in *Araripesuchus* and *Anatosuchus*. Together with the dorsal parietal region, these two bones are the most profusely decorated elements in the skull (figure 2A).

Parietal. The parietal occupies most of the dorsal and posterior region of the skull. Posteriorly, the contact with the supraoccipital is V-shaped. The medial border of the supratemporal fenestra is elongated and oblique to the sagittal plane. In the holotype, the supratemporal fenestrae are more circular in shape. The extensive contact with the squamosal forms an irregular suture where a foramen is observed (figure 2A).

Squamosal. Both squamosals are only preserved in the dorsal portion, lacking the lateral and lateropos-

Figure 2. Skull of *Comahuesuchus brachybuccalis* Bonaparte (P 6131 MOZ) in dorsal (A), ventral (B), and lateral (C) views. Broken bone indicated with parallel lines. Regular dotted denotes area covered with sediment / Cráneo de *Comahuesuchus brachybuccalis* Bonaparte (P 6131 MOZ) en vista dorsal (A), ventral (B) y lateral (D). Líneas paralelas indican hueso roto. Punteado regular indican áreas cubiertas con sedimento.

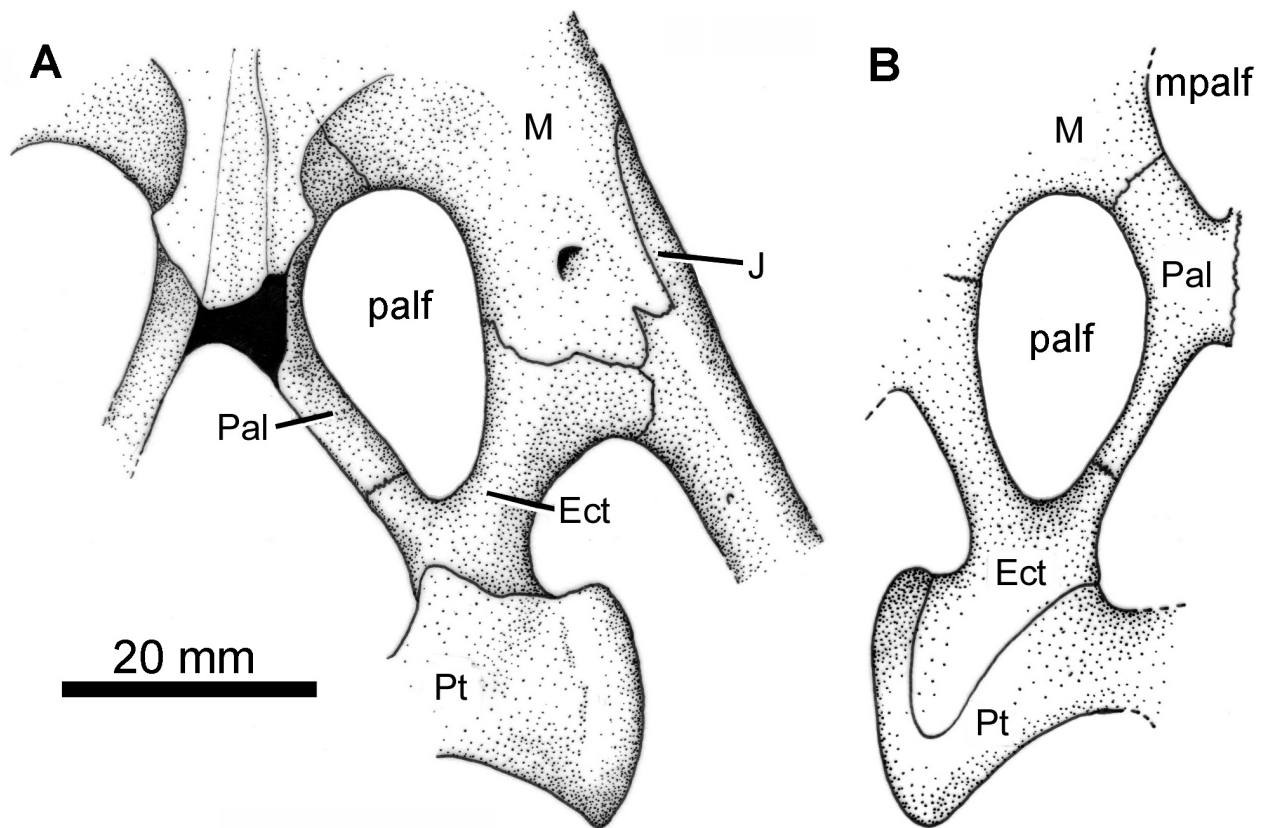


Figure 3. Palatine region of the skull of *Notosuchus terrestris* Woodward (MACN-RN 1040) in dorsal (**A**), and ventral (**B**) views / *Región palatina del cráneo de Notosuchus terrestris* Woodward (MACN-RN 1040) en vista dorsal (**A**) y ventral (**B**).

terior borders. The squamosal is ornamented with irregular furrows on the dorsolateral surface (figure 2A). In the holotype, the posterolateral corner of the squamosal forms a slightly posteriorly projected process (Bonaparte, 1991a) as in *Notosuchus*, but it is not strongly developed as in *Malawisuchus* and *Simosuchus*.

Supraoccipital. The supraoccipital is exposed on the dorsal aspect of the skull (figure 2A). In *Notosuchus* the dorsal exposure is smaller and it is absent in *Malawisuchus*, *Simosuchus* and *Anatosuchus*. In posterior view, it is triangular with a thick medial crest.

Palatine. The palatines are transversely narrow, bearing a shallow medial concavity with a small foramen. The left palatine also has an accessory smaller foramen (figure 2B). The contact with the maxilla is flat with a rounded lateral border. The posterior process of the palatine reaches between the pterygoid and the ectopterygoid, forming a sharp angle (figure 2B), differing from that observed in *Notosuchus* (figure 3). In *Malawisuchus* (Gomani 1997), *Simosuchus* (Buckley *et al.*, 2000), *Anatosuchus* (Serenó *et al.*, 2003) and

Araripesuchus (Price, 1959; Ortega *et al.*, 2000) there is no contact with the ectopterygoid. Even in *Simosuchus*, there is no axial contact between both palatines. This element contributes to the palatine fenestra forming its medial and posteromedial edge. The internal nares are not evident.

Ectopterygoid. In the holotype (Bonaparte, 1991a), the ectopterygoids were not preserved. The ectopterygoid is a large flattened bar that is ventrally exposed and anterolaterally oriented. The most lateral region widens and reaches below the pterygoid wing where it contacts the palatine. The lateral edge of the ectopterygoid fits with the ventrolateral border of the pterygoid wing (figure 2B). In *Notosuchus* (MACN RN-1037 and MACN RN-1040) the lateral border of the pterygoid wing is more laterally placed (figure 3). The anterior process is very well developed and has an extensive anteroposterior contact with the jugal and reduced contact with the maxilla (figure 2.B). In *Notosuchus*, the ectopterygoid suture with the maxilla is proportionally wide and transversely oriented, and the posterior process is small and contacts

with the jugal (figure 3). The shape and contacts of this element in *Simosuchus* (Buckley *et al.*, 2000) differ greatly from that observed in *Comahuesuchus*. In *Simosuchus*, the ectopterygoid is reduced and square in shape, forming the anterolateral border of the palatine fenestra and without any contact with the palatine. The relationships of the ectopterygoid with the pterygoid, the maxilla and the jugal are quite different from that observed in *Comahuesuchus*.

The posterolateral border of the palatine fenestra is delimited by the ectopterygoid where it contacts the palatine medially (figure 2.B). In *Notosuchus* (figure 3), contrary to the observations of Gasparini (1971), the posterior and posterolateral border of the palatine fenestra is defined by the ectopterygoid. Also, the ectopterygoid has a small process anteromedially projected that contacts the palatine (figure 3).

Pterygoid. The pterygoid wings are only partially preserved. The available section is thin and slopes toward the medial plane. The palatine contacts the ectopterygoid on the pterygoid wing excluding the pterygoid from palatine fenestra edge as in *Notosuchus* (figures 2.B and 3). This differs from *Protosuchus haughtoni* (Gow, 2000), *Malawisuchus* (Gomani, 1997), *Simosuchus* (Buckley *et al.*, 2000), *Araripesuchus* (Price, 1959; Ortega *et al.*, 2000), and most crocodyliforms in which the pterygoid largely contributes to the edge of the palatine fenestra.

Jugal. In lateral aspect, the jugal is low and mainly concave, with a laterally projected dorsal crest. In *Chimaerasuchus* and *Sphagesaurus* there is a similar feature, but the crest is more laterally developed and more ventrally located (Wu and Sues, 1996; Pol, in press). In *Notosuchus*, the jugal has a convex lateral surface. It has no, or very shallow, ornamentation. The anterior process that defines the anterolateral border of the orbit lies on the posteromedial region of the paracanine fossa (figure 2.A, C). In inner aspect, the anterior process of the jugal is concave and lies on the most medial wall of the paracanine fossa of the maxilla. The body of the jugal contacts broadly with the ectopterygoid. The left jugal bears the base of the postorbital process, directed slightly posteriorly (figure 2.A) and cylindrical in cross section.

Exoccipital. The exoccipital is badly preserved. In posterior aspect, it is observed the partial oblique contact with the supraoccipital and the dorsal border of the foramen magnum. In ventral view, there is a ventrally shifted fragment that contacts the basioccipital. Its bears a narrow and elongate foramen which may be for the cranial nerve XII (i.e. the hypoglossal foramen).

Basioccipital and Basisphenoid. The poorly preserved, incomplete, and broken basicranial elements were shifted from their original position and the sutures are not

clear. Because this area offers several difficulties for its correct characterization, it does not provided new information and it is not described or figured.

Lower Jaws (Figure 4)

Only the anterior halves of both lower jaws are preserved. In lateral view, the dentary is long. It is deepest just behind the caniniform. It is very low anteriorly and bears procumbent incisiform teeth. It has a lateral groove with numerous vascular foramina distributed along a descending pattern between the fifth tooth and the caniniform area, after which these foramina begin to ascend on the dentary (figure 4.A). The mandibular symphysis is anteroposteriorly elongated and flat. This region is very wide and well exposed ventrally with the posterior edge at the level of the ninth tooth, differing notably from other Cretaceous mesoeucrocodylians. The anterior and posterior edges are concave and convex, respectively (figure 4.C, D). In the holotype, these edges are more angular, and the mandibular branches become almost parallel each other. In this specimen, the mandibular branches are slightly divergent posteriorly. Dorsally, numerous foramina surround the alveolar edge. The anterior region, close to the symphysis, is edentulous. The lateral and inferior dentary surface and the symphyseal ventral region have a light ornamentation of furrows (figure 4). In the holotype, the dentary extends posteriorly beneath the mandibular fenestra.

The splenial forms part of the symphysis posteriorly, where it rises to the alveolar border of the caniniform. The splenial is anteroposteriorly short and reaches the ventral border. Internally, the anterior border of the intermandibularis oralis foramen (Iordansky, 1973) is present (figure 4.B, D). It is large, almost circular in shape and located immediately behind the symphyseal border. This location is farther anterior compared to the condition found in *Notosuchus*. Because this foramen is posteriorly closed by the angular, it has an important contribution in the inner wall of the lower jaw. In *Notosuchus* (MACN-RN 1037), this foramen is contained exclusively within the splenial.

Dentition (Figures 2B, C; 4)

Comahuesuchus brachybuccalis possesses a dental morphology unique among Crocodyliformes, suggesting a novel adaptive type for the Cretaceous of Gondwana (Bonaparte, 1991a). The premaxillary teeth are not preserved, but four small alveoli of square cross section are located on its posterior region. In MUCPv 202 the crown base of the four premaxillary teeth is present. The anterior area of the premaxilla is broken and possibly edentulous, as sug-

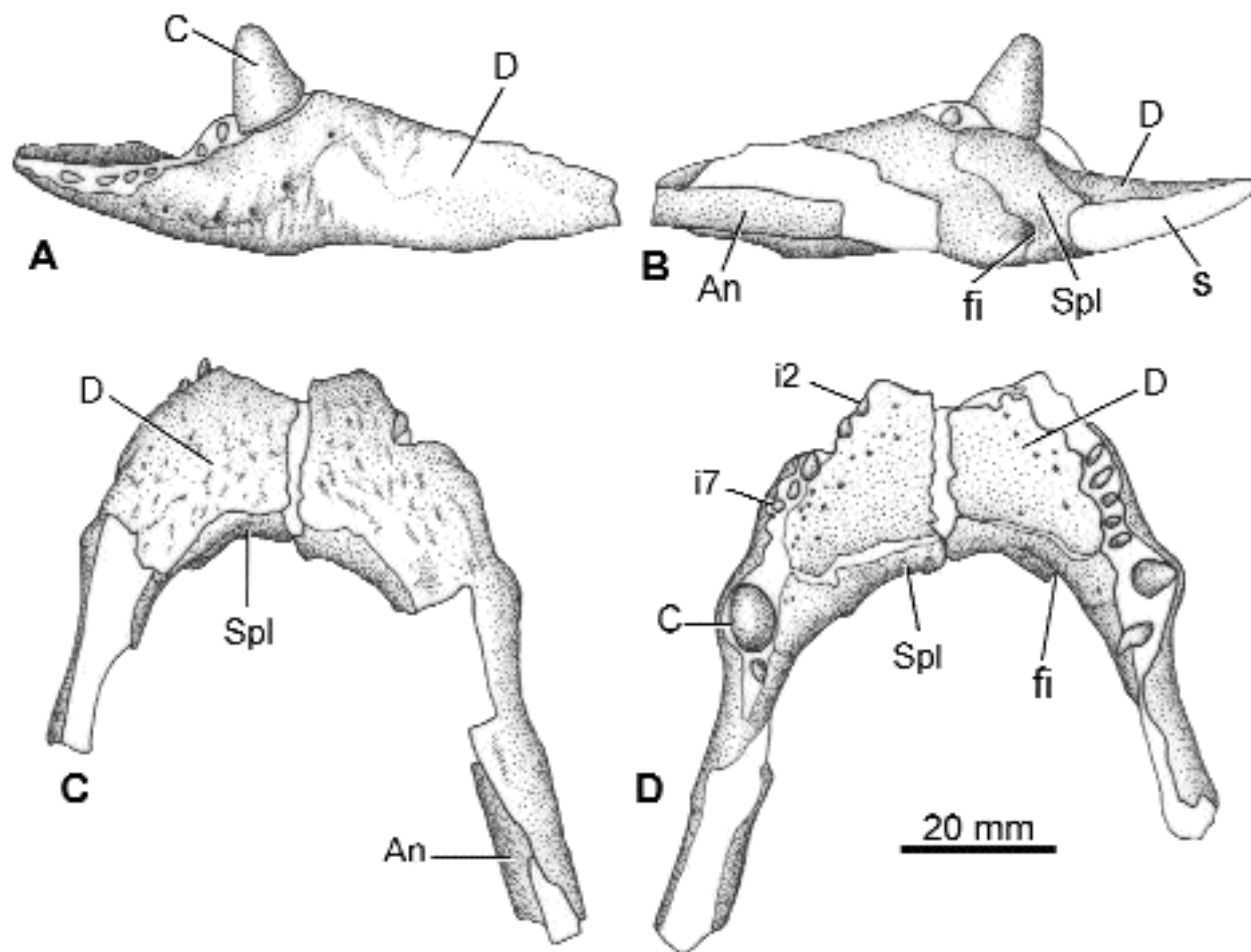


Figure 4. Lower jaws of *Comahuesuchus brachybuccalis* Bonaparte (P 6131 MOZ) in lateral (A), medial (B), ventral (C), and dorsal (D) views. White denotes areas covered with sediment / Mandíbulas de *Comahuesuchus brachybuccalis* Bonaparte (P 6131 MOZ) en vistas lateral (A), medial (B), ventral (C) y dorsal (D). Blanco indica áreas cubiertas con sedimento.

gested by the lower jaw in which there are no teeth close to the area of the mandibular symphysis. The maxilla has five teeth before the paracanine fossa. The two anteriormost teeth are very small, possibly similar to those of the premaxilla. As in *Anatosuchus*, *Araripesuchus*, basal eusuchians (e.g. *Pelagosaurus* and *Theriosuchus*; Buffetaut, 1980; Clark, 1986), and less notorious in *Notosuchus*, the third tooth is the hypertrophied caniniform, which curves slightly backwards, and is implanted in a wide alveolar process. The two post-caniniform teeth are small and all the cheek teeth are implanted in separate alveoli.

The dentary bears nine teeth anterior to the caniniform. They are small and their orientation in the dentary varies. The anterior teeth do not reach the anterior sector of the dentary and are procumbent while posteriorly the teeth are vertically implanted. This is related to the particular morphology of the dentary and the symphysis. The hypertrophied caniniform is transversely narrow and high. Behind it, there is a small conical tooth not observed in the other specimens. As in *Notosuchus* the teeth are im-

planted in a groove instead of being in separate alveoli. Anteriorly the alveoli begin to close.

In the maxilla there is an enlarged and relatively wide area, slightly convex, with shallow pits and irregular furrows located behind the paracanine fossa (figure 2.B) at the level of the maxillary tooth row. This structure is unusual among crocodyliforms and would have been used for the intraoral treatment of food. Bonaparte (1991a) suggested the lack of anteroposterior movements in the lower jaws of *Comahuesuchus* due to the presence of the paracanine fossa and the close fit among maxilla and dentary. However, the ventral opening of the fossa is a little more than twice the anteroposterior diameter of the dorsal opening. This together with the lesser dimensions of the lower caniniform tooth would have allowed anteroposterior displacements. Moreover, the great development of the pterygoid wing and palatine fenestra denote the presence of highly developed muscles (pterygoideous muscles; Schumacher, 1973) capable of producing anteroposterior movement in the lower jaws. Additionally, in *Malawisuchus*, *Notosuchus* and

Chimaerasuchus the anteroposterior lengthening of the glenoid surface of the articular lacking a posterior transversal ridge, and in *Sphagesaurus* the wear facet on its teeth allows for anteroposterior movements in their lower jaws (Clark *et al.*, 1989; Gomani, 1997; Bonaparte, 1991a; Wu *et al.*, 1995; Wu and Sues, 1996; Pol, in press). In extant crocodylians the pterigoideous muscles are also strongly developed and are the main muscle responsible for jaw adduction (Busbey, 1989), but the presence of a posterior prominent transversal ridge in the deeply concave glenoid surface of the articular limit anteroposterior madibular movements. In *Comahuesuchus*, the jaw joint is yet unknown.

Variability

Comahuesuchus brachybuccalis is based on the holotype and three more specimens. The material here described differs from the holotype in having the following features: fused frontals; greater dorsal exposure of the premaxilla and supraoccipital; broader contact between prefrontal and frontal; a post-caniniform tooth in the lower jaw; and mandibular branches slightly divergent posteriorly. Because the new specimen of *Comahuesuchus* is about 25% larger than the holotype (MACN-N 30 and 31 have approximately the same size than MUCPV 202), these differences are considered to be the result either of a different stage of the ontogenetic development or as intraespecific variations.

Discussion

Comahuesuchus brachybuccalis was originally assigned to *Notosuchia*, within the grade Protosuchia (Bonaparte, 1991a). The proposal of including it inside Protosuchia was supported by plesiomorphic features present in the Notosuchia. These features are the "...amplia región basicraneana con un complejo sistema de cavidades neumáticas y posición relativamente anterior del ala de los pterigoides" (Bonaparte 1991a: 46). The inclusion of *Comahuesuchus* in Notosuchia was justified by the following features: "Basicráneo amplio, robusto, con cavidades neumáticas y amplio proceso ánteromedial del cuadrado en posición más ventral que el cóndilo occipital; cráneo de hocico corto, con órbitas grandes proyectadas lateralmente, y narinas de posición vertical; depresiones supratemporales axialmente largas, con la fenestra temporal ubicada en la mitad anterior, y diseño de las crestas parietales semejantes a las de Notosuchidae; similar morfología y proporciones de la región interorbitaria" (Bonaparte, 1991a: 58–59). Notosuchia was proposed by Gasparini (1971), to include two South American terrestrial mesosuchian families: Notosuchidae Dollo (*Notosuchus terrestris* Woodward) and Uruguaysuchidae Gasparini (*Uruguaysuchus aznarezi* Rusconi, *U. terrai*

Rusconi and *Araripesuchus gomesii* Price). This group has been proposed as polyphyletic because their members were not considered closely related in current phylogenetic analyses (e.g. Benton and Clark, 1988; Gasparini *et al.*, 1991; Clark, 1994; Ortega *et al.*, 2000). Subsequently, Ortega *et al.* (2000) erected the broader taxon Ziphosuchia that involves *Notosuchus* (and their close relatives), *Libycosuchus* and *Sebecosuchia*; and interpreted *Araripesuchus* (and possibly *Uruguaysuchus*) as sister taxon of Notosuchia. Later, Sereno *et al.* (2001) redefined Notosuchia using phylogenetic taxonomy, as a stem group composed by all crocodyliforms more closely related to *Notosuchus terrestris* than *Crocodylus niloticus*. In his analysis, this clade included *Araripesuchus* and *Sebecosuchia*.

In most phylogenetic analyses concerning basal crocodyliforms, *Comahuesuchus brachybuccalis* was not considered (e.g. Clark, 1994; Ortega *et al.*, 2000). Gomani (1997) excluded *Comahuesuchus* from the metasuchian clade (*sensu* Benton and Clark, 1988) because the presence of unfused frontals. However, the specimen reported here demonstrates that it is a doubtful or a possibly juvenile feature of the holotype. Also, Gomani (1997) interpreted erroneously that in *Comahuesuchus* the nasals do not reach the anterior end of the snout and that it lacks teeth posterior to the caniniform.

A cladistic analysis was performed to test the phylogenetic relationships of *Comahuesuchus brachybuccalis* among other basal crocodyliforms. The Late Triassic and Early Jurassic protosuchians *Hemiprotosuchus leali* (Bonaparte, 1971) and *Protosuchus richardsoni* (Colbert and Mook, 1951) were used as outgroup to root the tree. Ingroup taxa are *Comahuesuchus brachybuccalis*, *Notosuchus terrestris*, *Malawisuchus mwakasyungutiensis*, *Sphagesaurus huenei*, *Chimaerasuchus paradoxus*, *Simosuchus clarki*, *Anatosuchus minor*, *Araripesuchus* (*A. gomesii* and *A. patagonicus*) were used as representative taxa; Price, 1959; Hecht, 1991; Ortega *et al.*, 2000) and Peirosauridae (*Lomasuchus palpebrosus* and *Peirosaurus tormini*) were used as representative taxa; Gasparini *et al.*, 1991).

Fifty one cranial characters were used (Appendix 1), of which 21 (Ch. 1–21) were taken from Clark (1994); 5 (Ch. 22–26) from Wu and Sues (1996); 2 (Ch. 27–28) from Gomani (1997); 6 (Ch. 29–34) from Pol (in press); 12 (Ch. 37–48) from Ortega *et al.* (2000); and 3 (Ch. 49–51) from Buckely *et al.* (2000). Some of these characters were modified and two new characters were considered (Ch. 35–36). Characters were not weighted and the multi-state characters were treated as unordered. Autapomorphic characters for terminal taxa were excluded from the analysis.

The data matrix (Appendix 2) was analyzed with NONA version 2.0 (Goloboff, 1993) and edited with

Winclada (Nixon, 1999), using a heuristic search with 100 replication and multiple tree bisection–reconnection (TBR)(mult*max*) algorithms.

Two most parsimonious trees (L: 87; Ci: 0.64; Ri: 0.69) and the strict consensus (L: 88; Ci: 0.63; Ri: 0.68) (figure 5) were obtained. The most parsimonious trees differ only in the placement of *Comahuesuchus* as sister taxon of *Chimaerasuchus*, or *Notosuchus* plus *Sphagesaurus*.

All mesoeucrocodylian taxa (Node 1) share nine unambiguous features (Appendix 3). Within this clade two major groups are defined. Node 2 comprises *Anatosuchus* and *Araripesuchus* plus Peirosauridae (figure 5). They share three unambiguous features, including the presence of external cranial surface ornamented with circular and subpolygonal pits (Ch. 1), quadrate bearing only one fenestra (Ch. 13), and the maxillary tooth row with waves of size variation (Ch. 40).

Araripesuchus and Peirosauridae (Node 3) share the presence of a transversely expanded dentary, almost as wide as high, with convex lateroventral surface (Ch. 42). The close relationships between *Araripesuchus* and Peirosauridae was previously established (e.g. Ortega *et al.*, 2000; Buckley *et al.*, 2001), and also, they were considered sister taxa of Neosuchia (Clark, 1994; Ortega *et al.*, 2000), but because neosuchians were excluded from this analysis it does not test this hypothesis.

Anatosuchus minor, from the Aptian–Albian of Niger was recently described and included within the Comahuesuchidae family (Sereno *et al.*, 2003). This inclusion was supported by three features not clearly observed in *Comahuesuchus* or present in other basal crocodyliforms: a) the dorsal (nasal) and ventral (premaxillary) borders of the external nares inset posteriorly from the anterior margin of the snout; b) presence of diastemata in median upper and lower teeth; and c) anterior upper tooth row offset labially and ventrally from the dentary tooth row. The feature a) is not clear in the specimens available of *Comahuesuchus* because in all of them the anteromedial process of the premaxilla (i.e. the anterior floor of external nares) is badly preserved (MUCPv 202; MACN–RN 30 and 31) or absent (P 6131 MOZ). Median diastemata among maxillary and dentary teeth (feature b) are also well developed in sebecid (e.g. *Sebecus*; Colbert, 1946), and less notorious in the upper teeth of *Araripesuchus patagonicus* (Ortega *et al.*, 2000: figure 4.A) and some specimens of *Notosuchus* (e.g. MACN–N 24). The feature c) is shared with *Comahuesuchus* but as well as in other basal crocodyliforms (e.g. *Malawisuchus*, *Simosuchus*, *Notosuchus*, and *Araripesuchus*). *Anatosuchus* and *Comahuesuchus* resemble clearly in the dorsal shape and proportions of the skull, but many features in the lower and upper dentition (number and type of in-

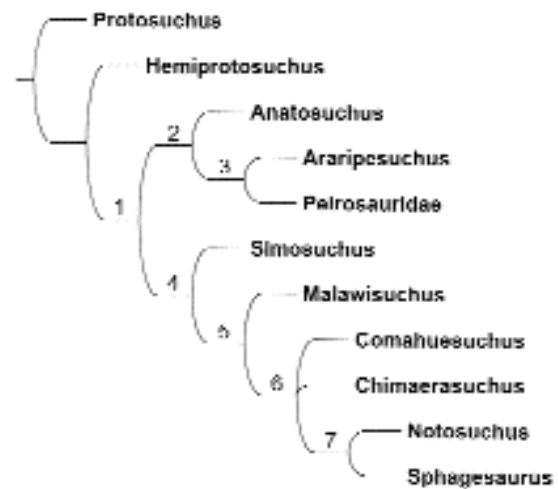


Figure 5. Strict consensus of the two most parsimonious trees obtained by NONA (Goloboff, 1993) and edited by Winclada (Nixon, 1999) (L: 88; Ci: 0.63; Ri: 0.68). The characters of each node are detailed in Appendix 3 / *Consenso estricto de los dos árboles más parsimoniosos obtenidos con NONA (Goloboff, 1993) y editados con Winclada (Nixon, 1999). Los caracteres de cada nodo son detallados en el Apéndice 3.*

plantement of teeth), mandibular symphysis (enlargement and dorsal exposure), palatal and skull roof areas allow to considered both genera as not closely related taxa. The inclusion of *Anatosuchus* within Comahuesuchidae is not supported by this cladistic analysis since *Anatosuchus* is depicted as more closely relative to *Araripesuchus* and Peirosauridae than to *Comahuesuchus* and other notosuchids.

Node 4 comprises a diverse assemblage of basal crocodyliforms that developed bizarre features in skull and dental elements. This node is diagnosed by having an unornamented region along the alveolar margin on the lateral surface of the maxilla and dentary bones (Ch. 24); and the presence of medially expanded quadrate condyles (Ch. 41). At this node, *Simosuchus* is the most basal member. Originally, this crocodyliform was nested with *Uruguaysuchus* and *Malawisuchus*, and four unequivocal and one equivocal synapomorphies diagnosed this node (Buckley *et al.*, 2000). They are the presence of a long process extending from the posterolateral edge of the squamosal; a cranioquadrate passage enclosed near the lateral edge of the skull by the quadrate, squamosal and otoccipital (unknown in *Uruguaysuchus*); and a retro-articular process that is attenuated and projects posteriorly from the ventral part of the mandible (Buckley *et al.*, 2000). Here, it is interpreted that in *Malawisuchus* the quadrate, squamosal, and exoccipital meet broadly lateral to the cranioquadrate passage (Gomani, 1997; contra Buckley *et al.*, 2000) (Ch. 14), as in most mesoeucrocodylians (Clark, 1994). The condi-

tion observed in *Simosuchus* (following Buckley *et al.*, 2000), is only present in thalattosuchians (Clark, 1994). Despite the similarities that *Simosuchus* and *Comahuesuchus* share in the shape of the skull, the detailed comparison shows remarkable differences between them and also with other notosuchids, especially in the structure and relationship of the palatine, the shape of the nasal and lachrymal, the contacts between maxilla–ectopterygoid and maxilla–prefrontal, the position of the wing of the pterygoid, the delimitation of the palatine fenestra, in the number and shape of the mandibular and maxillary teeth and in the structure of the mandibular symphysis.

The Node 5 (figure 5) is regarded as notosuchians. In *Malawisuchus*, *Chimaerasuchus*, *Comahuesuchus*, *Notosuchus*, and *Sphagesaurus* the external surface of the premaxilla and maxilla has two plane of exposure, one faces laterally (almost vertical) and the other dorsolaterally (almost horizontal) (Ch. 34); and the dentary extends beneath the mandibular fenestra (Ch. 20). Also, they have a reduced number of maxillary teeth (Ch. 25). At this node, unique among crocodyliform, the articular facet for the quadrate condyle is almost twice as long as wide and lacks a posterior transversely ridge (Ch. 22) (uncertain in *Comahuesuchus* and *Sphagesaurus*), that indicate capacity of fore–aft movement in the jaw and produce derived patterns of occlusion (Clark *et al.*, 1989; Wu *et al.*, 1995; Wu and Sues, 1996; Pol, in press). This node also is diagnosed by having less than five premaxillary teeth (Ch. 25; ambiguous) and the external nares confluent (Ch. 18; ambiguous).

Node 6 (figure 5) is diagnosed by having a notch in the premaxilla located on the laterodorsal edge of the external nares (Ch. 30); a contact between the ectopterygoid and the posterior part of the palatine, excluding the pterygoid from the palatine fenestra (Ch. 35; uncertain in *Chimaerasuchus* and *Sphagesaurus*); and the suture between the nasal and the frontal obliquely oriented (Ch. 36; uncertain in *Chimaerasuchus* and *Sphagesaurus*).

Notosuchus and *Sphagesaurus* (Node 7) only share one unambiguous feature: the presence of compressed maxillary teeth obliquely disposed (Ch. 33).

When *Comahuesuchus* is nested with *Chimaerasuchus* in one of two most parsimonious trees, they share the lack of contact between the nasal and the lachrymal (Ch. 5), only reported in the peirosaurid *Lomasuchus* (Gasparini *et al.*, 1991), and in the non-mesoeucrocodylian crocodyliforms *Orthosuchus* (Lower Jurassic of South Africa; Nash, 1975) and *Gobiosuchus* (Late Cretaceous of Mongolia; Osmólska and Buffetaut, 1997). In the phylogenetic analysis of Wu and Sues (1996), *Chimaerasuchus* was nested together with *Notosuchus* and *Malawisuchus*, while *Comahuesuchus* resulted to be more closely re-

lated to derived crocodyliforms than to notosuchian.

The current analysis nests *Comahuesuchus* within the notosuchian clade as was previously considered (Bonaparte, 1991a; Pol, in press). In addition to *Comahuesuchus* and *Notosuchus*, from the same geological unit was discovered another crocodyliform, *Cynodontosuchus rothi* (Woodward, 1896), based on an incomplete rostrum and anterior part of the lower jaws. At first, this species was considered as a closed relative taxon to *Notosuchus*, but posteriorly interpreted as a *Baurosuchidae* (Price, 1945, 1959; Gasparini, 1972). Some derived feature of *Comahuesuchus* (and other notosuchians) such as the lack of antorbital fenestra and reduced maxillary teeth are shared with *Cynodontosuchus* (and also with *Baurusuchus*), but both differs because the later taxon has an extremely laterally compressed rostrum, only three premaxillary teeth, the maxilla facing laterally, and a high mandibular symphysis (Gasparini, 1972). In the phylogenetic analysis of Buckley *et al.* (2000), *Comahuesuchus* is sister taxon of a Gondwanan clade that includes: ((*Notosuchus*, *Libycosuchus* (*Malawisuchus* (*Uruguaysuchus* + *Simosuchus*))) (*Sebecus* + *Baurusuchus*)). This hypothesis is taxonomically consistent with the Ziphosuchia clade proposed by Ortega *et al.* (2000) as well as with the Notosuchia clade of Sereno *et al.* (2001). South American taxa such as *Baurusuchus* and *Sebecus* were not considered in the analysis but clear affinities with the notosuchian group are observed (Pol, 1999, in press; Ortega *et al.*, 2000; Buckley *et al.*, 2000; Sereno *et al.*, 2001).

Conclusions

The description of this new specimen of *Comahuesuchus brachybuccalis* expands the knowledge of this form and provides new evidence about the Cretaceous diversification of notosuchians in Gondwana. *Comahuesuchus* represents a bizarre adaptative type among crocodyliforms, showing highly specialized features in the skull such as the presence of an extremely short and wide snout, a transversely wide and anteroposterioly elongated mandibular symphysis, robust upper and lower caniniforms, and a dorsally open paracanine fossa in the posterior region of the maxilla.

The phylogenetic analysis include *Comahuesuchus brachybuccalis* within the notosuchian clade, also represented by *Malawisuchus mwakasyungutiensis* and *Chimaerasuchus paradoxus* from the Early Cretaceous of Africa and China, and *Notosuchus terrestris* and *Sphagesaurus huenei* from the Late Cretaceous of South America.

With the exception of *Chimaerasuchus* (Wu and Sues, 1996), the remaining notosuchian species are

distributed among Gondwanan regions (South America and Africa) corroborating the hypothesis of a Cretaceous Gondwanan fauna (Bonaparte, 1986). This is also justified by the predominance of other groups such as abelisaurid theropods (e.g. Bonaparte, 1991b; Sampson *et al.*, 1998), titanosaurid sauropods (e.g. Bonaparte and Kielan-Jaworowska, 1987; Curry Rogers and Forster, 2001), madtsoiid snakes (e.g. Hoffstetter, 1961; Albino, 1996), pipid and "leptodactylid" frogs (e.g. Estes, 1975; Báez, 1987) and gondwanatherian mammals (e.g. Krause *et al.*, 1997). However, non-gondwanic records of some taxa such as notosuchians (e.g. *Chimaerasuchus paradoxus*, Lower Cretaceous of China; Wu *et al.*, 1995), titanosaurids (e.g. *Ophisthocelicaudia skarzynskii*, Late Cretaceous of China; Borsuk-Bialynicka, 1977), and madtsoiids (Late Cretaceous unnamed species from Spain and France; Rage, 1996; Sigé *et al.*, 1997), among others, are pointing that the paleobiogeography of Gondwana was more complex than previously known.

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Appendix 1

List of the characters used in the phylogenetic analysis. The original number of characters derived from other authors (see discussion) is indicated in brackets.

Character 1 (1) (modified by Ortega *et al.*, 2000) – Ornamentation of external surface of cranial dermal smooth or formed by grooves and ridges (0), or with circular to subpolygonal pits (1)

Character 2 (2) (modified) – Rostrum narrower anterior to orbits (0), or broad throughout (1)

Character 3 (7) – Palatal part of premaxilla do not meet posterior to incisive foramen (0), or meet posteriorly along contact with maxillae (1)

Character 4 (10) – Posterior ends of maxillae do not meet on palate anterior to palatines (0), or ends do meet (1)

Character 5 (11) – Nasals contact lachrymal (0), or do not (1)

Character 6 (15) (modified) – Descending process of prefrontal does not contact palate (0), or contacts palate and the process transversely expanded (1), or contact palate and the process transversely expanded in the dorsal part and columnar ventrally (2)

Character 7 (17) (modified) – Anterior part of jugal about twice as broad as posterior part (0), or as broad as posterior part (1)

Character 8 (23) (modified) – Frontal extends only slightly or not at all into supratemporal fossa (0), or extends well (1)

Character 9 (33) – Parietal with broad, sculpted region separating fossae (0), or with sagittal crest between supratemporal fossae (1)

Character 10 (36) – Posterior edge of squamosal nearly flat (0), or posterolateral edge of squamosal extends posteriorly as a long process (1)

Character 11 (40) (modified) – Palatal surface of pterygoid sculpted (0), or smooth (1)

Character 12 (41) – Pterygoids separate posterior to choanae (0), or are fused (1)

Character 13 (45) – Quadrate without fenestrae (0), or with a single fenestra (1), or with two or more fenestrae on dorsal and postero-medial surfaces (2)

Character 14 (49) – Quadrate, squamosal, and exoccipital do not meet to enclose cranioquadrate passage (0), enclose passage near lateral edge of skull (1), or meet broadly lateral to passage (2)

Character 15 (55) – Basisphenoid similar in length to basioccipital, with flat or concave ventral surface (0), or basisphenoid shorter than basioccipital (1)

Character 16 (59) – Cranial nerves IX–XI pass through common large foramen vagi in exoccipital (0), or cranial nerve IX passes medial to nerves X and XI in separate passage (1)

Character 17 (62) (modified) – Exoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (0), or supraoccipital forms dorsal edge of foramen magnum (1)

Character 18 (66) – External nares divided (0), or confluent (1)

Character 19 (67) (modified) – Antorbital fenestra about half the di-

ameter of the orbit (0), or much smaller than orbit (1), or absent (2)
Character 20 (70) (modified) – Dentary does not extend posteriorly beneath mandibular fenestra (0), or extend beneath fenestra (1)
Character 21 (78) (modified) – Posterior two premaxillary teeth much longer than anterior teeth (0), or similar in size (1)
Character 22 (23) – Articular facet for quadrate condyle wider than long and with pronounced posterior edge (0), or almost twice as long as wide and without posterior edge (1)
Character 23 (27) (modified by Ortega *et al.*, 2000) – Premaxilla with five or more teeth (0), or less teeth (1)
Character 24 (29) – Unsculptured region along alveolar margin on lateral surface of both maxilla and dentary absent (0), or present (1)
Character 25 (30) – Maxilla with eight or more teeth (0), or seven or fewer teeth (1)
Character 26 (31) – Maxillary tooth row extending posterior to anterior border of orbit (0), or terminating in front of orbit (1) in lateral view
Character 27 (4) (modified) – Prefrontals broad (0), or narrow and elongated (1)
Character 28 (46) (modified by Buckley *et al.*, 2000) – Maxillary teeth multicusped: absent (0), in one longitudinal row (1), or in three longitudinal rows (2)
Character 29 (122) – Jugal does not exceed the anterior margin of the orbit (0), or exceeds (1)
Character 30 (123) – Notch in the premaxilla, at 2/3 height of the lateral vertical margin of the external nares: absent (0), or present (1)
Character 31 (133) – Anterior process of ectopterygoid, developed (0), or reduced-absent (1)
Character 32 (134) – Posterior process of ectopterygoid, developed (0), or reduced-absent (1)
Character 33 (137) – Compressed crown of maxillary teeth oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1)
Character 34 (139) – Maxilla and premaxilla with one vertical plane of exposure (0), or one plane laterally (tall) and other dorsolaterally exposed (1)
Character 35 – Ectopterygoid does not contact posterior part of palatine (0), or contacts palatine, excluding the pterygoid of the posterior edge of the fenestra palatina (1)
Character 36 – Nasal-frontal suture transversely oriented (0), or obliquely oriented (1)
Character 37 (18) (modified) – Relative position of the last maxillary tooth with anterior edge of palatine fenestra: last maxillary tooth anterior to the level of the anterior edge of palatine fenestra (0), or last maxillary tooth posterior to the level of the anterior edge of palatine fenestra (1)
Character 38 (19) (modified) – Dental upper implantation: teeth set in isolated alveoli (0), or teeth set disposed in a groove (1)
Character 39 (19) (modified) – Dental lower implantation: teeth set in isolated alveoli (0), or teeth set disposed in a groove (1)
Character 40 (20) – Size of maxillary teeth: all maxillary teeth similar in size or with the largest alveolus placed at middle of maxillary

row (0), or tooth row with waves of size variation (1)
Character 41 (53) – Quadrate condyles: almost aligned (0), or medial condyle expands ventrally (1)
Character 42 (81) – Mandibular compression: dentary compressed, formed by almost vertical lateral and medial laminae (0), or dentary transversely expanded, almost as wide as high, and with convex lateroventral surface (1)
Character 43 (132) – Heterodonty of maxilla and dentary teeth: homodonty (0), or with different dental morphologies (heterodonty) (1)
Character 44 (139) – Depression on primary pterygoidean palate posterior to internal nares: depression wider than palatine bar (0), or narrower than palatine bar between palatal fenestrae (1)
Character 45 (147) – Medial shelf of retroarticular process: vertical and facing medially (0), or facing dorsally (1)
Character 46 (156) – Teeth at the anterior part of the maxilla: no prominent tooth (0), or second or third alveoli enlarged (1), or fourth or fifth alveoli enlarged (2)
Character 47 (175) – Palatal surface concave (0), or plane (1)
Character 48 (176) – Occipital condyle posteriorly directed (0), or posteroventrally directed (1)
Character 49 (115) – Vomer exposed (0), or not exposed (1) on palate
Character 50 (116) – Posterior cheek teeth conical (0), or laterally compressed (1), or strongly spatulate (2)
Character 51 (117) – Cheek teeth not constricted at the base of crown (0), or constricted (1)

Appendix 3

Characters and character states defining the nodes in the strict consensus of two most parsimonious trees shown in Figure 5. Equivocal characters are indicated with an asterisk (*).

Node 1: (Mesoeucrocodylia): 9(0); 10(1); 11(1); 14(2); 16(1); 19(1); 27(1); 29(1); 48(1).
Node 2: 1(1); 13(1); 21*(1); 40(1); 46*(1); 47*(1).
Node 3: 42(1).
Node 4: 24(1); 41(1).
Node 5: (Notosuchia): 18*(1); 20(1); 22(1); 23*(1); 25(1); 34(1).
Node 6: 30(1); 35(1); 36*(1).
Node 7: 7*(0); 33(1).

Abbreviations: **An**, angular; **C**, caniniform; **ca**, caniniform alveolus; **ch**, choanal opening; **D**, dentary; **dp**, depression for the palpebral bone; **Ect**, ectopterygoid; **fi**, foramen intermandibularis caudalis; **fmax**, foramen of the maxilla; **Fr**, frontal; **i**, lower incisivi-form; **J**, jugal; **L**, lachrymal; **M**, maxilla; **mpalf**, maxilla-palatine fenestra; **N**, nasal; **P**, parietal; **Pal**, palatine; **palf**, palatine fenestra; **pc**, paracanine fossa; **Pfr**, prefrontal; **Pm**, premaxilla; **pn**, premaxillary notch; **Po**, postorbital; **Pt**, pterygoid; **s**, symphysis; **Soc**, supraoccipital; **Spl**, splenial; **Sq**, squamosal; **stf**, supratemporal fenestra; **vf**, vascular foramen.

Appendix 2

Distribution of character states. “0” denotes primitive character state, “1” and “2” derived character states, “?” missing information or uncertain character states.

	1	2	3	4	5
<i>Protosuchus</i>	1234567890	1234567890	1234567890	1234567890	12345678901
<i>Hemiprotosuchus</i>	0000?00010	0020100000	0000000000	??00010000	0000?000?00
<i>Notosuchus</i>	00?0?01110	0?20100000	?0?0000000	?0?0?10000	000?0000?00
<i>Malawisuchus</i>	011010000	1122010101	0111110011	1011110110	10000001110
<i>Comahuesuchus</i>	00?10?1001	1122?10111	0111101100	?010000000	10100101111
<i>Sphagesaurus</i>	01?11?1000	1???0?0121	1?11111011	0101110010	101??101100
<i>Chimaerasuchus</i>	00?1?0?0??	11?0?0?12?	0?1111?011	1111?00000	??1?0?1?1??
<i>Simosuchus</i>	00??1?????	???????111	0111111211	?01???0000	?01?00?1?0
<i>Anatosuchus</i>	01100?1101	1101110010	0001011110	1100000000	1010?001021
<i>Araripesuchus</i>	10?1?21000	111?1??110	1000001010	?000001001	?00??111100
<i>Peirosauridae</i>	1011021100	1112110010	1010001010	?000001001	01111111110
	1111120100	111211001?	10000110?0	?0000010?1	?111?110110