



## THE FIRST “PROTOSUCHIAN” (ARCHOSAURIA: CROCODYLIFORMES) FROM THE CRETACEOUS (SANTONIAN) OF GONDWANA<sup>1</sup>

(With 16 figures)

LUCAS E. FIORELLI<sup>2</sup>  
JORGE O. CALVO<sup>3</sup>

**ABSTRACT:** The remains of “protosuchians” from the Cretaceous come, to exception of “Las Hoyas crocodyliform” from the Lower Cretaceous of Spain, exclusively of Central Asia: *Zaraasuchus*, *Gobiosuchus*, *Zosuchus*, and *Artzosuchus* from the Upper Cretaceous of Mongolia; *Tagarosuchus* from Lower Cretaceous of Southern Siberia; *Edentosuchus*, *Sichuanosuchus*, and *Shantungosuchus* from Lower Cretaceous of China. We report a new basal crocodyliform taxon, *Neuquensuchus universitas* gen.nov., sp.nov., from Neuquén Province, Argentina, belonging to Bajo de la Carpa Formation, representing the first and only “protosuchian” from the Cretaceous of Gondwana. The articulated and fragmentary materials belonged to a willowy, slender species, with very long and thin extremities. As in *Shantungosuchus*, the cervical centers are lengthened, with prominent ventral keel and well developed anteroventral parapophyses. As in basal crocodylomorphs, it possesses two sacral vertebrae. Also, a much enlarged scapular blade, with well developed acromial ridge and the posterior edge similar to *Sichuanosuchus*. The pronounced deltopectoral crest in the complete humerus is equivalent to *Sichuanosuchus* and as this, a circular, elongated and thin shaft with the medial condyle longer than the lateral one. Also, the complete ulna and radius is similar in their proportions to *Sichuanosuchus*. As this, the pubis is lengthened, very thin in the half section and not very expanded distally. The femur, tibia and fibula are elongated and similar to other non-derived crocodyliforms. Besides representing the first Cretaceous “protosuchian” of Gondwana, the occurrence of these outside of Asia and Europe during the Cretaceous offers new evidence of pre-Albian dispersion between Gondwana and Central Asia through Europe.

**Key words:** Crocodylomorpha. Protosuchian. *Neuquensuchus universitas* gen.nov., sp.nov. Cretaceous. Gondwana.

**RESUMEN:** El primer “protosuquio” (Archosauria: Crocodyliformes) del Cretácico (Santoniano) de Gondwana. Los restos de “protosuquios” del Cretácico provienen, a excepción del “crocodyliforme de Las Hoyas” del Cretácico Inferior de España, exclusivamente de Asia Central: *Zaraasuchus*, *Gobiosuchus*, *Zosuchus* y *Artzosuchus* del Cretácico Superior de Mongolia; *Tagarosuchus* del Cretácico Inferior del sur de Siberia; *Edentosuchus*, *Sichuanosuchus* y *Shantungosuchus* del Cretácico Inferior de China. Aquí reportamos un nuevo taxón de crocodyliforme basal, *Neuquensuchus universitas* gen.nov., sp.nov., de la provincia de Neuquén, Argentina, correspondiente a la Formación Bajo de la Carpa, representando el primer y único “protosuquio” del Cretácico de Gondwana. Los materiales fragmentarios y articulados corresponden a una especie esbelta y delgada, con extremidades largas y delgadas. Al igual que en *Shantungosuchus*, los centros cervicales son alargados, con una quilla ventral prominente y parapófisis anteroventrales bien desarrolladas. Como en los crocodyliformes basales, *Neuquensuchus* posee dos vértebras sacras. Además, una hoja escapular muy expandida, con un puente acromial bien desarrollado y el borde posterior similar a *Sichuanosuchus*. La cresta deltopectoral pronunciada en el húmero es equivalente a la de *Sichuanosuchus* y al igual que este, la diáfisis es circular, alargada y delgada con el cóndilo medial mayor que el lateral. Asimismo, las proporciones del radio y la úlna son similares a *Sichuanosuchus*. Como este, el pubis es alargado, muy delgado en su sección media y poco expandido distalmente. El fémur, tibia y fibula son alargados y similares a otros crocodyliformes no derivados. Además de representar el primer “protosuquio” cretácico de Gondwana, su presencia fuera de Asia y Europa durante el Cretácico ofrece nueva evidencia de un evento de dispersión pre-Albiano entre Gondwana y Asia Central a través de Europa.

**Palabras clave:** Crocodylomorpha. Protosuquio. *Neuquensuchus universitas* gen.nov., sp.nov. Cretácico. Gondwana.

<sup>1</sup> Submitted on September 14, 2006. Accepted on October 24, 2007.

<sup>2</sup> Centro Regional de Investigaciones Científicas y Transferencia Tecnológica (CRILAR). Entre Ríos y Mendoza s/n, CP 5301, Anillaco, La Rioja, Argentina.  
E-mail: lfiorelli@crilar-conicet.com.ar.

<sup>3</sup> Centro Paleontológico Lago Barreales (CePaLB), Universidad Nacional del Comahue. Ruta Provincial 51, km 65, Neuquén, Argentina.

## INTRODUCTION

Fossil remains of basal non-Metasuchia Crocodyliformes from Cretaceous come almost exclusively from the Asian continent, to exception of “Las Hoyas Crocodyliform” (SANZ *et al.*, 1988) (Fig.1) from the Lower Cretaceous of Las Hoyas, Spain (upper Barremian; DIEGUEZ *et al.*, 1995). The Asian forms are represented by species coming from China, Mongolia and Russia. From China comes *Edentosuchus tienshanensis* (YOUNG, 1973; POL *et al.*, 2004), a Protosuchia from the Lower Cretaceous of Tugulu Group, Xinjiang; *Shantungosuchus hangjinensis* (WU *et al.*, 1994) from the Luohandong Formation, Zhidan Group, Inner Mongolia and *Sichuanosuchus shuhanensis* (WU *et al.*, 1997) from an uncertain locality of Sichuan. From Mongolia come forms belonging to the Campanian age. *Gobiosuchus kielanae* (OSMÓLSKA, 1972; OSMÓLSKA *et al.*, 1997) comes from the Bayan Zak locality; *Gobiosuchus* (?) *parvus* (EFIMOV, 1983), later considered conspecific of *G. kielanae* (OSMÓLSKA *et al.*, 1997), comes from Üüden Sair locality; *Zosuchus davidsoni* (POL & NORELL, 2004a) and *Zaraasuchus shepardi* (POL & NORELL, 2004b) come from Zos Canyon locality; *Artzosuchus brachicephalus* (EFIMOV, 1983), a very fragmentary form of uncertain filiation, comes from the same locality that *G. (?)parvus*. Lastly, *Tagarosuchus kulemzini* (ALIFANOV *et al.*, 1999), with practically complete skull, comes from the Lower Cretaceous of Shestakovo locality, South Siberia.

Here we present a new basal form of crocodyliform from the Upper Cretaceous of Northern Patagonia, Neuquén Province, Argentina. The remains come from the Bajo de la Carpa Formation, Neuquén Group (Fig.2), and represent the first “protosuchian” form for the Cretaceous of Gondwana. In this paper, we describe the anatomy of this new Crocodyliform together with a parsimony analysis of their phylogenetic relationships.

## MATERIAL AND METHODS

The remains were found and gathered by Mr. Oscar de Ferrariis (at that time Director of the Museum of the National University of Comahue), together with J.O.C. The materials of this new basal crocodyliform were originally referred as *Notosuchus* (MUCPv-137) and were collected in 1987. The study of the museum collection allowed us to find one more specimen represented by fragmentary postcranial material but in good preservation (Fig.3).

Institutional abbreviations: GMPKU, Geological Museum, School of Earth and Space Sciences, Peking University, Beijing, People’s Republic of China; IGM, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People’s Republic of China; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MUCP, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; UNC, Department of Geological Sciences, University of North Carolina at Chapel Hill; ZDM, Zigong Dinosaur Museum, Zigong, Sichuan, China; ZPAL, Instytut Paleobiologii PAN, Warszawa, Poland.

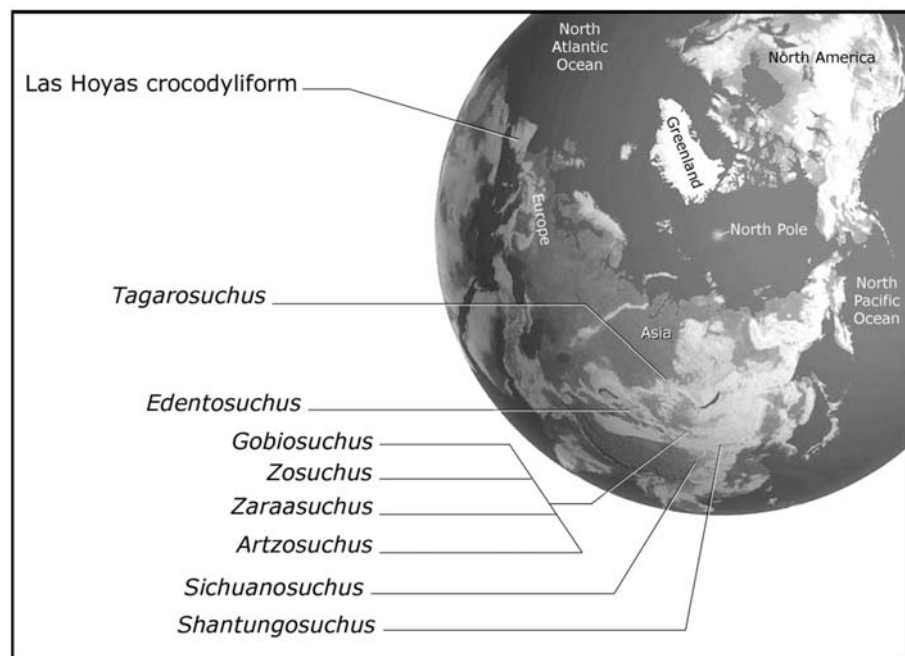


Fig.1- Map of Eurasia showing the places of origin of the species of Cretaceous protosuchians.

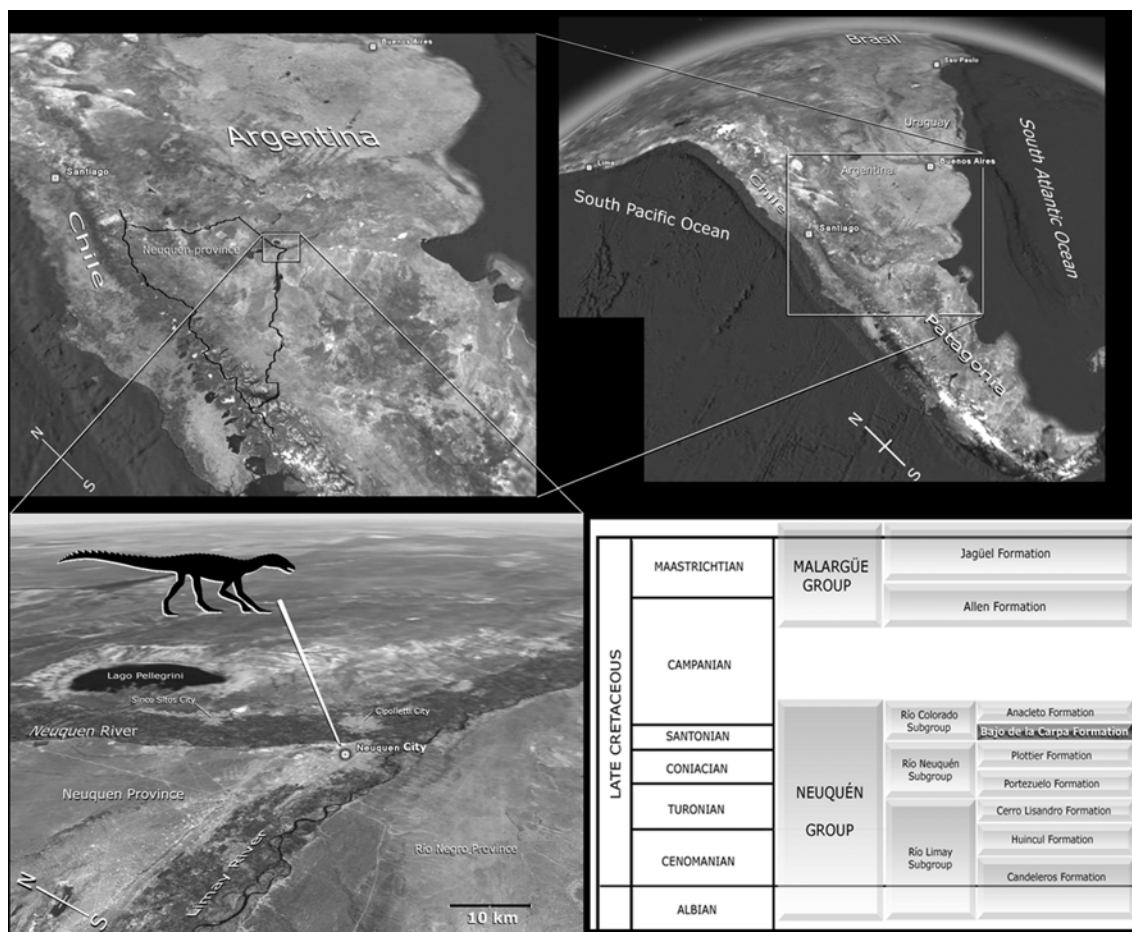


Fig.2- Up right: satellital map showing the location of Argentina and Patagonia in South America; up left: satellital map of Northpatagonic region, showing the location of the Neuquén Province; below left: area of Comahue where were found and collected the materials of *Neuquensuchus universitas*, gen.nov., sp.nov. (scale bar = 10km - right inferior bar). Below right: stratigraphy of the Cretaceous of Neuquén Basin and stratigraphic column of the Neuquén Group (based on LEANZA *et al.*, 2004). (Satellital images taken from GoogleEarth).

## RESULTS

### GEOLOGY

The Río Colorado subgroup constitutes the top of the Neuquén Group; it is widely distributed in the South of the Neuquén Basin. The subgroup is divided in two formations: Bajo de la Carpa (lower) and Anacleto (upper) (LEANZA *et al.*, 2004) (Fig.2). Bajo de la Carpa Formation is composed of coarse-grained, light violet and pink sandstones of fluvial origin. The age has been dated as Santonian (LEANZA *et al.*, 2004) (Fig.2).

Outcrops in the area have given a wide variety of fauna such as carnosaurine abelisaurid theropod (PORFIRI & CALVO, 2006) and the avian

dinosaur *Alvarezsaurus calvoi* BONAPARTE, 1991 and *Velocisaurus unicus* BONAPARTE, 1991; sauropod dinosaurs as cf. *Laplatasaurus* (LEANZA *et al.*, 2004), Titanosauridae indet. (CHIAPPE & CALVO, 1994; pers.obs.), *Neuquensaurus* sp. (pers.obs.), *Antarctosaurus* and the peculiar beaked sauropod *Bonitasaura salgadoi* APESTEGUÍA, 2004. Birds as *Neuquenornis volans* CHIAPPE & CALVO, 1994 and *Patagopteryx deferrariisi* ALVARENGA & BONAPARTE, 1992, snakes as *Dinilysia patagonica* WOODWARD, 1901, bird eggs in nests (SCHWEITZER *et al.*, 2002), dinosaur eggs named *Megaloolithus patagonicus* CALVO *et al.*, 1997. Crocodyles are represented by *Notosuchus terrestris* WOODWARD, 1896, *Comahuesuchus brachybuccalis* BONAPARTE, 1991,

*Cynodontosuchus rothi* WOODWARD, 1896, and postcranials articulated remains of a new peirosaurian crocodyliform (FIORELLI *et al.*, 2007). The remains of this new “protosuchian” have been gathered on the South margin of Neuquén River (North Neuquén City) increasing the number of crocodyliforms found in the formation.

#### SYSTEMATIC PALEONTOLOGY

Crocodylomorpha WALKER, 1970

Crocodyliformes HAY, 1930

(*sensu* BENTON & CLARK, 1988)

Mesoeucrocodylia WHETSTONE & WHYBROW, 1983

*Neuquensuchus universitas*, nov. gen. et nov. sp.

Etymology – Generic name “Neuquén” in reference to the Neuquén City; “suchus”, Greek for crocodile. Specific name “universitas” in reference to the university campus, where the

materials were collected.

Holotype – MUCPv-47 (Fig.3). Six cervical vertebrae, first four dorsal vertebrae, two sacral vertebrae and first five caudal vertebrae. Posterior cervical ribs and anterior dorsal ribs. Fragmentary right scapula, humerus, ulna and rights radius; left scapula and humerus. Right pubis, fragment of right ischium, femur, tibia and right fibula; fragment of the left ilium.

Referred specimens – MUCPv-161 (Fig.3). Proximal end of left tibia, distal end of left fibula and left astragalus.

Type locality – The remains were found in the North of the Neuquén City on the campus of the Universidad Nacional del Comahue (National University of Comahue), Neuquén Province, Argentina (Fig.2).

Type horizon – Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (Santonian; LEANZA *et al.*, 2004) (Fig.2).

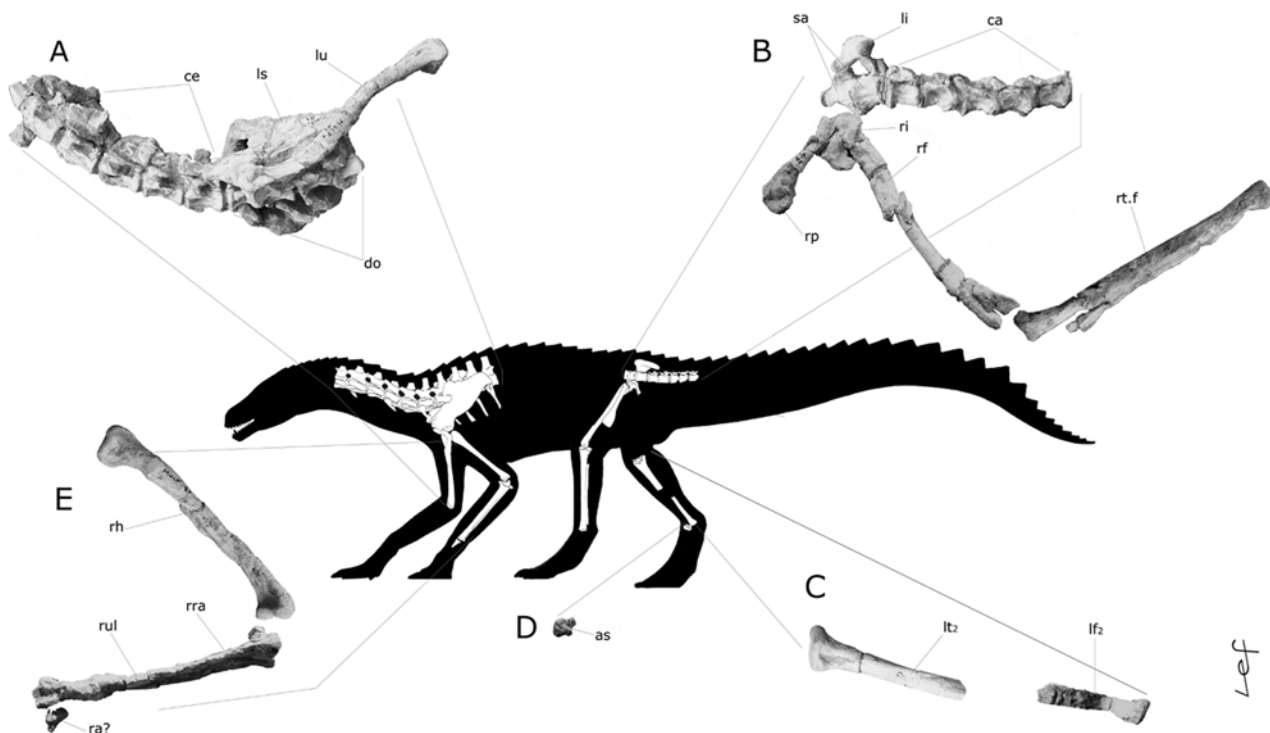


Fig.3- *Neuquensuchus universitas* gen.nov., sp.nov. Referred material. MUCPv-47 (holotype): A, B and E; MUCPv-161 (referred specimens): C and D. A, cervical vertebrae, first dorsal vertebrae, left scapula and left humerus. B, sacral and first caudal vertebrae and right pubis, ischium, femur, tibia and fibula. C, left tibia and fibula. D, left astragalus. E, right humerus, ulna, radius and radial. (Abbreviations in the Appendix IV).

Diagnosis – Relatively small, thin and slender crocodyliform, diagnosed by the following combination of poscranial characters: lengthened cervical vertebrae with low ventral keel, parapophysis and diapophysis anteroposteriorly lengthened. Neural spines elongated in dorsal vertebrae, with their centra lengthened without ventral keel but with a very low anterior hypapophysis. Two laterally enlarged sacral vertebrae. First caudal vertebra with a tenuous opisthocoealous and elongated anterior caudal vertebra, relatively low. Scapula with an important dorsal expansion and a good development of the posterodorsal hook. Humerus with a good development of the lateroproximal expansion, long and thin diaphysis of the humerus with the medial condyle biggest than the lateral one. Very lengthened and thin ulna, with olecranon process. Very thin and proximally expanded radius. Thin and long pubis with a very light distal expansion. Non-sigmoid and lengthened femur, smaller than the tibia.

#### DESCRIPTION AND COMPARISONS

##### AXIAL SKELETON

The specimen MUCPv-47 of *Neuquensuchus universitas* possesses incomplete axial remains but in good preservation state. It includes the last six

articulate cervical vertebrae with the first four dorsal, two sacral vertebrae and relatively well preserved five anterior caudal vertebrae that are articulated to the sacral vertebra.

Regarding the cervical section (Fig.4), this specimen possesses a relatively long and thin neck, similar to those other basal crocodylomorphs, as for example *Terrestriusuchus* (CRUSH, 1984) and *Gobiosuchus* (OSMÓLSKA *et al.*, 1997). On the cervical sequence, the first one, here considered the fourth, is incomplete, preserving just the posterior portion of the centrum (Fig.4). All cervical vertebrae and preserved dorsal are slightly amphicoelous. The long and thin cervical centra are parallelogram-shaped in lateral view, with an elevation of the anterior face of the centrum, similarly to *Terrestriusuchus* (CRUSH, 1984), *Dibothrosuchus elaphros* (WU & CHATTERJEE, 1993), *Zaraasuchus* (POL & NORELL, 2004b, IGM 100/1321), *Shantungosuchus* (YOUNG, 1961, IVPP V2484; WU *et al.*, 1994, IVPP V10097) and other cervicals of Crocodylia (ROMER, 1956; HOFFSTETTER & GASC, 1969). *Neuquensuchus* possess medially constricted, well marked cervical centra, similar to some basal crocodyliforms, such as *Zaraasuchus* (POL & NORELL, 2004b) and *Shantungosuchus* (YOUNG, 1961; WU *et al.*, 1994) and different to other protosuchids and mesoeucrocodylians, as *Edentosuchus* (LI, 1985) and *Notosuchia* (WU & SUES, 1996; FIORELLI, 2005; POL, 2005), that possess short and compressed cervical centra, without medial constriction.

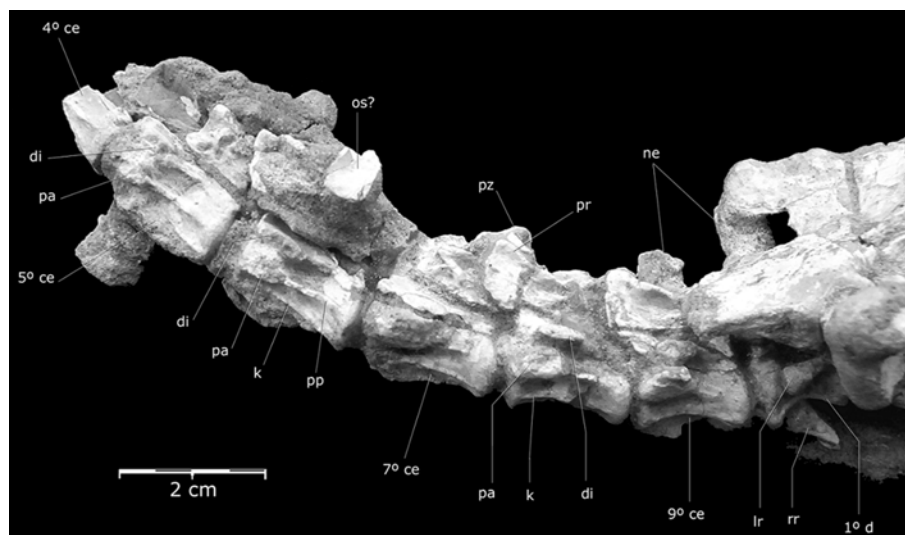


Fig.4- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Cervical vertebrae in left lateral view. (Abbreviations in the Appendix IV).

This structure indicates wide lateral movements of the long neck in this basal patagonian crocodyliform. In another sense, each one of the cervical centra possesses a long keel that runs anteroposteriorly in the whole ventral surface, forming deep furrows toward both sides of this and ventrally to the parapophysis (Figs.5B, 5C, 5D). Even so, the ninth centrum also possesses a less marked and lower keel, with shallow lateral furrows than those present in anterior cervicals. These keels are similar to those observed in “protosuchians” and notosuchians, like in the axis of *Shantungosuchus hangjinensis* (WU *et al.*, 1994, IVPP V10097), in the cervical vertebrae of *Protosuchus* (COLBERT & MOOK, 1951), *Sichuanosuchus huidongensis* (PENG, 1996), *Notosuchus* (POL, 2005; FIORELLI, 2005, MACN-RN 1037 and MUCPv-137) and *Chimaerasuchus* (WU & SUES, 1996, p.692-693, IVPP V8274) but the long extension is a plesiomorphic character. The parapophysis are very wide, well developed and robust with a lengthened articulate facet for the capitulum of the cervical ribs (Figs.5C, 5D). The articulated facets of these parapophysis possess an antero-lateroventral direction, similar to other basal crocodylomorphs as in the first cervical ones of *Terrestriusuchus* (CRUSH, 1984), in the posterior cervical vertebra of *Zaraasuchus* (POL & NORELL, 2004b) or in the axis of *Shantungosuchus* (YOUNG, 1961; WU *et al.*, 1994). Lateroventrally projected parapophysis of *Neuquensuchus universitas* possesses a long parapophyseal ridge posteriorly. Posterior cervical vertebrae have the surfaces for the capitulum enlarged and lengthen, covering practically the anterior half of the extensive centrum (Fig.5D). Between the parapophysis and diapophysis there is a prolonged depression, this character has been recorded in *Zaraasuchus* (POL & NORELL, 2004b) and *Protosuchus* (COLBERT & MOOK, 1951). The diapophyses are lengthened in the first cervical vertebra and they are anteriorly located below the neurocentral sutures. Nevertheless, in the seventh cervical, the diapophyses are anteroventrally located on the suture. In the eighth cervical, the diapophysis spreads rounding the tubercular process. Lastly, in the ninth cervical, the diapophysis is located more dorsally, as in *Terrestriusuchus*. All cervicals possess an important postdiapophyseal ridge, like in *Zaraasuchus*. The neural spines are not complete but they seem to be high and dorsoventrally lengthened, centrally located in the neural arches, contrary to the posterior cervical vertebrae of *Zaraasuchus* (POL &

NORELL, 2004b). Laterally, in the base of the neural spines, there is a cavity between the pre and postzygapophysis, nearly delimited by a small developed suprapostzygapophyseal lamina (Fig.5A). Prezygapophysis and postzygapophysis, in dorsal view are robust, laterally high and slightly curved laterally. Prezygapophysis articulate facets are dorsomedially directed and postzygapophysis articulate facets are lateroventrally directed, like in *Zaraasuchus*. Ventrally, the prezygapophysis possesses a well developed lamina posteroventrally directed, that continues with the anterior border of diapophysis; it directs anterodorsally the prezygapophysis base (Fig.5D). There is a very marked border, that extends toward posterior among the articular facets of the pre and postzygapophysis, on the whole lateral surface of the neural pedicelous. Similar condition has been observed in *Zaraasuchus* (Fig.5D).

Regarding the dorsal vertebrae, only the first four have been preserved, with their corresponding articulate ribs (Fig.6). It is observed that these dorsals, corresponding to the tenth to twelfth vertebrae, possess the same anteroposterior length, but they fall in relation with the posterior cervical ones. In *Notosuchus* and other *Metasuchia* there is a light increase in the longitude of the tenth (last cervical in *Notosuchus*) and eleventh dorsal centrum, compared with the short cervical ones (POL, 2005; FIORELLI, 2005). All the centra are amphicoelous and strongly constrained in the half section. Therefore, proximal and distal facets are very wide and inflated (Figs.6C, 6D) like in *Sichuanosuchus huidongensis* (PENG, 1996). The first dorsal vertebra does not possess a ventral keel and a true reduced hypapophysis appears (Fig.6D). In the first two dorsal vertebrae, the parapophyses are anteriorly located, ventrally directed and rounded. The third dorsal vertebra has the parapophysis small and dorsoventrally longer. Diapophyses are well developed. The cavities in the base of the neural spines are wider and shallower, not very deep but limited posteriorly by high and well-developed suprapostzygapophyseal laminae (Figs.6A, 6B). In lateral view, neural spines in anterior dorsals are very elongated and laminar (Figs.6A, 6B).

In MUCPv-47, the poorly preserved sacral vertebrae are articulated with the anterior five caudals (Fig.7). They are jointed by a suture. Centra are short and very wide, flat and massive. (Figs.7C, 7E). The preserved transverse processes seem to have been wide, similar to those of basal crocodylomorphs as *Dromicosuchus* (SUES *et al.*, 2003).

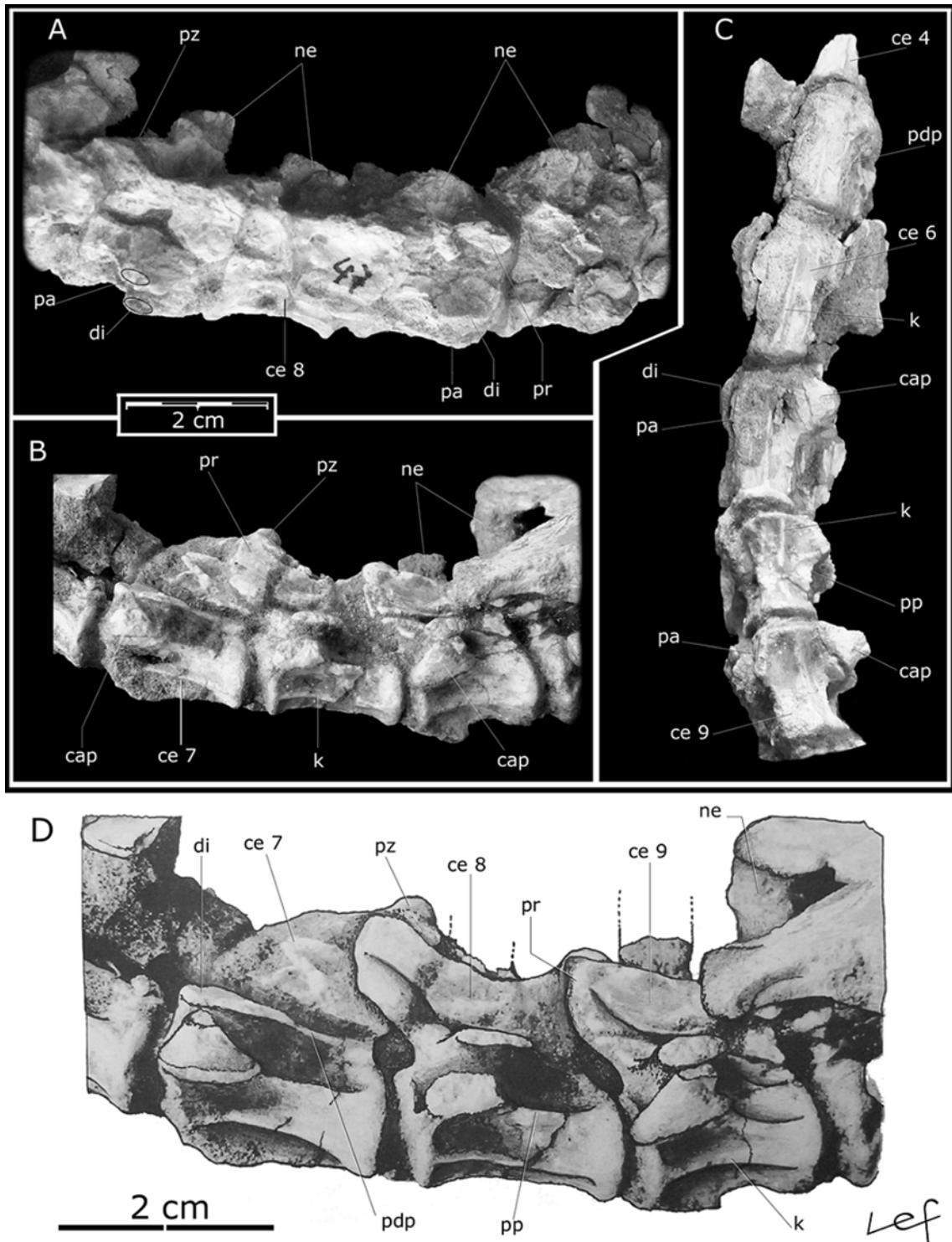


Fig.5- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Posterior cervical vertebrae. A, right lateral view; B and D, left lateral view; C, ventral view. (Abbreviations in the Appendix IV).

Anterior caudals correspond to the five firsts (Figs.7A, 7B). Just centra and some pre and postzygapophyses are preserved; they are more rounded and lengthened than in *Notosuchus*. In *Neuquensuchus universitas* centra are similar to the first caudal vertebrae of *Shantungosuchus* (Wu *et al.*, 1994) and other basal crocodyliforms. The first caudal possesses a centrum very slightly opisthocoelic. Transverse processes in the second and third caudals are slightly square in transverse section and they placed at the same level than the zygapophysis. Pre and postzygapophyses, in caudals, do not possess an extensive dorsal development as those in *Notosuchus* and other notosuchian and neosuchian, such as in *Mahajangasuchus* (BUCKLEY & BROCHU, 1999) and Dyrosauridae (SCHWARZ *et al.*, 2006). Articulation surfaces of the

prezygapophysis, in the third and fourth caudals, are inclined ventromedially. Hemals arches have not been preserved but the articulated surfaces for the same one appear from the second caudal vertebra.

#### APPENDICULAR SKELETON

MUCPv-47 includes both scapulae, the left humerus (Fig.6), ulna and right radius, left ilium, right pubis, proximal right ischium, femur, tibia and fragment of the right fibula. MUCPv-161 includes a very well preserved proximal left tibia, distal left fibula, and fragmentary remains of tarsus – left astragalus (Fig.3). It is referred to *Neuquensuchus* due to their characters and similar proportions with MUCPv-47.

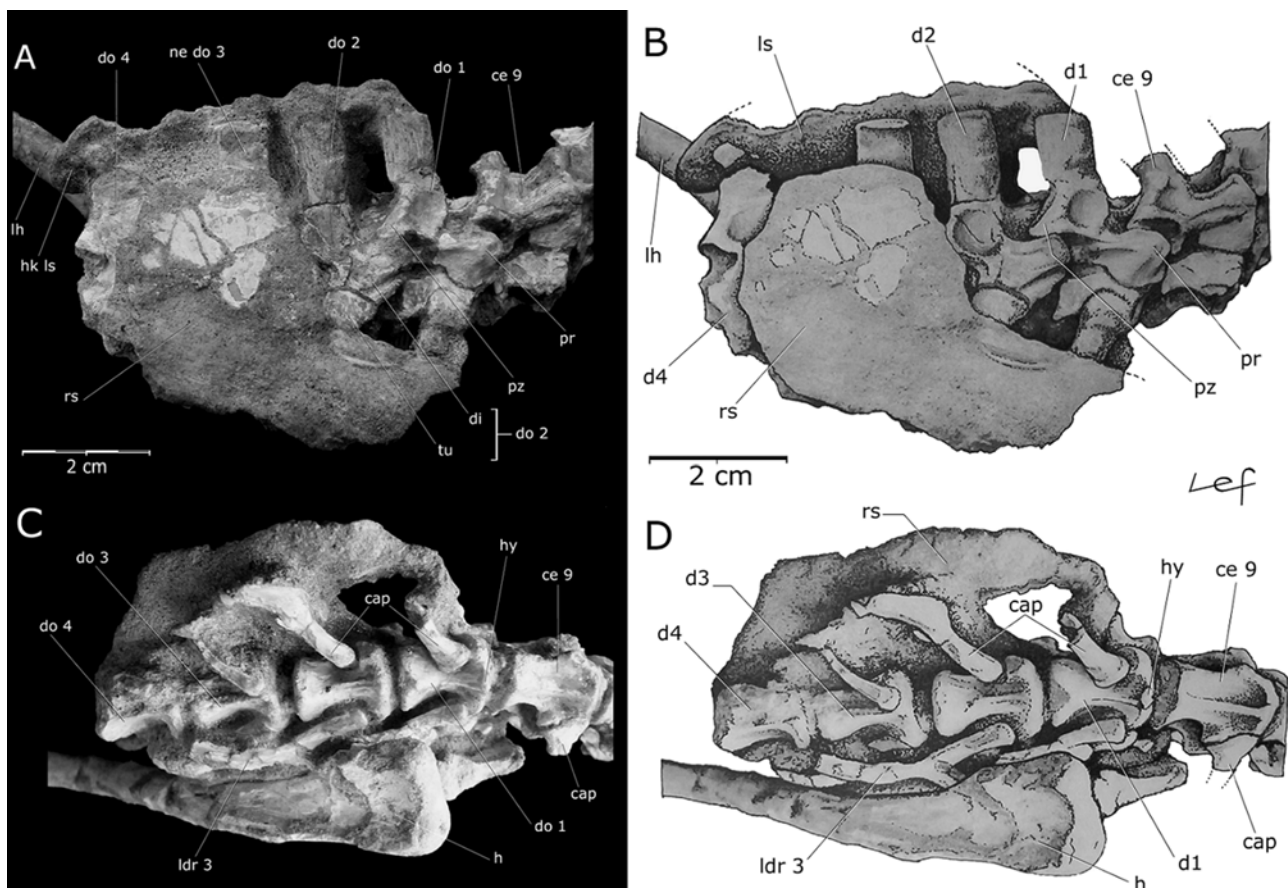


Fig.6- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. First dorsal vertebrae. A and B, right lateral view; C and D, ventral view. (Abbreviations in the Appendix IV).



## SCAPULA

The scapula of *Neuquensuchus universitas* (Figs. 6, 8) is quite similar to that of *Notosuchus* (POL, 2005; FIORELLI, 2005) and *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). However it differs from *Notosuchus* in having a less marked constriction above the ventral expansion and a slender dorsal expansion. In notosuchians the dorsal expansion is very developed and more anteroposteriorly extensive (POL, 2005; FIORELLI, 2005). As in *S. shuhanensis*, *Neuquensuchus universitas* has the anterior concave border of the scapular blade wider than the posterior one and a well-developed acromial ridge, extended along the anterior margin of ventral portion (Fig. 8). The hook, or projection in the posterodorsal vertex, is posteriorly directed and the dorsal border is convex. It is only shared with *Sichuanosuchus shuhanensis* (WU *et al.*, 1997) and also in part with *Sichuanosuchus huidongensis* (PENG, 1996). The hook is also visible in some sphenosuchians as in *Pseudhesperosuchus* but in this Triassic crocodylomorph the posterior border is much wider and it tapers abruptly and more centrally (BONAPARTE, 1971). However, in *Junggarsuchus* (CLARK *et al.*, 2004) the hook is dorsoposteriorly directed and the dorsal border is slightly concave.

Another important characteristic is the relationship between the dorsoventral length of scapula and the total length of the humerus; only in *Terrestriusuchus*, *Gobiosuchus*, *Sichuanosuchus* and *Neuquensuchus universitas* this scapular longitude represents less than 70% of the longitude of the humerus, while in the remaining crocodylomorphs – included all the Metasuchia –, it is always bigger.

## HUMERUS

MUCPv-47 preserves both humera (Figs. 9-10). They are very long and thin (100.8mm), and similar in all its proportions and characteristic to that of *Gobiosuchus kielanae* (OSMÓLSKA *et al.*, 1997, ZPAL MgR-II/67), *Zaraasuchus* (POL & NORELL, 2004b, IGM 100/1321), and *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). The relationship between the distal extension of the deltopectoral crest and the total length of humerus in *Neuquensuchus universitas* is 23.5%. In *Sichuanosuchus* it is also 23.5% and in *Shantungosuchus* it is 23% (WU *et al.*, 1997). This is different to the other Metasuchia where this relationship is always bigger than 27%.

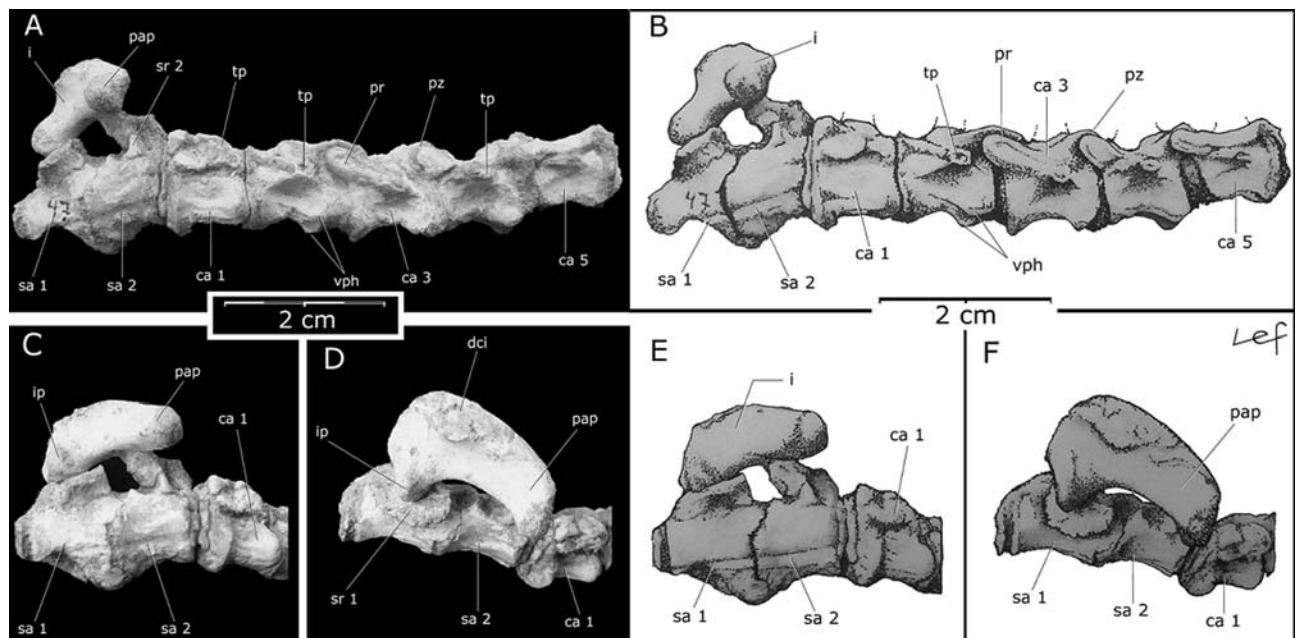


Fig. 7- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Sacral and first caudal vertebrae and left ilium. A and B, in left lateral view. C and E, sacral and left ilium in ventral view. D and F, sacral and left ilium in left lateral view. (Abbreviations in the Appendix IV).

On the other hand, the diameter of the shaft in relation to the total length of the humerus is, in *Neuquensuchus* (6.5%) similar to the other named “protosuchians” (e.g., *Sichuanosuchus*, *Shantungosuchus*, and *Zaraasuchus*), where it never overcomes 7%, but this contrast with the mesoeucrocodylians *Metasuchia* where this relationship is always bigger than 9%. Moreover, in *Neuquensuchus universitas* the relationship between the total length and width of the proximal end of the humerus is approximately 5%, similar to those of *Crocodylia*, *sphenosuchians*, *Protosuchia* and more basal *crocodyliform*, while in *Metasuchia non-Crocodylia* it is not bigger than 4%.

The proximal end of the humerus shows the articular surface lateromedially elongated, strongly curved medially and relatively thin anteroposteriorly, like that present in *Gobiosuchus* and *Sichuanosuchus* (Fig.10C). The lateroproximal expansion and the rectangular proximal shape of the humerus of *Neuquensuchus universitas* (Fig.10C) are very similar to those of *Notosuchus* (POL, 2005, MACN-RN 1037 and 1042), *Chimaerasuchus paradoxus* (WU & SUES, 1996, IVPP V8274), and *Araripesuchus patagonicus* (ORTEGA *et al.*, 2000, MUCPv-267), suggesting some relationships between *Neuquensuchus* and these

notosuchians. However, this characteristic is also similar to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088) and some *Protosuchia* and *sphenosuchians*, as for example *Dibothrosuchus* (WU & CHATTERJEE, 1993, IVPP V7907). This indicates that the character in question does not throw overwhelming phylogenetic information because it possesses a high distributional disparity inside *Crocodylomorpha* representing possible convergences in the different groups. However, the internal tuberosity of *Neuquensuchus universitas* is more similar to that of *Sichuanosuchus* (WU *et al.*, 1997). The lateral facet of the deltopectoral crest has the border anterolaterally directed like in *Notosuchus* and in the rest of the *crocodyliforms* it is laterally directed; however, in *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088) this lateral facet is seemingly also anterolaterally directed.

Distally, the medial condyle is bigger than the lateral one and its general form and proportions are identical to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997). The posterolateral surface of the humerus is strongly concave and the posterior intercondylar groove is broad, like in *Sichuanosuchus huidongensis* (PENG, 1996, ZDM 3404).

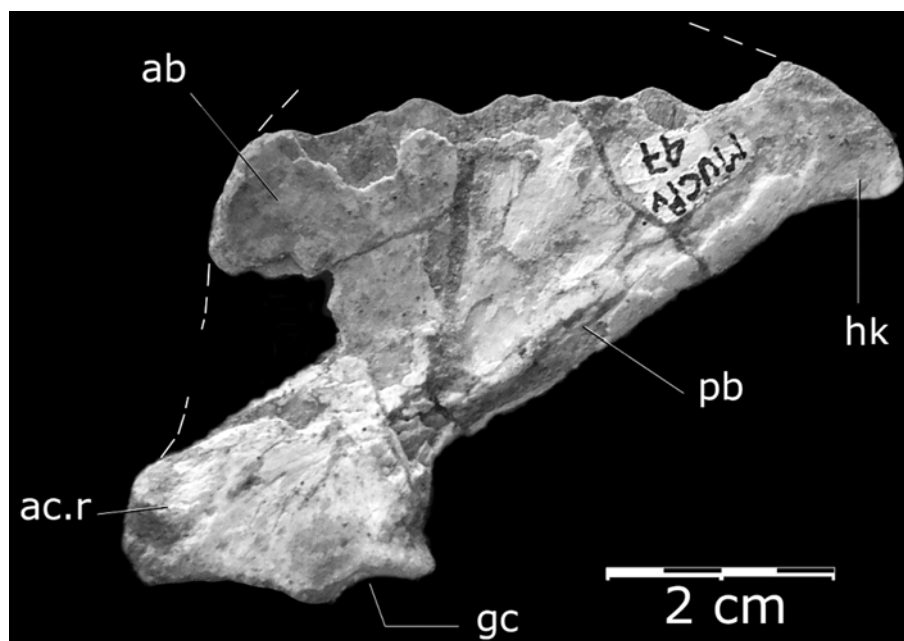


Fig.8- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Left scapula in lateral view. (Abbreviations in the Appendix IV).

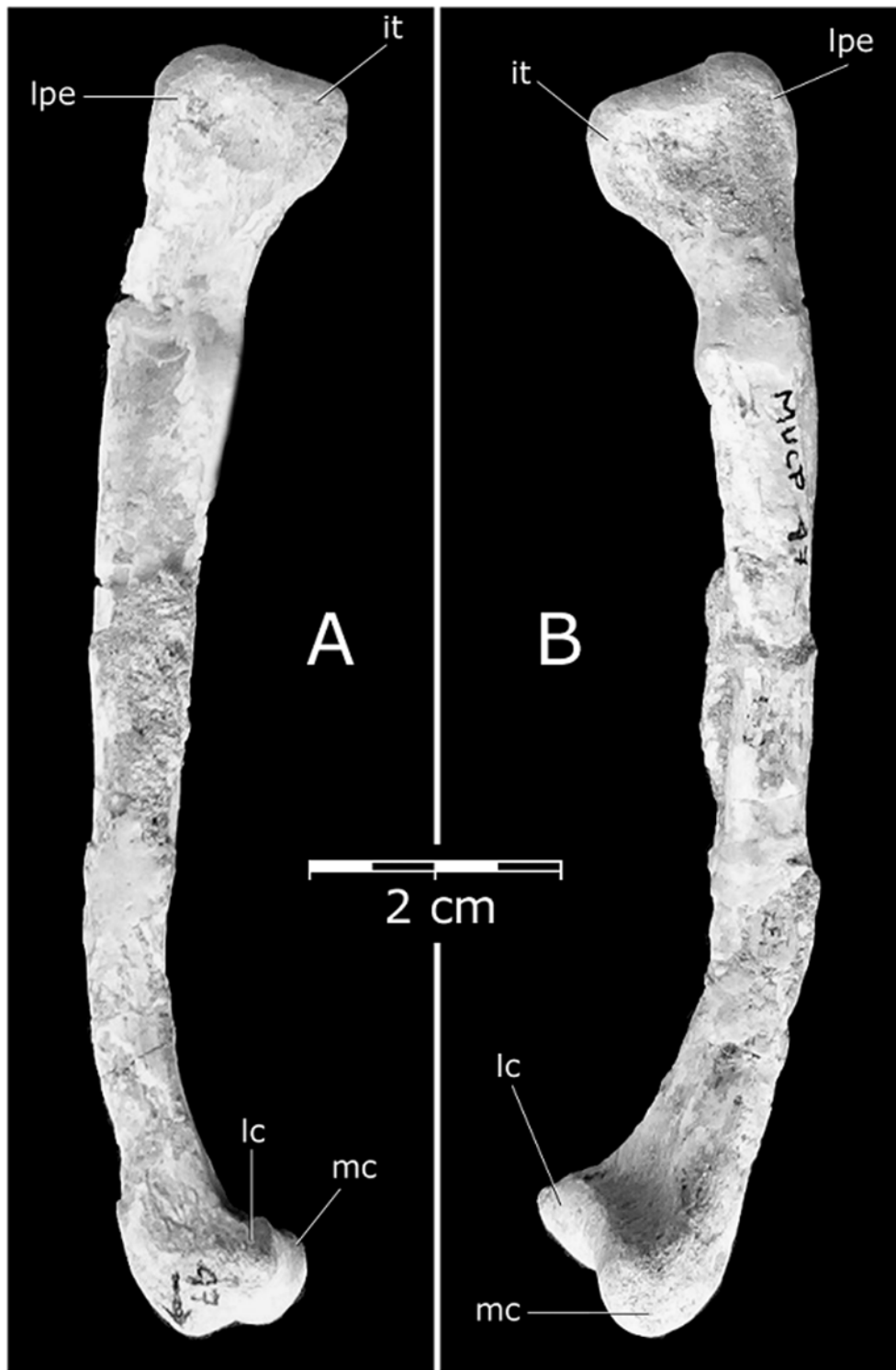


Fig.9- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right humerus in anterior (A) and posterior (B) views. (Abbreviations in the Appendix IV).

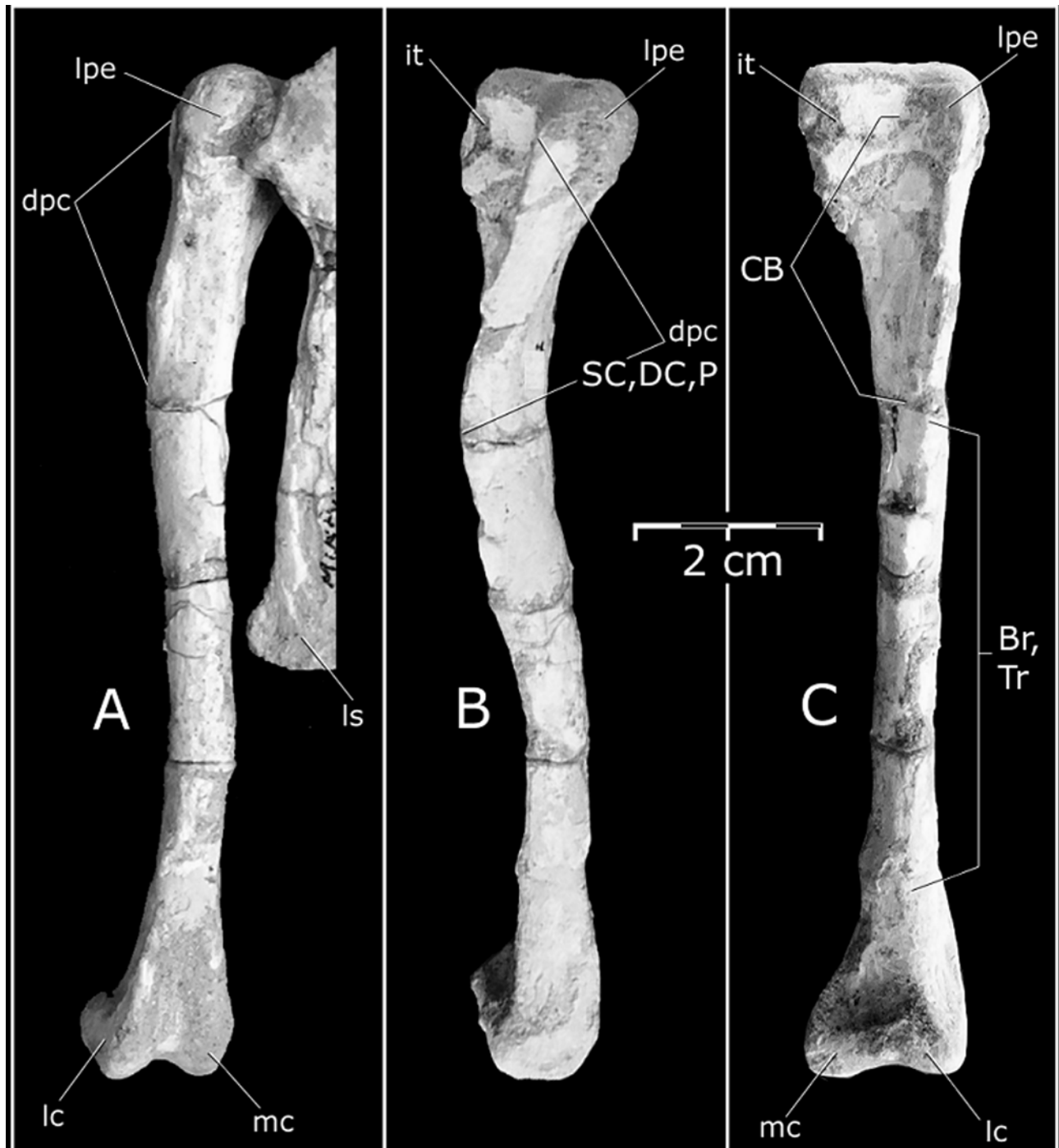


Fig.10- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Left humerus in posterolateral (A), lateral (B) and anterior view (C). (Abbreviations in the Appendix IV).

## ULNA

The ulna of *Neuquensuchus universitas* is straight (Fig.11), with a long and thin shaft, slightly compressed lateromedially as in *Sichuanosuchus*. It possesses a small proximal expansion, and a convex surface for the lateral condyle of the humerus. As in other basal crocodylomorphs, like some sphenosuchians but contrary to notosuchians, the ulna possesses a prominent olecranon process. The right ulna, although incomplete, has a length of 107.5 mm and it is longer than the humerus. This character is only shared with some sphenosuchians (e.g., *Terrestriusuchus*, *Dibothrosuchus*, and *Dromicosuchus*), representing an autapomorphy of *Neuquensuchus* and a convergent feature shared with these sphenosuchians but related to the cursorial habits of this crocodyliforms. However, in *Neuquensuchus universitas* the relationship between the width of the shaft (5.7mm) and their total length (107.5mm) is 5.3%; it is comparable to other "protosuchian" forms (*Zaraasuchus* <6%; *Gobiosuchus* = 5%; *Shantungosuchus* = 5.6%; *Sichuanosuchus* = 5.3%) and differs from other mesoeucrocodylians metasuchian where it is bigger than 7% (notosuchians and neosuchians).

## RADIUS

The right radius (Fig. 11) is a very long and thin bone. It is similar in its general form to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). Its proximal end is strongly expanded and the thin shaft is circular in transverse section. The relationship between the diameter of the shaft (3.9mm) and total length of the radius (105mm) in *Neuquensuchus universitas* is 3.7%, which is similar to *Sichuanosuchus shuhanensis* (3.6%). By contrast in *Terrestriusuchus* it is 2.9% and in the other sphenosuchians it is bigger (for example in *Pseudhesperosuchus* it is 5% and in *Hesperosuchus* it is 5.75%). In more derived members of Mesoeucrocodylia this relationship always surpasses 5% (*Araripesuchus patagonicus*: 5.5%; *Notosuchus*: 8.05%; *Chimaerasuchus*: >8%; *Simosuchus*: >8%; Crocodylia: = 8%) contrary to *Araripesuchus tsangatsangana* (TURNER, 2006) where it is 4.52%.

The specimen MUCPv-47 possesses a small proximal fragment of the radial, articulated to the end of the right radius, which is very similar to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997).

## ILIUM

Only the posterior fragment of the left ilium has been preserved in MUCPv-47 (Fig.7). It includes the posterior border of the acetabular cavity, the ischiadic peduncle and postacetabular process. The posterior part of dorsal crest in *Neuquensuchus universitas* is low and snub, different to *Notosuchia* (POL, 2005; FIORELLI, 2005) where there is a very laterally extended marked acetabular roof. The length between the dorsal end of the crest and the distal end of the ischiadic peduncle is very short, indicating an ilium dorsoventrally low. It differs from more derived Mesoeucrocodylia (*Metasuchia*) where the ilium is very wide dorsoventrally. The ischiadic peduncle is small and the surface for the articulation of the ischium is reduced. The postacetabular process is dorsoventrally thin and markedly posteriorly projected, with its distal extreme lateroventrally directed, like in *Protosuchus* (COLBERT & MOOK, 1951) and other "protosuchian" forms.

## PUBIS

The right pubis of *Neuquensuchus universitas* (MUCPv-47) is practically complete. It is associated to the proximal end of the right ischium, sacral and caudal vertebrae, left ilium and femur, tibia and right fibula (Figs.12-13). The pubis is a long and thin bone (rod-like shaped), mainly in the section of the shaft, similar to basal forms of Crocodylomorpha, as *Terrestriusuchus* (CRUSH, 1984), *Protosuchus* (COLBERT & MOOK, 1951), *Sichuanosuchus* (IVPP V12088), and a basal innominate form of China (POL *et al.*, 2004, GMPKU-P 200102). The small proximal expansion supports a convex facet for the ilium and for the pubic process of the ischium (Fig.12B). This character is similar to that of *Sichuanosuchus* and other "protosuchians", and it implies that the pubis is partially introduced inside the acetabulum. The pubis is slightly expanded distally, as in GMPKU-P 200102 (POL *et al.*, 2004) and *Sichuanosuchus*. In *Neuquensuchus universitas* the relationship between the length of the pubis (39.5mm) and the width of the distal expansion (10.8mm) is 27%, similar to *Sichuanosuchus* (26%) and *Gobiosuchus* (23-24%). In more derived Mesoeucrocodylia – metasuchian forms –, this proportion is always superior to 30%. Lastly, the diameter of the pubic shaft, in relation to the total length, resembles that of other "protosuchians". In *Neuquensuchus*, this relationship is 7%, similar to *Sichuanosuchus*

(6.5%) and *Gobiosuchus* (<7%) and very different from *Metasuchia* (>8%).

The existent relationship between the total length of the pubis and the total length of femur is a characteristic only shown by *Gobiosuchus*, *Shantungosuchus* and *Neuquensuchus* being smaller than 45%, while in *Terrestriusuchus*, *Protosuchus*, and *Metasuchia* the proportion between pubis and femur is always bigger due mainly to the reduction of the pubis, to exception of *Mahajangasuchus*.

#### ISCHIUM

Only the proximal end of the right ischium has

been preserved in MUCPv-47, together with a slight impression (Fig.12B). It is very similar in its construction to *Protosuchus*, *Sichuanosuchus* and GMPKU-P 200102 (POL *et al.*, 2004). The pubis process of ischium is slightly narrower than the proximal end of the pubis, like in *Sichuanosuchus*, and it contacts with the pubis in its posterodorsal extreme. For this reason, the ischium partially excludes the pubis of the acetabulum. The half section of the proximal shaft shows that it is quite narrow but it spreads to distally expanded according to the impression of the same similar to *Protosuchus* and *Gobiosuchus*.

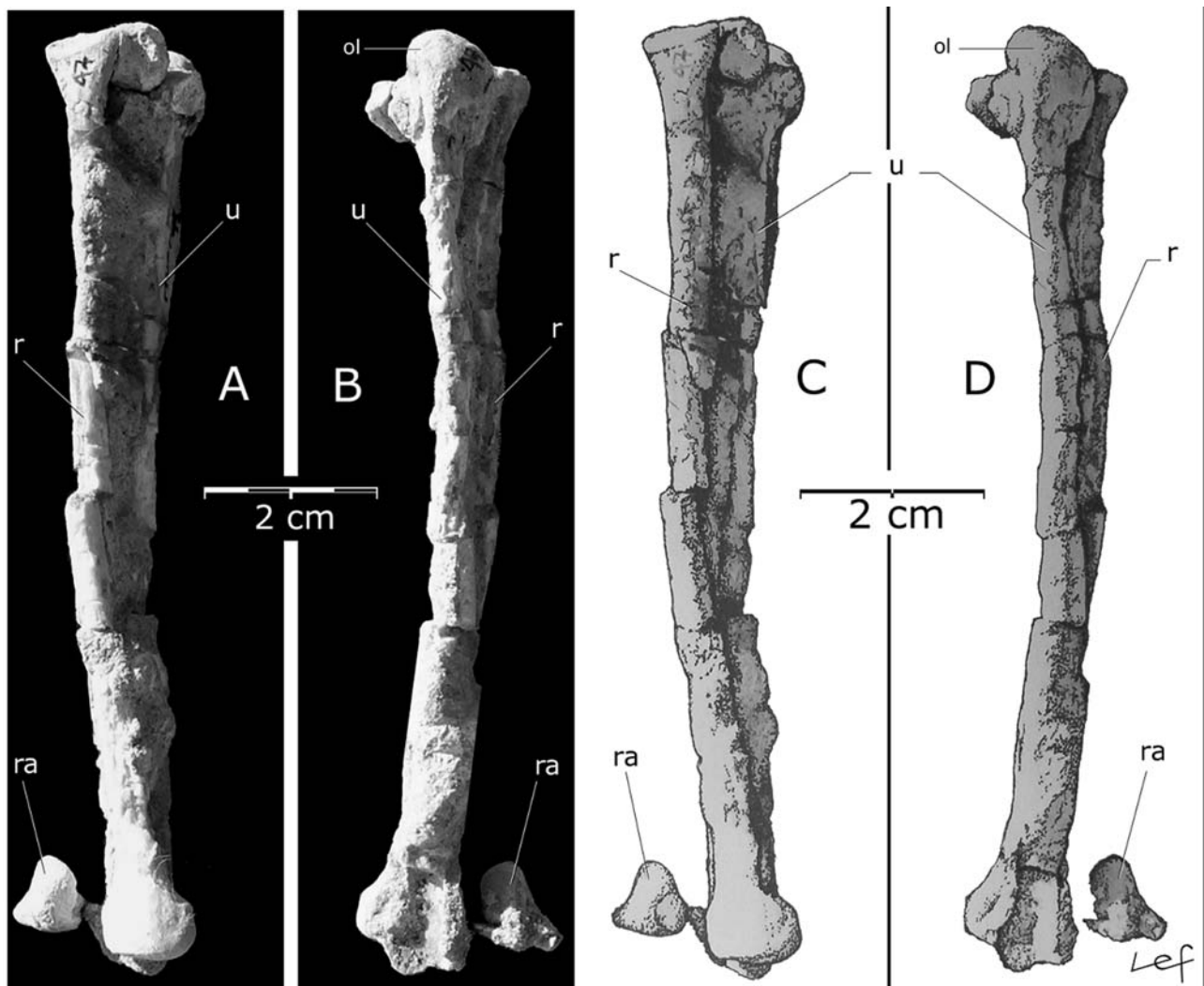


Fig.11- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right ulna, radius and radial in lateral (A and C) and medial (B and D) views. (Abbreviations in the Appendix IV).

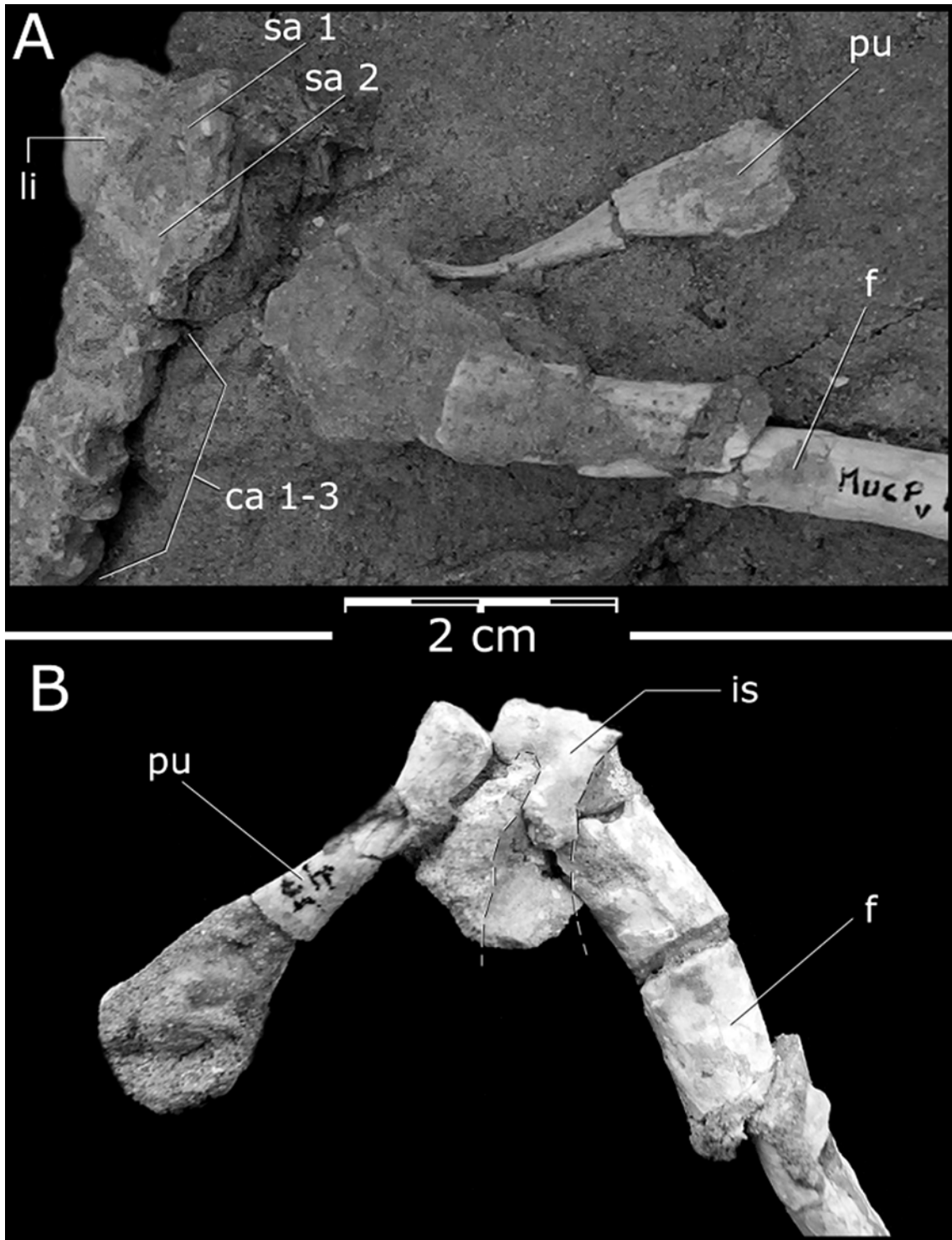


Fig. 12- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. A, right pubis and femur in lateral view; B, right pubis, ischium and femur in medial view. (Abbreviations in the Appendix IV).

## FEMUR

Only in the specimen MUCPv-47 of *Neuquensuchus universitas* the right femur have been preserved (Figs. 3D, 13, 14). In the holotype, the right femur articulates with the tibia and fibula (Figs. 12-13) as likewise with the right ilium, sacral and first caudals vertebrae. The long and thin femur is like in basal crocodylomorphs. It is mostly practically straight and the sigmoid form is not conspicuous or not very marked. The condyle on the femoral head is slightly expanded (Fig. 14). This characteristic differs from other sphenosuchians, such as *Terrestrisuchus* (CRUSH, 1984), *Dromicosuchus* (SUES *et al.*, 2003, UNC 15574), *Macelognathus* (GÖHLICH *et al.*, 2005, LACM 4684/128272), and derived mesoeucrocodylians. The femur of *Neuquensuchus universitas* possesses a lengthened furrow similar in its proportions and muscular dispositions to that observed in

the femoral fragment of *Shantungosuchus hangjinensis* (WU *et al.*, 1994, IVPP V10097). *Neuquensuchus universitas* as in other basal crocodyliforms lacks of a prominent anteromedial process of the femur medially placed on the proximal end of shaft. This process is very marked in *Notosuchia* (POL, 2005; FIORELLI, 2005; fig. 14B) and other metasuchians such as *Mahajangasuchus* (BUCKLEY & BROCHU, 1999). Although in MUCPv-47 the distal end is damaged we can observe that the lateral condyle (fibular c.) is slightly bigger with respect to the medial one. An important character in *Neuquensuchus* is the relationship of the diaphyseal width (7mm) and the total length of the femur (94mm) equal to 7.5%. This is similar to some basal crocodyliforms (*Gobiosuchus* = 6.3%; *Shantungosuchus* = 7.6%), differing from *Protosuchus* and more derived mesoeucrocodylians – Metasuchia – where it is always bigger than 9%.

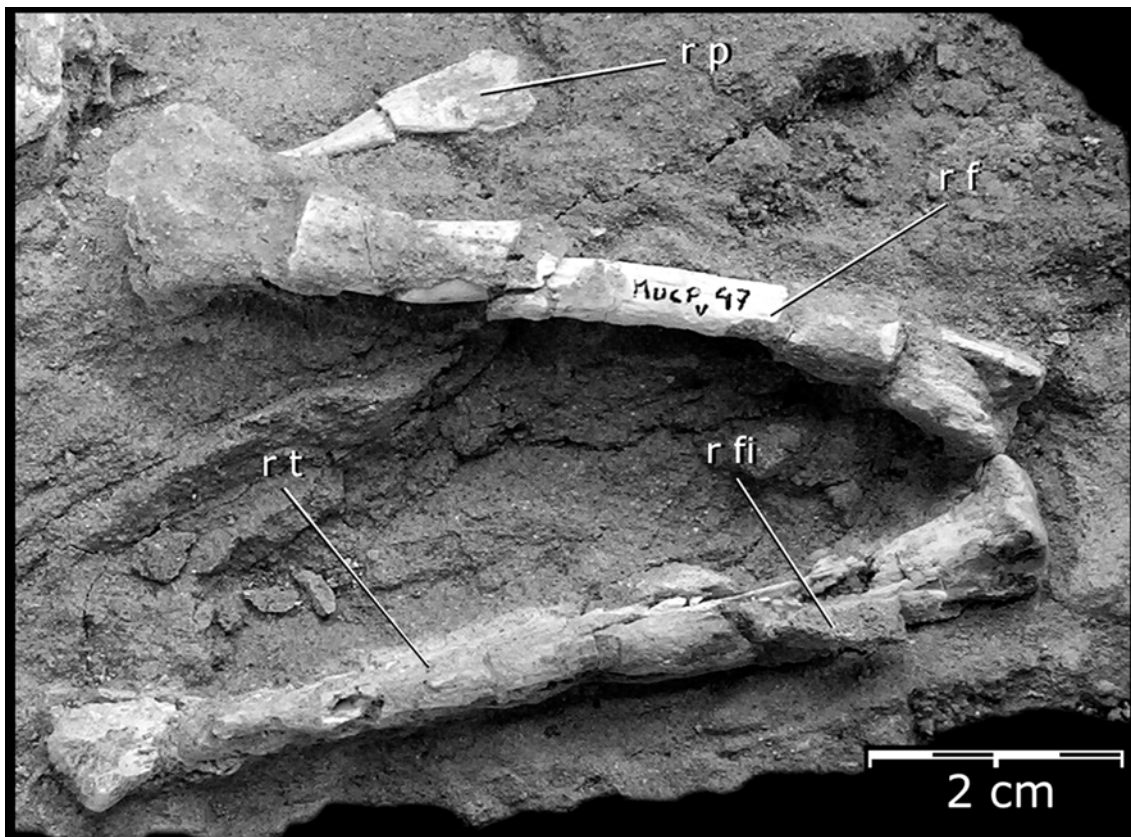


Fig.13- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right pubis, femur, tibia and fibula in lateral view. (Abbreviations in the Appendix IV).



## TIBIA

The right tibia in MUCPv-47 is complete (Fig.13), while in MUCPv-161 just the proximal end is preserved (Fig.14). The tibia possesses a very long, straight and thin shaft, similar to that present in some most basal Crocodylomorpha, as in sphenosuchians like *Macelognathus*, *Dromicosuchus*, *Hesperosuchus*, and *Terrestriusuchus* (CRUSH, 1984; CLARK *et al.*, 2000; SUES *et al.*, 2003; GÖHLICH *et al.*, 2005). However, in some "protosuchian" forms the tibia is too similar, such as in *Shantungosuchus chuhsienensis* (YOUNG, 1961; WU *et al.*, 1994, IVPP V2484) and *Gobiosuchus kielanae* (OSMÓLSKA, 1972; OSMÓLSKA *et al.*, 1997, ZPAL MgR-II/67). The proximal end is broad and the distal end has a small lateromedial expansion. *Neuquensuchus universitas* does not possess a developed cnemial crest and the femoral condyles form a marked notch in the distal end (Figs.14A, 14C).

In MUCPv-47, the tibia (105.3mm) is longer than the femur (94.5mm) comprising 89.7% of the tibial

length. This possibly represents one of the most important characters in the species because this feature character is only shared with *Shantungosuchus*, where the length of the femur is 95% of the tibial length (WU *et al.*, 1994) (see Fig.13). By contrast in all other crocodyliforms the femur is always longer than the tibia (WU *et al.*, 1994). Even so, in early ontogenetic states of Crocodylia the femur is always longer than the tibia (DODSON, 1975). Inside Crocodylomorpha, some sphenosuchians as *Terrestriusuchus* or *Macelognathus* have the tibia longer than the femur (SERENO, 1991; CRUSH, 1984; GÖHLICH *et al.*, 2005). On the other hand, the relationship between the diaphyseal width (5.6mm) and the tibia length (105mm; 5.3%) is identical to that of *Shantungosuchus* (5.3%), differing from those of *Protosuchus* and *Metasuchia* that is always bigger than 8%. The discussions and evolutionary consequences on these characteristics are offered later on (see Discussion).

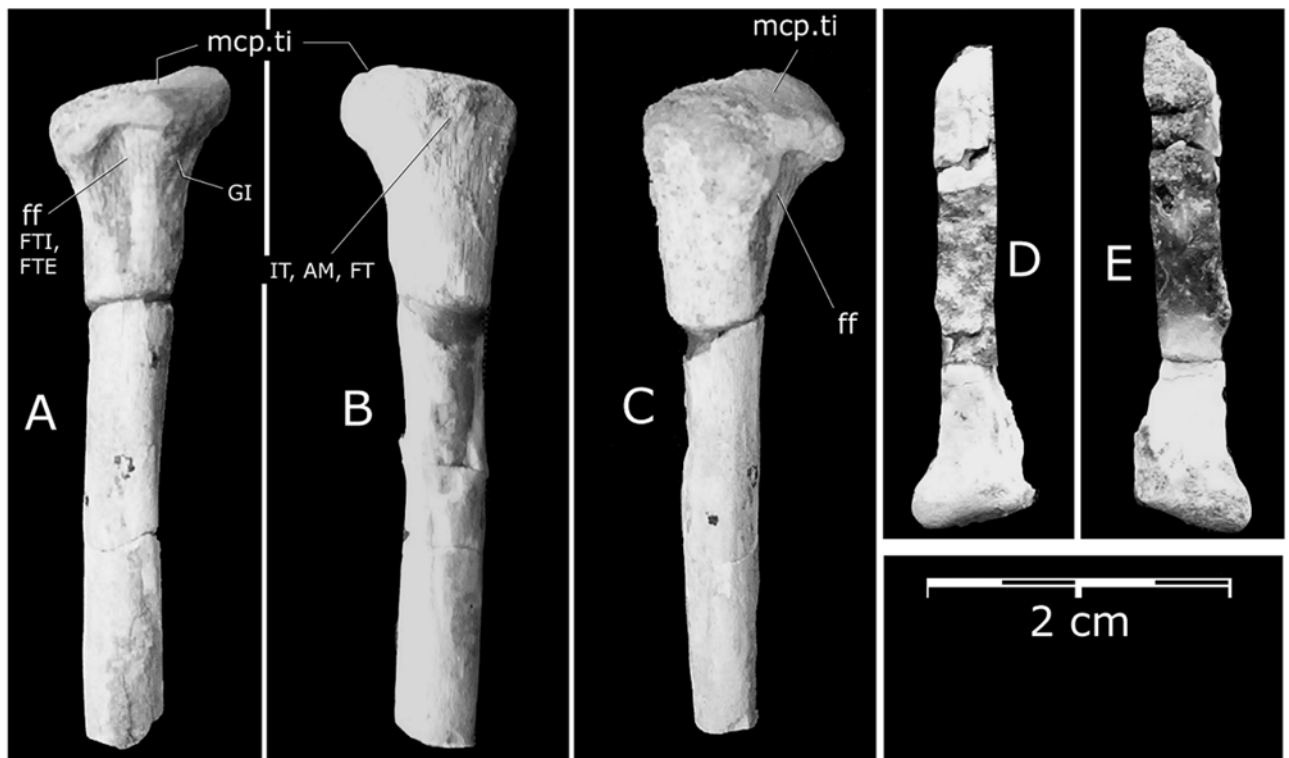


Fig.14- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-161. A, B and C, proximal end of left tibia; D and E, distal end of left fibula. Tibia in posterior (A), anterior (B) and lateral (C) view. Fibula in medial (D) and lateral (E) views. (Abbreviations in the Appendix IV).

## FIBULA

Few fibular materials have been preserved. In MUCPv-47, the partial and very fragmentary right fibula (Fig. 13) is thin and long. In MUCPv-161 the distal end of fibula possesses a thin shaft with D-shaped in cross-section (Figs. 14D, 14E).

## TARSUS

Only conserved in MUCPv-161, the left astragalus is incompletely preserved (Fig. 3D). In spite of it, we can see morphological characters in the articulations that are present in typical Crocodyliformes tarsus. For instance, a good marked process supporting the square fibular facet and a lateromedially wide tibial facet. The articulate surface for the metatarsals is rounded and width with a deep anterior hollow.

## PHYLOGENETIC RELATIONSHIPS

Although *Neuquensuchus universitas* gen.nov., sp.nov. is represented just by postcranial remains, it was possible to establish its phylogenetic relationships based on parsimony analysis. For this analysis, we used a modified data set taken of recent publications (POL & NORELL, 2004b; POL *et al.*, 2004), which was based on the addition of several characters of previously published matrix (CLARK, 1994; WU & SUES, 1996; GOMANI, 1997; WU *et al.*, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000). We have included new characters not included in previous publications that were defined by WU & SUES (1996), MARTINELLI (2003), and FIORELLI (2005). Moreover, sixteen new characters were added and new taxa were included. The matrix includes 231 characters and 51 taxa (see appendixes I and II). The present work tries to focus mainly in non-neosuchian basal crocodyliforms. In the present analysis, characters were taken with equal weight using NONA (GOLOBOFF, 1993) and published with Winclada (NIXON, 1999). An heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult\*1000; max\*), holding 20 trees per replication (hold/20;). Thirty six (36) most parsimonious trees of 839 steps (CI 0.34; RI 0.65) were found in all of replications. The 36 phylogenetic hypotheses differ in the relationships of some neosuchian crocodyliforms like for instance Peirosaurid forms and derived

neosuchian group. However, *Notosuchia* as well as the basal groups of crocodyliformes stayed constant in the different hypotheses as we can observe in the strict consensus tree (Fig. 15).

In all more parsimonious hypotheses, *Neuquensuchus universitas* represents the sister taxa of *Shantungosuchus hangjinensis* from the Lower Cretaceous of Inner Mongolia (Northern China). Both shared the character 91 “hypapophyses present only in cervical vertebrae” and character 226 “Tibia longer than the femur” (Node 11 of the figure 15). This last character is ambiguous in *Sichuanosuchus shuhanensis* and *Zosuchus davidsoni*. In another sense, just two diagnostic character separating *Neuquensuchus* from *Shantungosuchus* (olecranon well developed [character 173-0] and the relationship between the ulna length and the humerus length [Character 220]; Node 12). The absence of additional autapomorphies in *Neuquensuchus* can be due to the fragmentarity of the available material, which does not possess cranial remains, the reason why we support the erection of this new taxon. The temporal and geographical separation goes in favor of this proposal. The resulting clade shows that *Neuquensuchus* and *Shantungosuchus* are the sister group of *Sichuanosuchus shuhanensis* from the Early Cretaceous of Sichuan, China (Node 10). This node is diagnosed by two unambiguous synapomorphies (palatines form palatal shelves that do not meet [Character 37]; posteroventral edge of mandibular ramus markedly deflected [Character 170]). However, both characters are ambiguous in *Neuquensuchus*. *Zosuchus davidsoni* from Upper Cretaceous of Gobi Desert (Mongolia), represents the sister taxa of the resulting node of the three previously taxa (Node 9), diagnosed by five unambiguous synapomorphies (characters 55, 143, 163, 169 and 178; see Appendix I).

The clade conformed by *Fruita* form, *Zosuchus*, *Sichuanosuchus*, *Shantungosuchus*, and *Neuquensuchus* (Node 8 from the figure 15), is closely related to *Hsisosuchus* and more derived mesoeucrocodylians than other Protosuchia (*Gobiosuchus*, *Protosuchus* and all their descendants). This conclusion is similar to that obtained in other works (POL, 2003; POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; FIORELLI, 2005; POL & APESTEGUÍA, 2005; ZAHER *et al.*, 2006), but differs of those in that it postulates a monophyly of protosuchids and “protosuchians” (e.g., WU *et al.*, 1994; WU & SUES, 1996; WU *et al.*, 1997; TYKOSKI *et al.*, 2002).

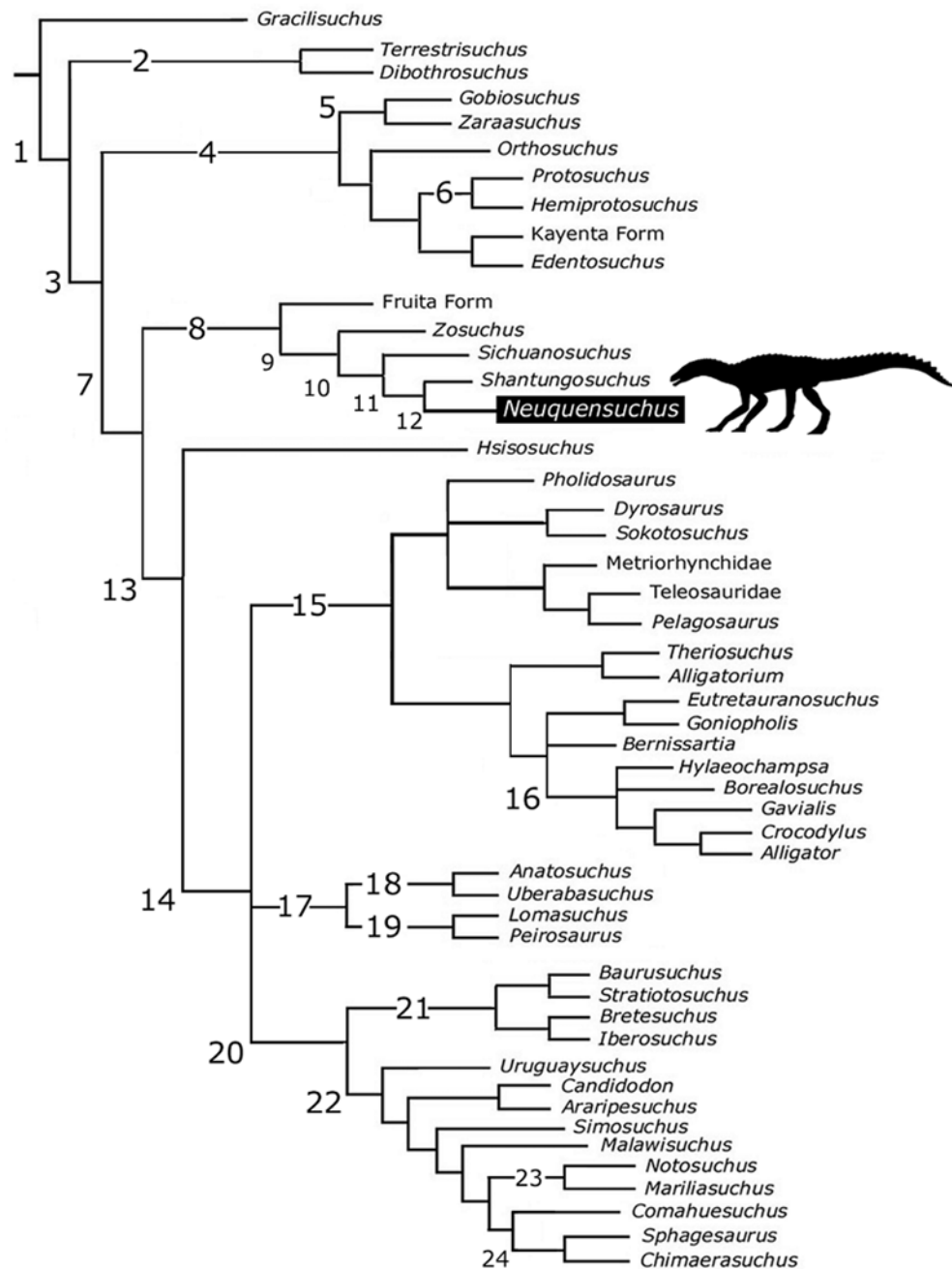


Fig.15- Strict consensus of the 36 most parsimonious topologies that resulted from a strict parsimony analysis obtained with NONA and published with Winclada. Tree length is 839 with a CI of .33 and a RI of .65. The tree shows the phylogenetic relationships of *Neuquensuchus universitas* gen.nov., sp.nov. performed a basal mesoecrocodylia. 1: Crocodylomorpha; 2: "Sphenosuchia"; 3: Crocodyliformes; 4: Protosuchia; 5: Gobiosuchidae; 6: Protosuchidae; 7: Mesoecrocodylia; 8, 9, 10 and 11: Innominated; 12: *Neuquensuchus universitas* gen.nov., sp.nov.; 13: "Mesosuchia"; 14: Metasuchia; 15: Neosuchia; 16: Eusuchia; 17: Peirosauridae; 18 and 19: Innominated; 20: Notosuchia; 21: Sebecosuchia; 22: Innominated; 23: Notosuchidae; 24: Sphagesauridae. *Araripesuchus* is used here like a terminal taxon although in the analyses it was used *A. gomesii* and *A. patagonicus*. Explanation and definitions of suprageneric taxa see Appendix V.

On the other hand and in contrast to some recent phylogenetic analysis (e.g., CLARK, 1994; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; TURNER, 2004; 2006; TURNER & CALVO, 2005) that placed *Araripesuchus* like basal member of Neosuchia, in our analyses this taxon appears as a basal member of notosuchian clade, an important result comparable with other recent phylogenetic studies (POL, 2003; POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; FIORELLI, 2005; POL & APESTEGUÍA, 2005; ZAHER *et al.*, 2006).

## DISCUSSION

*Neuquensuchus universitas* gen.nov., sp.nov. represents the first basal Mesoeucrocodylia non Metasuchia from the Cretaceous, not only from Argentina but also from South America and Gondwana (Fig.16). Mesoeucrocodylia is defined here like the most inclusive clade containing *Crocodylus* but not *Protosuchus* (BENTON & CLARK, 1988; CLARK, 1994; *sensu* SERENO *et al.*, 2001; 2005). Without doubts, the Triassic argentinean and gondwanic forms of basal crocodyliforms, such as *Hemiprotosuchus* (BONAPARTE, 1967; 1971), *Protosuchus* sp. (ALCOBER *et al.*, 2004), *Orthosuchus* (NASH, 1975), and *Baroqueosuchus haughtoni* (BUSBEY & GOW, 1984) are not related directly to *Neuquensuchus universitas*, because it integrates the most basal group of Mesoeucrocodylia (Figs.15-16) due to the intimate relationships with other so formerly called "protosuchians" and more derived form like *Hsisosuchus*. Then, it demonstrates that *Neuquensuchus* does not represent a derived form from the Upper Triassic/Early Jurassic Gondwana taxa. Therefore, it comes from highly more derived taxa from the Early Cretaceous of Central Asia, such as *Shantungosuchus* and *Sichuanosuchus* (Figs. 15, 16). It would be possible that related form of "Las Hoyas crocodyliform" is closely related, but there is not a detailed data of this specimen to include it in the phylogenetic analyses, although in recent studies "Las Hoyas crocodyliform" is intimately related to *Gobiosuchus* (see ORTEGA *et al.*, 2000). Regarding to the Cretaceous paleobiogeography, *Neuquensuchus universitas* throws more problems than answers inside the classics paleogeographic models used until now (e.g., BONAPARTE, 1986; BUFFETAUT, 1982; SERENO, 1999). This problematic disjunct distributional Cretaceous pattern is similar to that observed in other groups of very diverse tetrapods, as for

example Lissamphibia (Discoglossidae, *Callobatrachus*), Mammaliamorpha (e.g., Peramura), Notosuchia (*Chimaerasuchus*) and Atoposauridae (cf. *Theriosuchus*). Even in countless groups of dinosaurs, for example Rebbachisauridae, Nemegtosauridae, Saltasauridae, Abelisauroidea, Spinosauroidea, Carcharodontosauridae, Deinonychosauria, Alvarezsauria, and some Ornithischia (*Valdosaurus*, *Ouranosaurus*). Summing up, it was suggested by different authors (e.g., WU & SUES, 1996; POL, 2003), that this rises many questions to the hypothesis of faunistic endemism in Gondwana during Cretaceous times, a classic hypothesis assumed by several authors (GASPARINI, 1971; BONAPARTE, 1986; 1991; CLARK *et al.*, 1989). The occurrence of *Neuquensuchus* in Gondwana does not indicate the presence of Pangeic lineage of this clade in Southern lands. The presence of this basal mesoeucrocodylian is more probably due to subsequent dispersion, as it has been postulated in recent studies by JUÁREZ VALLIERI & FIORELLI (2002; 2003) and FIORELLI (2005). These authors propose a dispersion event among Gondwana, Europe and Central Asia during the Early Cretaceous (Berriasian–Aptian), producing a faunistic interchange poorly recognized previously (BRETT-SURMAN, 1979). Probably it occurred in both ways: from Central Asia to Gondwana through Europe as well as in the opposite direction. This new hypothesis agrees with the distributional pattern of all fossil groups and is perfectly adjusted with recent genetic studies carried out on current vertebrates (see HAY *et al.*, 1995; HEDGES & POLING, 1999; HEDGES, 2001; COOPER *et al.*, 2001; MURPHY *et al.*, 2001; MEYER & ZARDOYA, 2003).

These basal mesoeucrocodylian non-Metasuchia were abundant during Jurassic and Cretaceous in Asia. Undoubtedly they came from basal forms of Upper Triassic or Early Jurassic times, which have suffered an adaptative radiation in that continent. Posteriorly in the Early Cretaceous, after the contact between Gondwana and Asia (JUÁREZ VALLIERI & FIORELLI, 2002; 2003; FIORELLI, 2005), dispersion toward Southern continents of well derived forms took place and for this reason *Neuquensuchus universitas* occurs in Northern Patagonia. Summing up, *Neuquensuchus* represents a clade of mesoeucrocodylian basal form with a purely Asian origin and dispersal center, at least during the Upper Jurassic, and with dispersion out of Asia toward Europe and Gondwana during the Early Cretaceous.

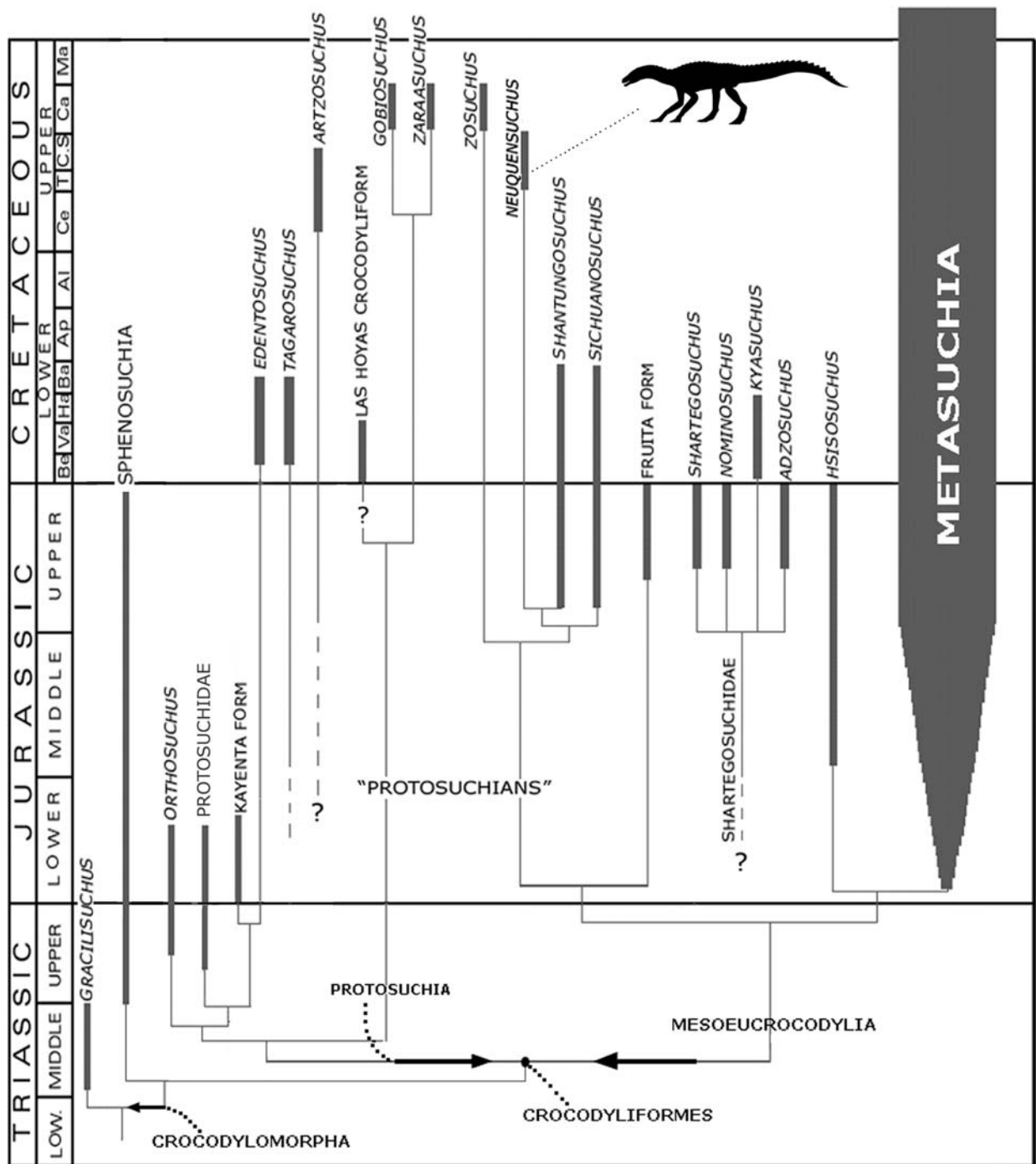


Fig.16- Chronological distribution of Crocodylomorpha. The “Shartegosuchidae” (EFIMOV, 1988) and other taxa not included in the phylogenetics analysis alone indicating here the highly endemic fauna of Crocodyliformes present in Central Asia during Jurassic and Cretaceous times; they do not indicate phylogenetic relationships with other groups in this chronology.

In the opposite way, we can explain the presence in the Early Cretaceous of China of the derived notosuchian *Chimaerasuchus paradoxus* (WU & SUES, 1996; MARTINELLI, 2003; POL, 2003; POL & NORELL, 2004a; 2004b; POL, 2005; FIORELLI, 2005) or the atoposarid neosuchian cf. *Theriosuchus* sp. (Wu *et al.*, 1996, IVPP V 10613). It seems that derived basal Crocodyliformes had an important adaptative success in Central Asia during Cretaceous times, for example by the occurrence of *Edentosuchus*, *Tagarosuchus*, *Artzosuchus*, *Gobiosuchus*, *Zaraasuchus*, *Shantungosuchus*, *Sichuanosuchus*, and *Zosuchus*. By contrast, in Neopangea it did not happen this way. The fact that in Gondwana, and mainly in South America, exist an acceptable Cretaceous crocodyliform record, the fragmentary remains of *Neuquensuchus* probably indicate their low abundance. Moreover they did not suffer an apparent adaptative radiation, as it occurred with Notosuchia, a properly gondwanic group. Together with previous protosuchid and "protosuchians" Asian taxa, the Upper Jurassic and Early Cretaceous forms includes in "Shartegosuchidae" – *Shartegosuchus* (EFIMOV, 1988), *Nominosuchus* (EFIMOV, 1996; KURZANOV *et al.*, 2003), *Kyasuchus* (EFIMOV & LESHCHINSKIY, 2000), and *Adzosuchus* (EFIMOV *et al.*, 2000) (see Fig.16) –, it is indicating the highly endemic fauna of Crocodyliformes present in Central Asia during Jurassic and Cretaceous times. In a recent work (FIORELLI *et al.*, 2006), it was demonstrated the monophyly and the Shartegosuchidae's endemic group, and they represent the most basal group of the mesosuchian clade (Fiorelli *et al.*, in prep.). The crocodyliforms fauna and other Asian continental tetrapods are correlated with the biogeographical hypothesis proposed by RUSSELL (1993) of a sequential partition of Pangea. He postulated the Asian isolation of Neopangea during the Upper Triassic or Early Jurassic.

In another sense, an interesting aspect that presents *Neuquensuchus universitas* derived from the present study is the important character related to the longitudinal ratio between the femur and tibia. Previously it was aforementioned that the femur comprises 89.7% of the tibial length, feature character only shared with *Shantugosuchus*, with a femoral length of 95% of the total tibial length (WU *et al.*, 1994) (see Fig.13). In the other crocodyliforms the femur is always longer than the tibia (WU *et al.*, 1994), even so in early ontogenetic states of Crocodylia (DODSON, 1975). Within Crocodylomorpha, only in some sphenosuchians

like *Terrestrisuchus* or *Macelognathus* the tibia is longer than the femur (SERENO, 1991; CRUSH, 1984; GÖHLICH *et al.*, 2005). Undoubtedly, this convergent characteristic was acquired independently by both groups, sphenosuchians – some species – and these two basal mesoeucrocodylian taxa, *Shantungosuchus* and *Neuquensuchus*.

As it has been suggested by diverse authors (CRUSH, 1984; SERENO, 1991; SERENO & WILD, 1992; CLARK *et al.*, 2000; SUES *et al.*, 2003; CLARK *et al.*, 2004; GÖHLICH *et al.*, 2005), sphenosuchians such as *Terrestrisuchus*, *Macelognathus*, *Junggarsuchus*, *Dromicosuchus*, and *Hesperosuchus*, would have presented a high capacity cursorial for the diverse characteristics of their extremities, mainly by the long and thin bones. Also, Wu *et al.* (1994) suggested that *Shantungosuchus* had a high cursorial capacity instead of very quick terrestrial displacement. The close relationships of forelimb with *Neuquensuchus* allow us to expect the same capacity of movement and cursorial capacity. In the more related taxa (*Sichuanosuchus* and *Zosuchus*), this characteristic – tibia > femur – is ambiguous. These important cursorial characteristic present in these crocodylomorphs possibly had a great influence in their spatial ranges and the amplification of ecological and territorial niches, allowing a bigger dispersal capacity.

Although postcranial remains of *Neuquensuchus universitas* gen.nov., sp.nov. reported here represent the first evident crocodyliform non-Metasuchia in gondwanic Cretaceous lands, we do not know too much about their anatomy and relationships. We believe that the strong phylogenetic relationships of *Neuquensuchus* produce important implications and give novel light about the paleobiogeographic issues. New exploratory works with the purpose of finding new remains of these original taxa, mainly cranial materials, will help to elucidate and know with more details their anatomy and phylogenetic relationships.

#### ACKNOWLEDGEMENTS

We want to express our most sincere gratefulness to the technicians of the Lake Barreales Paleontological Center for partly preparation of the material; to the members of the CePaLB for the collaboration during the study of the material. Additional gratefulness to MSc. Marco Brandalise de Andrade and to Dr. Diego Pol is here expressed for the informations given and the valuable

comments to the improvement of this work. We also thank to Mr. Carlos Muñoz, director of the Provincial Museum "Carlos Ameghino" of the Cipolletti City, and Dr. Leonardo Salgado (MUCP), to allow us the observation of diverse materials. A special grateful to A.Averianov, J.M.Parrish, A.D.Buscalioni, D.Pol and X.C.Wu, for the disinterested correspondences and papers sent; to Alexander Kellner for their constant help and Rubén Juárez Valieri, Augusto Haro, and Guillermo Salinas for their help, observations, and papers sent. Funding comes from National University of Comahue and Proyecto Dino.

#### REFERENCES

- ALCOBER, O.A.; MARTINEZ, R.N.; HEREDIA, G.; COLOMBI, C.; OLIVARES, I. & TROTTEYN, M., 2004. New vertebrate findings in the Upper Triassic Los Colorados Formation, Ischigualasto Basin, Northwestern Argentina. In: ANNUAL MEETING OF THE SOCIETY OF VERTEBRATE PALEONTOLOGY. 64., 2004, Denver. **Abstracts...** Northbrook: Society of Vertebrate Paleontology. p.34A.
- ALIFANOV, V.R.; EFIMOV, M.B.; NOVIKOV, I.V. & MORALES, M., 1999. A new Psittacosaurian complex of tetrapods from the Lower Cretaceous Shestakovo Locality (Southern Siberia). **Doklady Earth Sciences**, **369**:1228-1230.
- ALVARENGA, H. & BONAPARTE, J.F., 1992. A new flightless landbird from the Cretaceous of Patagonia. In: CAMPBELL, K.E. (Ed.) **Papers in Avian Paleontology**. Los Angeles: Natural History Museum of Los Angeles County, Science Series, **36**:51-64.
- ANTUNES, M.T., 1975. *Iberosuchus*, crocodile Sebecosuchien nouveau, l'Eocene iberique au Nord de la Chaîne Centrale, et l'origine du Canyon de Nazare. **Comunicações dos Serviços Geológicos de Portugal**, **59**:285-330.
- APESTEGUÍA, S., 2004. *Bonitasaura salgadoi* gen. et sp. nov.: a beaked sauropod from the Late Cretaceous of Patagonia. **Naturwissenschaften**, **91**:493-497.
- BENTON, M.J. & CLARK, J.M., 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: BENTON, M.J. (Ed.) **Phylogeny and Classification of the Tetrapods: Amphibians, Reptiles and Birds**. Oxford: Clarendon Press. Vol. 1. Systematics Association Special Publication, 35A. p.295-338.
- BONAPARTE, J.F., 1967. Dos nuevas "faunas" de reptiles triásicos de Argentina. In: SYMPOSIUM ON GONDWANA STRATIGRAPHY, 1., 1967, Mar del Plata. **Actas 2...**: 283-306.
- BONAPARTE, J.F., 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. **Opera Lilloana**, **22**:1-184.
- BONAPARTE, J.F., 1986. History of the terrestrial vertebrates of Gondwana. CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, 4., 1986, Mendoza. **Actas...**, **2**. p.63-95.
- BONAPARTE, J.F., 1991. Los vertebrados fósiles de la Formación Río Colorado, de la Ciudad de Neuquén y cercanías, Cretácico Superior, Argentina. **Revista del Museo Argentino de Paleontología "Bernardino Rivadavia" - Paleontología**, **4**:17-123.
- BRETT-SURMAN, M.K., 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. **Nature**, **277**:560-562.
- BROCHU, C.A., 1997a. Fossils, morphology, divergence timing, and the phylogenetic relationships of *Gavialis*. **Systematic Biology**, **46**:479-522.
- BROCHU, C.A., 1997b. A review of "*Leidyosuchus*" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. **Journal of Vertebrate Paleontology**, **17**:679-697.
- BUCKLEY, G.A. & BROCHU, C.A., 1999. An enigmatic new crocodile from the Upper Cretaceous of Madagascar. **Special Papers in Palaeontology**, **60**:149-175.
- BUCKLEY, G.A.; BROCHU, C.A.; KRAUSE, D.W. & POL, D., 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. **Nature**, **405**:941-944.
- BUFFETAUT, E., 1978. Les Dyrosauridae (Crocodylia, Mesosuchia) des phosphates de l'Eocene inferieur de Tunisie: *Dyrosaurus*, *Rhabdognathus*, *Phosphatosaurus*. **Geologie Méditerranéenne**, **5**:237-256.
- BUFFETAUT, E., 1979. *Sokotosuchus ianwilsoni* and the evolution of the Dyrosaurid crocodylians. **Nigerian Field Monographs**, **1**:31-41.
- BUFFETAUT, E., 1982. Radiation évolutive, paleoecologie et biogeographie des crocodyliens mesosuchiens. **Memoires de la Société Géologique de France**, **60**:1-88.
- BUSBY, A.B. & GOW, C., 1984. A new protosuchian crocodile from the Upper Triassic Elliot Formation of South Africa. **Palaeontologia Africana**, **25**:127-149.
- BUSCALIONI, A.D. & SANZ, J.L., 1988. Phylogenetic relationships of the Atoposauridae (Archosauria, Crocodylomorpha). **Historical Biology**, **1**:233-250.
- BUSCALIONI, A.D. & SANZ, J.L., 1990. The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). **Bulletin de l'Institut Royal des Sciences Naturelles de Belgique**, **60**:129-150.

- CALVO, J.O.; ENGELLAND, S.; HEREDIA, S. & SALGADO, L., 1997. First record of dinosaur eggshells (?Sauropoda-Megaloolithidae) from Neuquén, Patagonia, Argentina. **Gaia**, **14**:23-32.
- CAMPOS, D.A.; MARTIN SUARES, J.M.; RIFF, D. & KELLNER, A.W.A., 2001. Short note on a new Baurusuchidae (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. **Boletim do Museu Nacional, Nova Série, Geologia**, **57**:1-7.
- CARVALHO, I.S., 1994. *Candidodon*: um crocodilo com heterodontia (Notosuchia, Cretáceo Inferior - Brasil). **Anais da Academia Brasileira de Ciências**, **66**:331-346.
- CARVALHO, I.S. & BERTINI, R.J., 1999. *Mariliasuchus*: um novo Crocodylomorpha (Notosuchia) do Cretáceo da Bacia Bauru, Brasil. **Geología Colombiana**, **24**:83-105.
- CARVALHO, I.S.; RIBEIRO, L.C.B. & AVILLA, L.S., 2004. *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. **Gondwana Research**, **7**:975-1002.
- CHIAPPE, L.M. & CALVO, J.O., 1994. *Neuquenornis volans*, a new Late Cretaceous bird (Enantiornithes: Avisauridae) from Patagonia, Argentina. **Journal of Vertebrate Paleontology**, **14**:230-246.
- CLARK, J.M., 1985. **A new crocodylomorph from the Late Jurassic Morrison Formation of Western Colorado, with a discussion of relationships within the 'Mesosuchia'**. 86p. M.Sc. Thesis, University of California, Berkeley.
- CLARK, J.M., 1986. **Phylogenetic relationships of the Crocodylomorph Archosaurs**. 556p. Ph.D. Dissertation, University of Chicago, Chicago.
- CLARK, J. M., 1994. Patterns of evolution in Mesozoic Crocodyliformes. In: FRASER, N.C. & SUES, H.-D. (Ed.) **In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods**. New York: Cambridge University Press. p.84-97.
- CLARK, J.M. & NORELL, M.A., 1992. The Early Cretaceous Crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. **American Museum Novitates**, **3032**:1-19.
- CLARK, J.M.; JACOBS, L.L. & DOWNS, W.R., 1989. Mammal-like dentition in a Mesozoic crocodylian. **Science**, **244**:1064-1065.
- CLARK, J.A.; SUES, H.-D. & BERMAN, D.S., 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. **Journal of Vertebrate Paleontology**, **20**:683-704.
- CLARK, J.M.; XU, X.; FORSTER, C.A. & WANG, Y., 2004. A Middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. **Nature**, **430**:1021-1024.
- COLBERT, E.C. & MOOK, C.C., 1951. The ancestral crocodile *Protosuchus*. **Bulletin of the American Museum of Natural History**, **97**:143-182.
- COOPER, A.; LALUEZA-FOX, C.; ANDERSON, S.; RAMBAUT, A.; AUSTIN, J. & WARD, R., 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. **Nature**, **409**:704-707.
- CRUSH, P.J., 1984. A late Upper Triassic sphenosuchid crocodylian from Wales. **Palaeontology**, **27**:131-157.
- DIÉGUEZ, C., MARTÍN-CLOSAS, C., MELÉNDEZ, N., RODRIGUEZ-LAZÁRO, J. & TRINÇO, P., 1995. Biostratigraphy, In: MELÉNDEZ, N. (Ed.) **Las Hoyas. A lacustrine Konservat-Lagerstätte, Cuenca, Spain**. International Symposium on Lithographic Limestones, 2., 1995. Field Trip Guide Book. Madrid: Ediciones Universidad Complutense de Madrid. p.77-79.
- DODSON, P., 1975. Functional and ecological significance of relative growth in *Alligator*. **Journal of Zoology**, **175**:315-355.
- EFIMOV, M.B., 1983. [Review of crocodylians from Mongolia.] **Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii**, **24**:79-96.
- EFIMOV, M.B., 1988. [On the fossil crocodiles of Mongolia and the USSR.] (in Russian). **Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii**, **34**:81-90.
- EFIMOV, M.B., 1996. The Jurassic crocodylomorphs of Inner Asia. **Bulletin of the Museum of Northern Arizona**, **60**:305-310.
- EFIMOV, M.B.; GUBIN, Y.M. & KURZANOV, S.M., 2000. New primitive crocodile (Crocodylomorpha: Shartegosuchidae) from the Jurassic of Mongolia. **Paleontologicheskii Zhurnal**, **34**:S238-S241.
- EFIMOV, M.B. & LESHCHINSKIY, S.V., 2000. First finding of the fossil crocodile skull in Siberia [in Russian]. In: KOMAROV, A.V. (Ed.) **Materialy regional'noj konferencii geologov Sibiri, Dal'nego Vostoka i Severo-Vostoka Rossii**. Tomsk: GalaPress. Tom II, p.61-363.
- ERICKSON, B.R., 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. **Monograph of the Science Museum of Minnesota Paleontology**, **2**:1-61.
- EUDES-DESLONGCHAMPS, J.A., 1863. Memoires sur les teleosauriens de l'Epoque Jurassique du Departement du Calvados. **Memoires de la Société Linneenne de Normandie**, **12**:1-138.
- FIORELLI, L.E., 2005. **Nuevos restos de Notosuchus terrestris Woodward, 1896 (Crocodyliformes:**



- Mesoeucrocodylia) del Cretácico Superior (Santoniano) de la Provincia de Neuquén, Patagonia, Argentina.** 79p. Tesis de Grado, Universidad Nacional de Córdoba, Córdoba.
- FIGLIOTTI, L.E.; JUÁREZ VALIERI, R.D. & SALINAS, G.C., 2006. Relaciones filogenéticas de "Shartegosuchidae" Efimov (Crocodyliformes: Mesoeucrocodylia) del Jurásico y Cretácico de Asia Central. In: CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, 9., 2006, Córdoba. **Resúmenes...** Córdoba. p.83.
- FIGLIOTTI, L.E.; POL, D.; PORFIRI, J.D.; CALVO, J.O. & JUÁREZ VALIERI, R.D., 2007. Peirosaurid affinities of a crocodyliform from the Bajo de la Carpía Formation, Upper Cretaceous, Neuquén. In: REUNIÓN ANUAL DE COMUNICACIONES DE LA ASOCIACIÓN PALEONTOLOGICA ARGENTINA, 2007. Corrientes. **Resúmenes...** Corrientes. p.28.
- GASPARINI, Z.B., 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo infraorden de Mesosuchia (Crocodylia). **Ameghiniana**, **8**:83-103.
- GASPARINI, Z.B.; CHIAPPE, L.M. & FERNANDEZ, M., 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodylians. **Journal of Vertebrate Paleontology**, **11**:316-333.
- GASPARINI, Z.B. & DIAZ, G.C., 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodylia, Thalattosuchia) a marine crocodile from the Jurassic (Callovian) of Chile, South America. **Neues Jahrbuch für Geologie und Paläontologie Abhandlungen**, **153**:341-360.
- GASPARINI, Z.B.; FERNANDEZ, M. & POWELL, J., 1993. New Tertiary Sebecosuchians (Crocodylomorpha) from South America: phylogenetic implications. **Historical Biology**, **7**:1-19.
- GÖHLICH, U.B.; CHIAPPE, L.M.; CLARK, J.M. & SUES, H.-D., 2005. The systematic position of the Late Jurassic alleged dinosaur *Macelognathus* (Crocodylomorpha: Sphenosuchia). **Canadian Journal of Earth Sciences**, **42**:307-321.
- GOLOBOFF, P.A., 1993. NONA version 1.9, program and documentation distributed by the author. San Miguel de Tucumán.
- GOMANI, E.M., 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds, Northern Malawi. **Journal of Vertebrate Paleontology**, **17**:280-294.
- HASTEAD, L.B., 1975. *Sokotosuchus ianwilsoni* n.g., n.sp., a new teleosaur crocodile from the Upper Cretaceous of Nigeria. **Journal of the Nigerian Mining, Geological, and Metallurgical Society**, **11**:101-103.
- HAY, J.M.; RUVINSKY, I.; HEDGES, S.B. & MAXSON, L.R., 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. **Molecular Biological Evolution**, **12**:928-937.
- HAY, O.P., 1930. **Second Bibliography and Catalogue of the Fossil Vertebrata of North America**. Washington: Carnegie Institution of Washington. 2v.
- HEDGES, S.B., 2001. Afrotheria: Plate tectonics meets genomics. **Proceedings of the National Academy of Sciences of the United States of America**, **98**:1-2.
- HEDGES, S.B. & POLING, L.L., 1999. A molecular phylogeny of reptiles. **Science**, **283**:998-1001.
- HOFFSTETTER, R. & GASC, J.P., 1969. Vertebrae and ribs of modern reptiles. In: GANS, C.; BELLAIRS, A.d'A. & PARSONS, T.S. (Eds.) **Biology of the Reptilia**. London & New York: Academic Press. 1v., p.201-210.
- JUÁREZ VALIERI, R.D. & FIGLIOTTI, L.E., 2002. Distribución de taxa de tetrápodos continentales mesozoicos: división de Gondwana y conexiones con otras masas continentales. In: CONGRESO LATINOAMERICANO DE PALEONTOLOGÍA DE VERTEBRADOS, 1., 2002, Santiago de Chile. **Resúmenes...** Santiago de Chile: Universidad de Chile. p.37.
- JUÁREZ VALIERI, R.D. & FIGLIOTTI, L.E., 2003. Posibles evidencias de intercambio de faunas entre Gondwana y Asia Central durante el Cretácico Inferior. **Ameghiniana**, **40**:59R.
- KÄLIN, J.A. 1955. Crocodylia. In: PIVETEAU, J. (Ed.) **Traité de Palaeontologie**. Paris: Masson et Cie. v.5, p.695-784.
- KURZANOV, S.M.; EFIMOV, M.B. & GUBIN, Y.M., 2003. New archosaurs from the Jurassic of Siberia and Mongolia. **Paleontologicheskii Zhurnal**, **37**:53-57.
- LEANZA, H.A.; APESTEGUÍA, S.; NOVAS, F.E. & DE LA FUENTE, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. **Cretaceous Research**, **25**:61-87.
- LI, J., 1985. A revision of *Edentosuchus tienshanensis* young from the Tugulu Group of Xinjiang Autonomous Region. (translated from Chinese). **Vertebrata Palasiatica**, **23**:196-206.
- LI, J.; WU, X.-C. & LI, X., 1994. New material of *Hsisosuchus chungkingensis* from Sichuan, China. **Vertebrata Palasiatica**, **32**:107-126.
- MARTINELLI, A.G., 2003. New cranial remains of the bizarre notosuchid *Comahuesuchus brachybuccalis* (Archosauria, Crocodyliformes) from the Late Cretaceous of Rio Negro Province (Argentina). **Ameghiniana**, **40**:559-572.

- MEYER, A. & ZARDOYA, R., 2003. Recent advances in the (molecular) phylogeny of vertebrates. **Annual Review of Ecology, Evolution and Systematics**, **34**:311-338.
- MOOK, C.C., 1942. Skull characters of *Amphicotylus lucasii* Cope. **American Museum Novitates**, **1202**:1-5.
- MOOK, C.C., 1967. Preliminary description of a new goniopholid crocodylian. **Kirtlandia**, **2**:1-10.
- MURPHY, W.J.; EIZIRIK, E.; JOHNSON, W.E.; ZHANG, Y.P.; RYDER, O.A. & O'BRIEN, S.J., 2001. Molecular phylogenetics and the origins of placental mammals. **Nature**, **409**:614-618.
- NASH, D.S., 1975. The morphology and relationships of a crocodylian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. **Annals of the South African Museum**, **67**:227-329.
- NIXON, K.C., 1999. *Winclada* (Beta) ver. 0.9.9. Publisher by the autor. Ithaca, New York.
- NOBRE, P.H. & CARVALHO, I.S., 2002. Osteologia do crânio de *Candidodon itapecuruense* (Crocodylomorpha, Mesoeucrocodylia) do Cretáceo do Brasil. In: SIMPÓSIO SOBRE O CRETÁCEO DO BRASIL, 6., / SIMPÓSIO SOBRE EL CRETÁCICO DE AMERICA DEL SUR, 2., 2002, São Pedro. **Boletim...** Rio Claro: Universidade Estadual Paulista. p.77-82.
- NORELL, M.A. & CLARK, J.M., 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. **Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre**, **60**:115-128.
- ORTEGA, F.; BUSCALIONI, A.D. & GASPARINI, Z.B., 1996. Reinterpretation and new denomination of *Atacisaurus crassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha: Metasuchia). **Geobios**, **29**:353-364.
- ORTEGA, F.; GASPARINI, Z.; BUSCALIONI, A.D. & CALVO, J.O., 2000. A new species of *Araripesuchus* (Crocodylomorpha: Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). **Journal of Vertebrate Paleontology**, **20**:57-76.
- OSMÓLSKA, H., 1972. Preliminary note on a crocodylian from the Upper Cretaceous of Mongolia. **Palaeontologica Polonica**, **27**:43-47.
- OSMÓLSKA, H.; HUA, S. & BUFFETAUT, E., 1997. *Gobiosuchus kielanae* (Protosuchia) from the Late Cretaceous of Mongolia: anatomy and relationships. **Acta Palaeontologica Polonica**, **42**:257-289.
- OWEN, R., 1878. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement VIII, Crocodylia (*Goniopholis*, *Petrosuchus* and *Suchosaurus*). **Palaeontographical Society of London Monograph**, **32**:1-15.
- OWEN, R., 1879. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement IX, Crocodylia (*Goniopholis*, *Brachydectes*, *Nannosuchus*, *Theriosuchus* and *Nuthetes*). **Palaeontographical Society of London Monograph**, **33**:1-19.
- PENG, G.Z., 1996. A Late Jurassic protosuchian *Sichuanosuchus huidongensis* from Zigong, Sichuan Province. (translated from chinese). **Vertebrata Palasiatica**, **34**:269-278.
- POL, D., 1999a. **El esqueleto postcraniano de *Notosuchus terrestris* (Archosauria: Crocodyliformes) del Cretácico Superior de la Cuenca Neuquina y su información filogenética**. 158p. Tesis de Licenciatura. Universidad de Buenos Aires, Buenos Aires.
- POL, D., 1999b. Basal mesoeucrocodylian relationships: new clues to old conflicts. **Journal of Vertebrate Paleontology**, **19**:69A.
- POL, D., 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. **Journal of Vertebrate Paleontology**, **23**:817-831.
- POL, D., 2005. Postcranial remains of *Notosuchus terrestris* (Archosauria: Crocodyliformes) from the Upper Cretaceous of Patagonia, Argentina. **Ameghiniana**, **42**:21-38.
- POL, D. & APESTEGUÍA, S., 2005. New *Araripesuchus* remains from the Early Late Cretaceous (Cenomanian-Turonian) of Patagonia. **American Museum Novitates**, **3490**:1-38.
- POL, D. & NORELL, M.A., 2004a. A new crocodyliform from Zos Canyon, Mongolia. **American Museum Novitates**, **3445**:1-36.
- POL, D. & NORELL, M.A., 2004b. A new Gobiosuchid Crocodyliform taxon from the Cretaceous of Mongolia. **American Museum Novitates**, **3458**:1-31.
- POL, D.; JI, S.; CLARK, J.M. & CHIAPPE, L.M., 2004. Basal crocodyliforms from the Lower Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*. **Cretaceous Research**, **25**:603-622.
- PORFIRI, J.D. & CALVO, J.O., 2006. A new record of Carnosaurinae (Theropoda: Abelisauridae) from the Upper Cretaceous of Neuquén, Patagonia. In: ANNUAL MEETING OF THE SOCIETY OF VERTEBRATE PALEONTOLOGY. 66., 2006, Ottawa. **Abstracts...** Northbrook: Society of Vertebrate Paleontology. p.111A-112A.

- PRICE, L.I., 1945. A new reptile from the Cretaceous of Brazil. **Notas Preliminares e Estudos, Serviço Geológico Mineralógico do Brasil**, **25**:1-8.
- PRICE, L.I., 1950. On a new crocodylian, *Sphagesaurus*, from the Cretaceous of the State of São Paulo, Brazil. **Anais Academia Brasileira de Ciências**, **22**:77-83.
- PRICE, L.I., 1955. Novos crocodylideos dos arenitos da Serie Baurú, Cretáceo do Estado de Minas Gerais. **Anais Academia Brasileira de Ciências**, **22**:487-498.
- PRICE, L.I., 1959. Sobre um crocodylideo notossúquio do Cretácico Brasileiro. **Boletim do Departamento Nacional da Produção Mineral, Diviso de Geologia e Mineralogia**, **188**:7-55.
- ROMER, A.S., 1956. **Osteology of the Reptiles**. Chicago: Chicago University Press. 772p.
- ROMER, A.S., 1972. The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanicorum*, gen. et sp. nov. **Breviora**, **389**:1-24.
- RUSCONI, C., 1933. Sobre reptiles cretácicos del Uruguay (*Uruguaysuchus aznarezi*, n. g. n. sp.) y sus relaciones con los notosúquidos de Patagonia. **Boletín Instituto de Geología y Perforaciones Montevideo Uruguay**, **19**:1-64.
- RUSSELL, D.A., 1993. The role of Central Asia in dinosaurian biogeography. **Canadian Journal of Earth Sciences**, **30**:2002-2012.
- SALISBURY, S.W.; WILLIS, P.M.A.; PEITZ, S. & SANDER, P.M., 1999. The crocodylian *Goniopholis simus* from the Lower Cretaceous of North-western Germany. **Special Papers in Palaeontology**, **60**:121-148.
- SANZ, J.L.; WENZ, S.; YÉBENES, A.; ESTES, R.; MARTÍNEZ-DELCLÒS, X.; JIMÉNEZ-FUENTES, E.; DIÉGUEZ, C.; BUSCALIONI, A.D.; BARBADILLO, L.J. & VÍA, L., 1988. An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). **Geobios**, **21**:611-635.
- SCHWARZ, D.; FREY, E. & MARTIN, T., 2006. The postcranial skeleton of the Hyposaurinae (Dyrosauridae; Crocodyliformes). **Paleontology**, **49**:695-718.
- SCHWEITZER, M. H.; JACKSON, F. D.; CHIAPPE, L. M.; SCHMITT, J. G.; CALVO, J. O. & RUBILAR, D. E. 2002. Late Cretaceous avian eggs with embryos from Argentina. **Journal of Vertebrate Paleontology**, **22**:191-195.
- SERENO, P.C., 1991. Basal archosaurs: phylogenetic relationships and functional implications. **Memoir of the Society of Vertebrate Paleontology**, **2**:1-53.
- SERENO, P.C., 1999. Dinosaurian biogeography: vicariance, dispersal and regional extinction. In: TOMIDA, Y.; RICH, T.H. & VICKERS-RICH, P. (Eds.) **Proceedings of the Second Gondwanan Dinosaur Symposium, National Science Museum Monographs**, **15**. Tokio. p. 249-257.
- SERENO, P.C.; LARSSON, H.C.E.; SIDOR, C.A. & GADO, B., 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. **Science**, **294**:1516-1519.
- SERENO, P.C.; MCALLISTER, S. & BRUSATTE, S.L., 2005. *TaxonSearch*: a relational database for suprageneric taxa and phylogenetic definitions. **PhyloInformatics**, **8**:1-20.
- SERENO, P.C.; SIDOR, C.A.; LARSSON, H.C.E. & GADO, B., 2003. A new notosuchian from the Early Cretaceous of Niger. **Journal of Vertebrate Paleontology**, **23**:477-482.
- SERENO, P.C. & WILD, R., 1992. *Procompsognathus*: theropod, "thecodont" or both? **Journal of Vertebrate Paleontology**, **12**:435-458.
- SUES, H.-D.; OLSEN, P.E.; CARTER, J.G. & SCOTT, D.M., 2003. A new crocodylomorph archosaur from the Upper Triassic of North Carolina. **Journal of Vertebrate Paleontology**, **23**:329-343.
- TURNER, A.H.T., 2004. Crocodyliform biogeography during the Cretaceous: evidence of Gondwanan vicariance from biogeographical analysis. **Proceedings of the Royal Society of London B**, **271**:2003-2009.
- TURNER, A.H.T., 2006. Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. **Historical Biology**, **18**:255-369.
- TURNER, A.H.T. & CALVO, J.O., 2005. A new sebecosuchian crocodyliform from the Late Cretaceous of Patagonia. **Journal of Vertebrate Paleontology**, **25**:87-98.
- TYKOSKI, R.S.; ROWE, T.B.; KETCHAM, R.A. & COLBERT, M.W., 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. **Journal of Vertebrate Paleontology**, **22**:593-611.
- WALKER, A.D., 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. **Philosophical Transactions of the Royal Society of London**, **257**:323-372.
- WELLNHOFER, P., 1971. Die Atoposauridae (Crocodylia, Mesosuchia) der Oberjura-Plattenkalke Bayerns. **Palaeontographica**, **138**:133-165.
- WHETSTONE, K.N. & WHYBROW, P.J., 1983. A "cursorial" crocodylian from the Triassic of Lesotho (Busotoland), Southern Africa. **Occasional Papers of the Museum of Natural History**, **106**:1-37.

- WOODWARD, A.S., 1896. On two Mesozoic crocodylians *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum), from the Red Sandstones of the Territory of Neuquén (Argentina Republic). **Anales del Museo de La Plata, Paleontología**, **4**:1-20.
- WOODWARD, A.S., 1901. On some extinct reptiles from Patagonia of the genera *Miolana*, *Dinilysia* and *Genyodectes*. **Proceedings of the Zoological Society of London**, **1**:169-184.
- WU, X.-C.; BRINKMAN, D.B. & LU, J.-C., 1994. A new species of *Shantungosuchus* from the Lower Cretaceous of Inner Mongolia (China), with comments on *S. chuhsienensis* Young, 1961, and the phylogenetic position of the genus. **Journal of Vertebrate Paleontology**, **14**:210-229.
- WU, X.-C. & CHATTERJEE, S., 1993. *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. **Journal of Vertebrate Paleontology**, **13**:58-89.
- WU, X.-C. & SUES, H.-D., 1996. Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. **Journal of Vertebrate Paleontology**, **16**:688-702.
- WU, X.-C.; SUES, H.-D. & BRINKMAN, D.B., 1996. An atoposaurid neosuchian (Archosauria: Crocodyliformes) from the Lower Cretaceous of Inner Mongolia (People's Republic of China). **Canadian Journal of Earth Sciences**, **33**:599-605.
- WU, X.-C.; SUES, H.-D. & DONG, Z.-M., 1997. *Sichuanosuchus shuhanensis*, a new ?Early Cretaceous protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. **Journal of Vertebrate Paleontology**, **17**:89-103.
- YOUNG, C.C., 1961. *Shantungosuchus chuhsienensis*, a new crocodile. **Vertebrata Palasiatica**, **5**:6-15.
- YOUNG, C.C., 1973. A new fossil crocodile from Wuerho. **Memoirs Institute Vertebrate Paleontology and Paleoanthropology**, **11**:37-44.
- YOUNG, C.C. & CHOW, M.C., 1953. New discovery of Reptilia from the Mesozoic of Sichuan. **Acta Palaeontologica Sinica**, New Series C, **1**:87-111.
- ZAHER, H.; POL, D; CARVALHO, A.B.; RICOMINI, C.; CAMPOS, D. & NAVA, W., 2006. Redescription of the cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). **American Museum Novitates**, **3512**:1-40.

## APPENDIX I

LISTS OF CHARACTERS CORRESPONDING TO THE DATA MATRIX  
(SEE APPENDIX III) USED IN THE PHYLOGENETIC ANALYSES

Definitions of the characters 1-101 were taken from CLARK (1994) and they have the same numeration like in the original publication. The character 5 was excluded of this analysis (due to the dependence with the modified definition of the character 6). Nevertheless, this exclusion does not affect the result of these analyses. The following ones, 102 to 192 characters, were taken from POL & NORELL (2004b). They are listed in order in relation to the same publication and the source mentioned together with the number of original character. The characters 193 and 194 were taken and designated by POL *et al.* (2004), corresponding originally to the characters 164 and 179, respectively. The characters 195, 196, and 197 were taken from WU & SUES (1996) that originally corresponded to the characters 6, 17 and 31, respectively. Although the characters 198 and 199 were taken from MARTINELLI (2003) they originally corresponded to the respective characters 35 and 36. The characters 200 and 210 were designated by FIORELLI (2005) and the numerations are the same ones. The characters 215 and 218 were taken and modified from POL (1999a) corresponding to the characters 192 and 191, respectively. Character 226 is taken and modified from SERENO (1991) corresponding to the character 27. The characters 1, 3, 6, 23, 37, 45, 49, 65, 67, 69, 73, 77, 79, 90, 91, 96, 97, 103, 104, 105, 107, 126, 143, 149, and 165 were taken as additive characters (also marked with "+" in this list). For finish, the characters 211-214, 216, 217, 219-225, and 227-231 are new, designated by the authors.

- CHARACTER 1 (modified from CLARK, 1994: character 1): + External surface of dorsal cranial bones: smooth (0), slightly grooved (1) and heavily ornamented with deep pits and grooves (2).
- CHARACTER 2 (modified from CLARK, 1994: character 2): Skull expansion at orbits: gradual (0), or abrupt (1).
- CHARACTER 3 (modified from CLARK, 1994: character 3): + Rostrum proportions: narrow oreinirostral (0), broad oreinirostral (1), nearly tubular (2), or platyrostral (3).
- CHARACTER 4 (CLARK, 1994: character 4): Premaxilla participation in internarial bar: forming at least the ventral half (0), or with little participation (1).
- CHARACTER 5 (CLARK, 1994: character 5): Premaxilla anterior to nares: narrow (0), or broad (1).
- CHARACTER 6 (modified from CLARK, 1994: character 6): + External nares facing anterolaterally or anteriorly (0), dorsally not separated by premaxillary bar from anterior edge of rostrum (1), or dorsally separated by premaxillary bar (2).
- CHARACTER 7 (CLARK, 1994: character 7): Palatal parts of premaxillae: do not meet posterior to incisive foramen (0), or meet posteriorly along contact with maxillae (1).
- CHARACTER 8 (CLARK, 1994: character 8): Premaxilla-maxilla contact: premaxilla loosely overlies maxilla (0), or sutured together along a butt joint (1).
- CHARACTER 9 (modified from CLARK, 1994: character 9): Ventrally opened notch on ventral edge of rostrum at premaxilla-maxilla contact: absent (0), present as a notch (1), or present as a large fenestra (2).
- CHARACTER 10 (CLARK, 1994: character 10): Posterior ends of palatal branches of maxillae anterior to palatines: do not meet (0), or meet (1).
- CHARACTER 11 (CLARK, 1994: character 11): Nasal contacts lacrimal (0), or does not contact (1).
- CHARACTER 12 (CLARK, 1994: character 12): Lacrimal contacts nasal along medial edge only (0), or medial and anterior edges (1).
- CHARACTER 13 (CLARK, 1994: character 13): Nasal contribution to narial border: yes (0), or no (1).
- CHARACTER 14 (CLARK, 1994: character 14): Nasal-premaxilla contact: present (0), or absent (1).
- CHARACTER 15 (modified from CLARK, 1994: character 15): Descending process of prefrontal: does not contact palate (0), or contacts palate (1).
- CHARACTER 16 (CLARK, 1994: character 16): Postorbital-jugal contact: postorbital anterior to jugal (0), or postorbital medial to jugal (1), or postorbital lateral to jugal (2).
- CHARACTER 17 (CLARK, 1994: character 17): Anterior part of the jugal with respect to posterior part: as broad (0), or twice as broad (1).
- CHARACTER 18 (CLARK, 1994: character 18): Jugal bar beneath infratemporal fenestra: flattened (0), or rod-shaped (1).
- CHARACTER 19 (CLARK, 1994: character 19): Quadratojugal dorsal process: narrow, contacting only a small part of postorbital (0), or broad, extensively contacting the postorbital (1).
- CHARACTER 20 (CLARK, 1994: character 20): Frontal width between orbits: narrow, as broad as nasals (0), or broad, twice as broad as nasals (1).
- CHARACTER 21 (CLARK, 1994: character 21): Frontals: paired (0), unpaired (1).
- CHARACTER 22 (CLARK, 1994: character 22): Dorsal surface of frontal and parietal: flat (0), or with midline ridge (1).
- CHARACTER 23 (modified from CLARK, 1994: character 23 by BUCKLEY & BROCHU, 1999: character 81): + Parieto-postorbital suture: absent from dorsal surface of skull roof and supratemporal fossa (0), absent from dorsal surface of skull roof but broadly present within supratemporal fossa (1), or present within supratemporal fossa and on dorsal surface of skull roof (2).

- CHARACTER 24 (CLARK, 1994: character 24): Supratemporal roof dorsal surface: complex (0), or dorsally flat “skull table” developed, with postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (1).
- CHARACTER 25 (modified from CLARK, 1994: character 25) Postorbital bar: sculpted (if skull sculpted) (0), or unsculpted (1).
- CHARACTER 26 (modified from CLARK, 1994: character 26): Postorbital bar: transversely flattened (0), or cylindrical (1).
- CHARACTER 27 (CLARK, 1994: character 27): Vascular opening in dorsal surface of postorbital bar: absent (0), or present (1).
- CHARACTER 28 (modified from CLARK, 1994: character 28): Postorbital anterolateral process: absent or poorly developed (0), or well developed, long, and acute (1).
- CHARACTER 29 (CLARK, 1994: character 29): Dorsal part of the postorbital: with anterior and lateral edges only (0), or with anterolaterally facing edge (1).
- CHARACTER 30 (CLARK, 1994: character 30): Dorsal end of the postorbital bar broadens dorsally, continuous with dorsal part of postorbital (0), or dorsal part of the postorbital bar constricted, distinct from the dorsal part of the postorbital (1).
- CHARACTER 31 (CLARK, 1994: character 31): Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0), or bar narrow, sculpting restricted to anterior surface (1).
- CHARACTER 32 (modified from CLARK, 1994: character 32): Parietal: with broad occipital portion (0), or without broad occipital portion (1).
- CHARACTER 33 (CLARK, 1994: character 33): Parietal: with broad sculpted region separating fossae (0), or with sagittal crest between supratemporal fossae (1).
- CHARACTER 34 (CLARK, 1994: character 34): Postparietal (dermosupraoccipital): a distinct element (0), or not distinct (fused with parietal?) (1).
- CHARACTER 35 (CLARK, 1994: character 35): Posterodorsal corner of the squamosal: squared off, lacking extra “lobe” (0), or with unsculptured “lobe” (1).
- CHARACTER 36 (modified from CLARK, 1994: character 36): Posterolateral process of squamosal: poorly developed and projected horizontally at the same level of the skull (0), elongated, thin, and posteriorly directed, not ventrally deflected (1), or elongated, posterolaterally directed, and ventrally deflected (2).
- CHARACTER 37 (CLARK, 1994: character 37): + Palatines: do not meet on palate below the narial passage (0), form palatal shelves that do not meet (1), or meet ventrally to the narial passage, forming part of secondary palate (2).
- CHARACTER 38 (CLARK, 1994: character 38): Pterygoid: restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of the trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).
- CHARACTER 39 (modified from CLARK, 1994: character 39): Choanal opening: continuous with pterygoid ventral surface except for anterior and anterolateral borders (0), or opens into palate through a deep midline depression (choanal groove) (1).
- CHARACTER 40 (CLARK, 1994: character 40): Palatal surface of pterygoids: smooth (0), or sculpted (1).
- CHARACTER 41 (CLARK, 1994: character 41): Pterygoids posterior to choanae: separated (0), or fused (1).
- CHARACTER 42 (modified from CLARK, 1994: character 42 by ORTEGA *et al.*, 2000: character 139): Depression on primary pterygoidean palate posterior to choana: absent or moderate in size being narrower than palatine bar (0), or wider than palatine bar (1).
- CHARACTER 43 (CLARK, 1994: character 43): Pterygoids: do not enclose choana (0), or enclose choana (1).
- CHARACTER 44 (modified from CLARK, 1994: character 44): Anterior edge of choanae situated near posterior edge of suborbital fenestra (or anteriorly) (0), or near posterior edge of pterygoid flanges (1).
- CHARACTER 45 (CLARK, 1994: character 45): + Quadrate: without fenestrae (0), with single fenestrae (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).
- CHARACTER 46 (CLARK, 1994: character 46): Posterior edge of quadrate: broad medial to tympanum, gently concave (0), or posterior edge of quadrate narrow dorsal to otoccipital contact, strongly concave (1).
- CHARACTER 47 (CLARK, 1994: character 47): Dorsal, primary head of quadrate articulates with squamosal, otoccipital, and prootic (0), or with prootic and laterosphenoid (1).
- CHARACTER 48 (CLARK, 1994: character 48): Ventrolateral contact of otoccipital with quadrate: very narrow (0), or broad (1).
- CHARACTER 49 (CLARK, 1994: character 49): + Quadrate, squamosal, and otoccipital: do not meet to enclose cranioquadrate passage (0), enclose passage near lateral edge of skull (1), or meet broadly lateral to the cranioquadrate passage (2).
- CHARACTER 50 (CLARK, 1994: character 50): Pterygoid ramus of quadrate: with flat ventral edge (0), or with deep groove along ventral edge (1).
- CHARACTER 51 (CLARK, 1994: character 51): Ventromedial part of quadrate: does not contact otoccipital (0), or contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (1).
- CHARACTER 52 (CLARK, 1994: character 52): Eustachian tubes: not enclosed between basioccipital and basisphenoid (0), or entirely enclosed (1).
- CHARACTER 53 (CLARK, 1994: character 53): Basisphenoid rostrum (cultriform process): slender (0), or dorsoventrally expanded (1).

- CHARACTER 54 (CLARK, 1994: character 54): Basispterygoid process: prominent, forming movable joint with pterygoid (0), or basispterygoid process small or absent, with basisphenoid joint suturally closed (1).
- CHARACTER 55 (modified from CLARK, 1994: character 55 by ORTEGA *et al.*, 2000: character 68): Basisphenoid ventral surface: shorter than the basioccipital (0), or wide and similar to, or longer in length than basioccipital (1).
- CHARACTER 56 (CLARK, 1994: character 56): Basisphenoid: exposed on ventral surface of braincase (0), or virtually excluded from ventral surface by pterygoid and basioccipital (1).
- CHARACTER 57 (CLARK, 1994: character 57): Basioccipital: without well-developed bilateral tuberosities (0), or with large pendulous tubera (1).
- CHARACTER 58 (CLARK, 1994: character 58): Otoccipital: without laterally concave descending flange ventral to subcapsular process (0), or with flange (1).
- CHARACTER 59 (CLARK, 1994: character 59): Cranial nerves IX–XI: pass through common large foramen vagi in otoccipital (0), or cranial nerve IX passes medial to nerves X and XI in separate passage (1).
- CHARACTER 60 (CLARK, 1994: character 60): Otoccipital: without large ventrolateral part ventral to paroccipital process (0), or with large ventrolateral part (1).
- CHARACTER 61 (CLARK, 1994: character 61): Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0), or horizontal (1).
- CHARACTER 62 (CLARK, 1994: character 62): Supraoccipital: forms dorsal edge of the foramen magnum (0), or otoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (1).
- CHARACTER 63 (CLARK, 1994: character 63): Mastoid antrum: does not extend into supraoccipital (0), or extends through transverse canal in supraoccipital to connect middle ear regions (1).
- CHARACTER 64 (CLARK, 1994: character 64): Posterior surface of supraoccipital: nearly flat (0), or with bilateral posterior prominences (1).
- CHARACTER 65 (modified from CLARK, 1994: character 65): + One small palpebral present in orbit (0), one large palpebral (1), or two large palpebrals (2).
- CHARACTER 66 (CLARK, 1994: character 66): External nares: divided by a septum (0), or confluent (1).
- CHARACTER 67 (CLARK, 1994: character 67): + Antorbital fenestra: as large as orbit (0), about half the diameter of the orbit (1), much smaller than the orbit (2), or absent (3).
- CHARACTER 68 (modified from CLARK, 1994: character 68 by ORTEGA *et al.*, 2000: character 41): Supratemporal fenestrae extension: relatively large, covering most of surface of skull roof (0), or relatively short, fenestrae surrounded by a flat and extended skull roof (1).
- CHARACTER 69 (modified from CLARK, 1994: character 69): + Choanal groove: undivided (0), partially septated (1), or completely septated (2).
- CHARACTER 70 (CLARK, 1994: character 70): Dentary: extends posteriorly beneath mandibular fenestra (0), or does not extend beneath mandibular fenestra (1).
- CHARACTER 71 (modified from CLARK, 1994: character 71): Retroarticular process: absent or extremely reduced (0), very short, broad, and robust (1), with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially (2), posteriorly elongated, triangular-shaped and facing dorsally (3), or posteroventrally projecting and paddleshaped (4).
- CHARACTER 72 (CLARK, 1994: character 72): Prearticular: present (0), or absent (1).
- CHARACTER 73 (modified from CLARK, 1994: character 73): + Articular without medial process (0), with short process not contacting braincase (1), or with process articulating with otoccipital and basisphenoid (2).
- CHARACTER 74 (CLARK, 1994: character 74): Dorsal edge of surangular: flat (0), or arched dorsally (1).
- CHARACTER 75 (CLARK, 1994: character 75): Mandibular fenestra: present (0), or absent (1).
- CHARACTER 76 (CLARK, 1994: character 76): Insertion area for M. pterygoideus posterior: does not extend onto lateral surface of angular (0), or extends onto lateral surface of angular (1).
- CHARACTER 77 (modified from CLARK, 1994: character 77): + Splenial involvement in symphysis in ventral view: not involved (0), involved slightly in symphysis (1), or extensively involved (2).
- CHARACTER 78 (CLARK, 1994: character 78): Posterior premaxillary teeth: similar in size to anterior teeth (0), or much longer (1).
- CHARACTER 79 (modified from CLARK, 1994: character 79): + Maxillary teeth waves: absent, no tooth size variation (0), one wave of teeth enlarged (1), or enlarged maxillary teeth curved in two waves ("festooned") (2).
- CHARACTER 80 (CLARK, 1994: character 80): Anterior dentary teeth opposite premaxilla-maxilla contact: no more than twice the length of other dentary teeth (0), or more than twice the length of other dentary teeth (1).
- CHARACTER 81 (modified from CLARK, 1994: character 81): Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: equal in size (0), or enlarged dentary teeth opposite to smaller teeth in maxillary toothrow (1).
- CHARACTER 82 (modified from CLARK, 1994: character 82 by ORTEGA *et al.*, 2000: character 120): Anterior and posterior scapular edges: symmetrical in lateral view (0), anterior edge more strongly concave than posterior edge (1), or dorsally narrow with straight edges (2).

- CHARACTER 83 (modified from CLARK, 1994: character 83 by ORTEGA *et al.*, 2000: character 121): Coracoid length: up to two-thirds of the scapular length (0), or subequal in length to scapula (1).
- CHARACTER 84 (CLARK, 1994: character 84): Anterior process of ilium: similar in length to posterior process (0), or one-quarter or less of the length of the posterior process (1).
- CHARACTER 85 (CLARK, 1994: character 85): Pubis: rodlike without expanded distal end (0), or with expanded distal end (1).
- CHARACTER 86 (CLARK, 1994: character 86): Pubis: forms anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from the acetabulum by the anterior process of the ischium (1).
- CHARACTER 87 (CLARK, 1994: character 87): Distal end of femur: with large lateral facet for the fibula (0), or with very small facet (1).
- CHARACTER 88 (CLARK, 1994: character 88): Fifth pedal digit: with phalanges (0), or without phalanges (1).
- CHARACTER 89 (CLARK, 1994: character 89): Atlas intercentrum: broader than long (0), or as long as broad (1).
- CHARACTER 90 (modified from CLARK, 1994: character 90): + Cervical neural spines: all anteroposteriorly large (0), only posterior ones rodlike (1), or all spines rodlike (2).
- CHARACTER 91 (modified from CLARK, 1994: character 91 by BUSCALIONI & SANZ, 1988: character 37 and by BROCHU, 1997a: character 7): + Hypapophyses in cervicodorsal vertebrae: absent (0), present only in cervical vertebrae (1), present in cervical and the first two dorsal vertebrae (2), present up to the third dorsal vertebra (3), or present up to the fourth dorsal vertebrae (4).
- CHARACTER 92 (CLARK, 1994: character 92): Cervical vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).
- CHARACTER 93 (CLARK, 1994: character 93): Trunk vertebrae: amphicoelous or amphiplatian (0), or procoelous (1).
- CHARACTER 94 (CLARK, 1994: character 94): All caudal vertebrae: amphicoelous or amphiplatian (0), first caudal biconvex with other procoelous (1), or procoelous (2).
- CHARACTER 95 (CLARK, 1994: character 95): Dorsal osteoderms: rounded or ovate (0), or rectangular, broader than long (1), or square (2).
- CHARACTER 96 (modified from CLARK, 1994: character 96, and BROCHU, 1997a: character 40): + Dorsal osteoderms: without articular anterior process (0), with a discrete convexity on anterior margin (1), or with a well-developed process located anterolaterally in dorsal parasagittal osteoderms (2).
- CHARACTER 97 (modified from CLARK, 1994: character 97 by ORTEGA *et al.*, 2000: characters. 107 and 108): + Rows of dorsal osteoderms: two parallel rows (0), more than two rows (1), or more than four rows with "accessory ranges of osteoderms" (*sensu* Frey, 1988) (2).
- CHARACTER 98 (CLARK, 1994: character 98): Osteoderms: some or all imbricated (0), or sutured to one another (1).
- CHARACTER 99 (CLARK, 1994: character 99): Tail osteoderms: dorsal only (0), or completely surrounded by osteoderms (1).
- CHARACTER 100 (CLARK, 1994: character 100): Trunk osteoderms: absent from ventral part of the trunk (0), or present (1).
- CHARACTER 101 (CLARK, 1994: character 101): Osteoderms: with longitudinal keels on dorsal surfaces (0), or without longitudinal keels (1).
- CHARACTER 102 (WU & SUES, 1996: character 14): Jugal: participating in margin of antorbital fossa (0), or separated from it (1).
- CHARACTER 103 (modified from WU & SUES, 1996: character 23): + Articular facet for quadrate condyle: equal in length to the quadrate condyles (0), slightly longer (1), or close to three times the length of the quadrate condyles (2).
- CHARACTER 104 (modified from WU & SUES, 1996: character 24 and WU *et al.*, 1997: character 124): + Jaw joint: placed at level with basioccipital condyle (0), below basioccipital condyle about above level of lower toothrow (1), or below level of toothrow (2).
- CHARACTER 105 (modified from WU & SUES, 1996: character 27 and ORTEGA *et al.*, 2000: character 133): + Premaxillary teeth: five (0), four (1), three (2), or two (3).
- CHARACTER 106 (modified from WU & SUES, 1996: character 29): Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0), or present (1).
- CHARACTER 107 (WU & SUES, 1996: character 30): + Maxilla: with eight or more teeth (0), seven teeth (1), six teeth (2), five teeth (3), or four teeth (4).
- CHARACTER 108 (WU & SUES, 1996: character 33): Coracoid: without posteromedial or ventromedial process (0), with elongate posteromedial process (1), or distally expanded ventromedial process (2).
- CHARACTER 109 (WU & SUES, 1996: character 40): Radiale and ulnare: short and massive (0), or elongate (1).
- CHARACTER 110 (WU & SUES, 1996: character 41): Postacetabular process: directed posteroventrally or posteriorly (0), or directed posterodorsally and much higher in position than preacetabular process (1).
- CHARACTER 111 (modified from GOMANI, 1997: character 4): Prefrontals anterior to orbits: elongated, oriented parallel to anteroposterior axis of the skull (0), or short and broad, oriented posteromedially-anterolaterally (1).
- CHARACTER 112 (modified from GOMANI, 1997: character 32): Basioccipital and ventral part of otoccipital: facing posteriorly (0), or facing posteroventrally (1).
- CHARACTER 113 (BUSCALIONI & SANZ, 1988: character 35): Vertebral centra: cylindrical (0), or spool shaped (1).
- CHARACTER 114 (modified from BUSCALIONI & SANZ, 1988: character 39): Transverse process of posterior dorsal vertebrae



dorsoventrally low and laminar (0), or dorsoventrally high (1).

CHARACTER 115 (BUSCALIONI & SANZ, 1988: character 44): Number of sacral vertebrae: two (0), or more than two (1).

CHARACTER 116 (BUSCALIONI & SANZ, 1988: character 49): Supra-acetabular crest: present (0), or absent (1).

CHARACTER 117 (BUSCALIONI & SANZ, 1988: character 54): Proximal end of radiale expanded symmetrically, similarly to the distal end (0), or more expanded proximomedially than proximolaterally (1).

CHARACTER 118 (ORTEGA *et al.*, 1996: character 5): Lateral surface of the dentary: without a longitudinal depression (0), or with a longitudinal depression (1).

CHARACTER 119 (ORTEGA *et al.*, 1996: character 9): Ventral exposure of splenials: absent (0), or present (1).

CHARACTER 120 (ORTEGA *et al.*, 1996: character 11, ORTEGA *et al.*, 2000: character 100): Tooth margins: with denticulate carinae (0), or without carinae or with smooth or crenulated carinae (1).

CHARACTER 121 (modified from POL, 1999a: character 133 and ORTEGA *et al.*, 2000: character 145): Lateral surface of anterior process of jugal: flat or convex (0), or with broad shelf below the orbit with triangular depression underneath it (1).

CHARACTER 122 (POL, 1999a: character 134): Jugal: does not exceed the anterior margin of orbit (0), or exceeds the anterior margin of orbit (1).

CHARACTER 123 (POL, 1999a: character 135): Notch in premaxilla on lateral edge of external nares: absent (0), or present on the dorsal half of the external nares lateral margin (1).

CHARACTER 124 (POL, 1999a: character 136): Dorsal border of external nares: formed mostly by the nasals (0), or by both the nasals and premaxilla (1).

CHARACTER 125 (POL, 1999a: character 138): Posterodorsal process of premaxilla: absent (0), or present extending posteriorly wedging between maxilla and nasals (1).

CHARACTER 126 (POL, 1999a: character 139 and ORTEGA *et al.*, 2000: character 9): + Premaxilla-maxilla suture in palatal view, medial to alveolar region: anteromedially directed (0), sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1), or posteromedially directed (2).

CHARACTER 127 (POL, 1999a: character 140): Nasal lateral border posterior to external nares: laterally concave (0), or straight (1).

CHARACTER 128 (POL, 1999a: character 141): Nasal lateral edges: nearly parallel (0), oblique to each other converging anteriorly (1), or oblique to each other diverging anteriorly (2).

CHARACTER 129 (POL, 1999a: character 143): Palatine anteromedial margin: exceeding the anterior margin of the palatal fenestrae wedging between the maxillae (0), or not exceeding the anterior margin of palatal fenestrae (1).

CHARACTER 130 (POL, 1999a: character 144): Dorsoventral height of jugal antorbital region respect to infraorbital region: equal or lower (0), or antorbital region more expanded than infraorbital region of jugal (1).

CHARACTER 131 (POL, 1999a: character 145): Maxilla-lacrimal contact: partially included in antorbital fossa (0), or completely included in antorbital fossa (1).

CHARACTER 132 (POL, 1999a: character 146): Lateral eustachian tube openings: located posteriorly to the medial opening (0), or aligned anteroposteriorly and dorsoventrally (1).

CHARACTER 133 (POL, 1999a: character 147): Anterior process of ectopterygoid: developed (0), or reduced-absent (1).

CHARACTER 134 (POL, 1999a: character 148): Posterior process of ectopterygoid: developed (0), or reduced-absent (1).

CHARACTER 135 (POL, 1999a: character 149 and ORTEGA *et al.*, 2000: character 13): Small foramen located in the premaxillo-maxillary suture in lateral surface (not for big mandibular teeth): absent (0), or present (1).

CHARACTER 136 (POL, 1999a: character 150): Jugal posterior process: exceeding posteriorly the infratemporal fenestrae (0), or not (1).

CHARACTER 137 (POL, 1999a: character 151): Compressed crown of maxillary teeth: oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1).

CHARACTER 138 (POL, 1999a: character 152): Large and aligned neurovascular foramina on lateral maxillary surface: absent (0), or present (1).

CHARACTER 139 (modified from POL, 1999a: character 153): External surface of maxilla and premaxilla: with a single plane facing laterally (0), or with ventral region facing laterally and dorsal region facing dorsolaterally (1).

CHARACTER 140 (POL, 1999a: character 154 and ORTEGA *et al.*, 2000: character 104): Maxillary teeth: not compressed laterally (0), or compressed laterally (1).

CHARACTER 141 (POL, 1999a: character 155): Posteroventral corner of quadratojugal: reaching the quadrate condyles (0), or not reaching the quadrate condyles (1).

CHARACTER 142 (POL, 1999a: character 156): Base of postorbital process of jugal: directed posterodorsally (0), or directed dorsally (1).

CHARACTER 143 (POL, 1999a: character 157): + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2).

CHARACTER 144 (POL, 1999a: character 158 and ORTEGA *et al.*, 2000: character 36): Postorbital-ectopterygoid contact: present (0), or absent (1).

CHARACTER 145 (POL, 1999a: character 161): Quadratojugal: not ornamented (0), or ornamented in the base (1).

- CHARACTER 146 (POL, 1999a: character 162): Prefrontal-maxillary contact in the inner anteromedial region of orbit: absent (0), or present (1).
- CHARACTER 147 (POL, 1999a: character 163): Basisphenoid: without lateral exposure (0), or with lateral exposure on the braincase (1).
- CHARACTER 148 (POL, 1999a: character 165): Quadrate process of pterygoids: well developed (0), or poorly developed (1).
- CHARACTER 149 (modified from POL, 1999a: character 166 and ORTEGA *et al.*, 2000: character 44): + Quadrate major axis directed: posteroventrally (0), ventrally (1), or anteroventrally (2).
- CHARACTER 150 (POL, 1999a: character 167): Quadrate distal end: with only one plane facing posteriorly (0), or with two distinct faces in posterior view, a posterior one and a medial one bearing the foramen aereum (1).
- CHARACTER 151 (POL, 1999a: character 168): Anteroposterior development of neural spine in axis: well developed covering all the neural arch length (0), or poorly developed, located over the posterior half of the neural arch (1).
- CHARACTER 152 (POL, 1999a: character 169): Prezygapophyses of axis: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of neural arch (1).
- CHARACTER 153 (POL, 1999a: character 170): Postzygapophyses of axis: well developed, curved laterally (0), or poorly developed (1).
- CHARACTER 154 (modified from POL, 1999b: character 212): Shape of dentary symphysis in ventral view: tapering anteriorly forming an angle (0), Ushaped, smoothly curving anteriorly (1), or lateral edges longitudinally oriented, convex anterolateral corner, and extensive transversally oriented anterior edge (2).
- CHARACTER 155 (POL, 1999b: character 213): Unsculpted region in the dentary below the tooth row: absent (0), or present (1).
- CHARACTER 156 (ORTEGA *et al.*, 1996: character 13 and BUCKLEY *et al.*, 2000: character 117): Cheek teeth: not constricted at base of crown (0), or constricted at base of crown (1).
- CHARACTER 157 (ORTEGA *et al.*, 2000: character 42): Outer surface of squamosal laterodorsally oriented: extensive (0), or reduced and sculpted (1), or reduced and unsculpted (2).
- CHARACTER 158 (ORTEGA *et al.*, 2000: character 74): Length/height proportion of infratemporal fenestra: higher than long or subequal (0), or very anteroposteriorly elongated (1).
- CHARACTER 159 (ORTEGA *et al.*, 2000: character 90): Foramen intramandibularis oralis: small or absent (0), or big and slotlike (1).
- CHARACTER 160 (ORTEGA *et al.*, 2000: character 146): Ectopterygoid medial process: single (0), or forked (1).
- CHARACTER 161 (modified from GOMANI, 1997: character 46 and BUCKLEY *et al.*, 2000: character 113): Cusps of teeth: unique cusp (0), one main cusp with smaller cusps arranged in one row (1), one main cusp with smaller cusps arranged in more than one row (2), several cusps of equal size arranged in more than one row (3), or multiple small cusps along edges of occlusal surface (4).
- CHARACTER 162 (POL & NORELL, 2004a: character 164): Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).
- CHARACTER 163 (POL & NORELL, 2004a: character 165): Palatine-ptyergoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).
- CHARACTER 164 (WU *et al.*, 1997: character 103): Squamosal descending process: absent (0), or present (1).
- CHARACTER 165 (modified from WU *et al.*, 1997: character 105): + Development of distal quadrate body ventral to otoccipital-quadrate contact: distinct (0), incipiently distinct (1), or indistinct (2).
- CHARACTER 166 (WU *et al.*, 1997: character 106): Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).
- CHARACTER 167 (WU *et al.*, 1997: character 108): Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).
- CHARACTER 168 (WU *et al.*, 1997: character 109): Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).
- CHARACTER 169 (WU *et al.*, 1997: character 110): Angular posterior to mandibular fenestra: widely exposed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).
- CHARACTER 170 (WU *et al.*, 1997: character 112): Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).
- CHARACTER 171 (modified from WU *et al.*, 1997: character 119): Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).
- CHARACTER 172 (WU *et al.*, 1997: character 121): Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).
- CHARACTER 173 (WU *et al.*, 1997: character 122): Olecranon: well developed (0), or absent (1).
- CHARACTER 174 (WU *et al.*, 1997: character 123): Cranial table width respect to ventral portion of skull: as wide as ventral portion of skull (0), or narrower than ventral portion of skull (1).
- CHARACTER 175 (WU *et al.*, 1997: character 127): Depression on posterolateral surface of maxilla: absent (0), or present (1).

- CHARACTER 176 (WU *et al.*, 1997: character 128): Anterior palatal fenestra: absent (0), or present (1).
- CHARACTER 177 (POL & NORELL, 2004a: character 179): Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).
- CHARACTER 178 (POL & NORELL, 2004a: character 180): Posterolateral end of quadratojugal: acute or rounded, tightly overlapping the quadrate (0), or with sinusoidal ventral edge and wide and rounded posterior edge slightly overhanging the lateral surface of the quadrate (1).
- CHARACTER 179 (POL & NORELL, 2004a: character 181): Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1).
- CHARACTER 180 (GASPARINI *et al.*, 1993: character 3): Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).
- CHARACTER 181 (POL & NORELL, 2004b: character 181): Palpebrals: separated from the lateral edge of the frontals (0), or extensively sutured to each other and to the lateral margin of the frontals (1).
- CHARACTER 182 (POL & NORELL, 2004b: character 182): External surface of ascending process of jugal: exposed laterally (0), or exposed posterolaterally (1).
- CHARACTER 183 (POL & NORELL, 2004b: character 183): Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0), or present (1).
- CHARACTER 184 (POL & NORELL, 2004b: character 184): Dorsal surface of posterolateral region of squamosal: without ridges (0), or with three curved ridges oriented longitudinally (1).
- CHARACTER 185 (POL & NORELL, 2004b: character 185): Ridge along dorsal section of quadrate-quadratojugal contact: absent (0), or present (1).
- CHARACTER 186 (POL & NORELL, 2004b: character 186): Sharp ridge along the ventral surface of angular: absent (0), or present (1).
- CHARACTER 187 (POL & NORELL, 2004b: character 187): Longitudinal ridge along the dorsolateral surface of surangular: absent (0), or present (1).
- CHARACTER 188 (POL & NORELL, 2004b: character 188): Dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges (fleur de lys pattern of OSMÓLSKA *et al.*, 1997): absent (0), or present (1).
- CHARACTER 189 (POL & NORELL, 2004b: character 189): Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0), or present (1).
- CHARACTER 190 (POL & NORELL, 2004b: character 190): Appendicular osteoderms: absent (0), or present (1).
- CHARACTER 191 (ORTEGA *et al.*, 2000: character 72): Supratemporal fenestra: present (0), or absent (1).
- CHARACTER 192 (POL & NORELL, 2004a: character 183): Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).
- CHARACTER 193 (POL *et al.*, 2004: caract. 164) Major axis of ectopterygoid body oriented: anterolaterally (0), or anteriorly (1).
- CHARACTER 194 (POL *et al.*, 2004: character 179): Ventral margin of infratemporal bar of jugal: straight (0), or dorsally arched (1).
- CHARACTER 195 (WU & SUES, 1996: character 6): Premaxilla-maxilla segment longer than (0) or shorter than (1) remainder of skull in lateral view.
- CHARACTER 196 (WU & SUES, 1996: character 17): Mandibular symphysis deep (0) or shallow and spatulate anteriorly (1).
- CHARACTER 197 (WU & SUES, 1996: character 31): Maxillary tooth row extending posterior to anterior border of orbit (0) or terminating in front of orbit (1) in lateral view.
- CHARACTER 198 (MARTINELLI, 2003: character 35): Ectopterygoid does not contact posterior part of palatine (0), or contact palatine, excluding the pterygoid of the posterior edge of the fenestra palatina (1).
- CHARACTER 199 (MARTINELLI, 2003: character 36): Nasal-frontal suture transversely oriented (0) or obliquely oriented (1).
- CHARACTER 200 (FIORELLI, 2005): Hipapophysis in cervical vertebrae: absent (0), like a vertical thorn slightly or well marked (1) or like keel-shaped running anteroposteriorly in ventral surface of centrum (2).
- CHARACTER 201 (FIORELLI, 2005): First and second pair of mandibular teeth directed, in relation to the vertical one, toward up practically vertical (0) or directed anterodorsally in an angle approximate of 45°-50° (1).
- CHARACTER 202 (FIORELLI, 2005): Postcanines teeth (molariforms) triangular in transverse section (0), rounded, cuspidate or tablets laterally (Ziphodont or basal type) (1).
- CHARACTER 203 (FIORELLI, 2005): Small and big neurovascular foramina aligned on lateral surface of dentary: absent (0) or present (1).
- CHARACTER 204 (FIORELLI, 2005): Anteroposterior crest directed in the glenoid fossa on articular shelf separating the articulation cavities for the respective condyles of quadrate: absent (0) or present (1).
- CHARACTER 205 (FIORELLI, 2005): Posterior Buttress on shelf of articular like top for the quadrate: absent (0) or present (1).
- CHARACTER 206 (FIORELLI, 2005): Rounded cervical centra (0) in transverse section or irregular polygonal (heptagonal) formed one of their vertexes the ventral keel (hipapophysis) (1).
- CHARACTER 207 (FIORELLI, 2005): Development of thin pre and postspinals sheets in anterior dorsal vertebrae: absent or little developed (0) or developed (1).

CHARACTER 208 (FIORELLI, 2005): Suprapostzygapophyseal laminae in cervical and cervicodorsal vertebrae: absent (0) or present (1).

CHARACTER 209 (FIORELLI, 2005): Development of the acetabular roof of ilium with a deep acetabular cavity: not developed (0) or well developed (1).

CHARACTER 210 (FIORELLI, 2005): Prominent process on femur (for *m. coccygeofemoralis*) located medially in the proximal end of shaft: absent or slightly developed (0) or very developed (1).

CHARACTER 211 Cervical vertebrae centra very anteroposteriorly lengthened (0), or shorter and tablets in anteroposterior sense (1).

CHARACTER 212 Articulation surface of the parapophysis for the chapter of the ribs in cervical vertebrae: anteroposteriorly lengthened –double long than wide or more– (0) or practically square or rounded – as long as wide – (1).

CHARACTER 213 Long postparapophyseal border in cervical vertebrae, anteroposteriorly directed until the posterior border of the centrum, forming deep furrows toward both sides (up and below) of the parapophyseal border: absent (0), present (1).

CHARACTER 214 Hook or expansion in the posterior vertex of the scapula formed by the posterior and dorsal border: absent (0), present (1).

CHARACTER 215 (POL, 1999a: character192) Lateral expansion in proximal extreme of the humerus: absent (0), present (1).

CHARACTER 216 Proportion among the long of the deltopectoral crest (Dc) in relation to the total length (TL) of the humerus (= Dc hu / TL hu): smaller than 25 % (0) or bigger than 25 % (1).

CHARACTER 217 Proportion among the diameter of the shaft (Dsh) of the humerus measured in half of their longitude in relation to the total length (TL) of the humerus (= Dsh hu/ TL hu): smaller or similar to 7 % (0) or bigger than 7 % (1).

CHARACTER 218 (modified from POL, 1999a: character 191) + Proportion among the total length of humerus and wide of proximal expansion: in the range between 2.15 and 2.3 (0), between 2.8 and 3.2 (1), bigger at 3.7 and 4.74 (2), same or bigger at 5.0 (3).

CHARACTER 219 Proportion among the diameter of the shaft (Dsh ra) of the radius measured in half of their longitude in relation to the total length (TL ra) of the radius (= Dsh ra / TL ra): smaller or similar to 4 % (0), between 4 % and 6 % (1) or bigger than 6 % (2).

CHARACTER 220 Relationship between the total length of the ulna and the total length of the humerus (= TL ul / TL hu): ulna < humerus (0) or ulna > humerus (1).

CHARACTER 221 Relationship between the broad of the shaft of ulna and their total length (= BS ul / TL ul): smaller than 5 % (0), between 5 % and 7 % (1) or bigger than 7 % (2).

CHARACTER 222 Broad of the femoral shaft in relation to their total length (= BS fe / TL fe): smaller than 9 % (0) or bigger than 9 % (1).

CHARACTER 223 Broad of the tibial shaft in relation to their total length (= BS ti / TL ti): smaller or similar to 7 % (0) or bigger than 7 % (1).

CHARACTER 224 Relationship among the broad of the distal expansion of pubis (B.d.e pu) and the total length (TL pu) of the same one (= B.d.e pu / TL pu): smaller or similar to 30 % (0) or bigger than 30 % (1).

CHARACTER 225 Relationship among the diameter of the pubic shaft (D.sh.pu) and the total length (TL pu) of the same one (= D.sh.pu / TL pu): smaller than 8 % (0) or bigger than 8 % (1).

CHARACTER 226 (modified from SERENO, 1991: character 27): Relationship between the total length of the femur and the total length of the tibia (= TL fe / TL ti): femur > tibia (0) or femur < tibia (1).

CHARACTER 227 Anteroposterior longitudinal relationship between the ventral scapular section (v.S) and dorsal scapular blade (d.S) [= v.S/d.S]: smaller than 55 % (0); between 55 % and 70 % (1); between 70 % and 100 % (2) or bigger than 100 % (3).

CHARACTER 228 Relationship between the anteroposterior length of dorsal scapular blade (d.S) and the major dorsoventral longitudinal axis (m.l.a.S) of the same one [= d.S/m.l.a.S]: smaller than 40 % (0); between 40 % and 55 % (1) or bigger than 55 % (2).

CHARACTER 229 Relationship between the diameter of the scapular half constriction (S.h.c) and the major dorsoventral longitudinal axis (m.l.a.S) of the same one [= S.h.c/ m.l.a.S]: less than 15 % (0); between 15 % and 20 % (1) or more than 20 % (2).

CHARACTER 230 Relationship between the major dorsoventral longitudinal axis of scapula (m.l.a.S) and the total length of the humerus (t.l.hu) [= m.l.a.S/t.l.hu]: less than 70 % (0) or more than 70 % (1).

CHARACTER 231 Relationship between the total length of the pubis (t.l.pu) and the total length of femur (t.l.fe) [= t.l.pu/t.l.fe]: less than 45 % (0) or more than 45 % (1).

## APPENDIX II

List of the 51 taxa used in the phylogenetic analysis (taken from POL & NORELL, 2004b; POL *et al.*, 2004). *Anatosuchus*, *Mariliasuchus*, *Candidodon*, *Stratiosuchus*, and *Uberabasuchus* are new taxa included in this paper.

*Gracilisuchus stipanicorum* (ROMER, 1972)  
*Terrestriusuchus gracilis* (CRUSH, 1984)  
*Dibothrosuchus elaphros* (WU & CHATTERJEE, 1993)  
*Protosuchus richardsoni* (COLBERT & MOOK, 1951)  
*Hemiprotosuchus leali* (BONAPARTE, 1971)  
 Kayenta Form (CLARK, 1986)  
*Edentosuchus tienshanensis* (YOUNG, 1973; POL *et al.*, 2004)  
*Orthosuchus stormbergi* (NASH, 1975)  
*Gobiosuchus kielanae* (OSMÓLSKA, 1972)  
*Zaraasuchus shepardi* (POL & NORELL, 2004b)  
*Shantungosuchus hangjinensis* (WU *et al.*, 1994)  
*Neuquensuchus universitas* (MUCPv-47, MUCPv-161)  
*Sichuanosuchus shuhanensis* (WU *et al.*, 1997)  
*Zosuchus davidsoni* (POL & NORELL, 2004a)  
 Fruita Form (CLARK, 1985, 1994)  
*Hsisosuchus chungkingensis* (YOUNG & CHOW, 1953; LI *et al.*, 1994; WU *et al.*, 1994)  
*Notosuchus terrestris* (WOODWARD, 1896; GASPARINI, 1971)  
*Anatosuchus minor* (SERENO *et al.*, 2003)  
*Comahuesuchus brachybuccalis* (BONAPARTE, 1991)  
*Mariliasuchus amarali* (CARVALHO & BERTINI, 1999)  
*Uruguaysuchus aznarezi* (RUSCONI, 1933)  
*Chimaeresuchus paradoxus* (WU & SUES, 1996)  
*Malawisuchus mvakasyungutiensis* (CLARK *et al.*, 1989; GOMANI, 1997)  
*Candidodon itapecuruense* (CARVALHO, 1994; NOBRE & CARVALHO, 2002)  
*Simosuchus clarki* (BUCKLEY *et al.*, 2000)  
*Sphagesaurus huenei* (PRICE, 1950; POL, 2003)  
*Araripesuchus gomesii* (PRICE, 1959)  
*Araripesuchus patagonicus* (ORTEGA *et al.*, 2000)  
*Baurusuchus pachecoi* (PRICE, 1945)  
*Stratiosuchus maxhechti* (CAMPOS *et al.*, 2001)  
*Bretesuchus bonapartei* (GASPARINI *et al.*, 1993)  
*Iberosuchus macrodon* (ANTUNES, 1975; ORTEGA *et al.*, 2000)  
*Lomasuchus palpebrosus* (GASPARINI *et al.*, 1991)  
*Peirosaurus torminni* (PRICE, 1955; GASPARINI *et al.*, 1991)  
*Uberabasuchus terrificus* (CARVALHO *et al.*, 2004)  
*Theriosuchus pusillus* (OWEN, 1879; CLARK, 1986, 1994; ORTEGA *et al.*, 2000)  
*Alligatorium* (WELNHOFER, 1971; CLARK, 1986, 1994)  
*Eutretauranosuchus delfsi* (MOOK, 1967; CLARK, 1986, 1994)  
*Goniopholis* (MOOK, 1942; CLARK, 1986, 1994; SALISBURY *et al.*, 1999)  
*Pholidosaurus decipiens* (OWEN, 1878; CLARK, 1986, 1994)  
*Dyrosaurus phosphaticus* (BUFFETAUT, 1978; CLARK, 1986, 1994)  
*Sokotosuchus ianwilsoni* (HALSTEAD, 1975; BUFFETAUT, 1979; CLARK, 1986, 1994)  
*Pelagosaurus typus* (EUDES-DESLONGCHAMPS, 1863)  
*Teleosauridae* (BUFFETAUT, 1982; CLARK, 1986, 1994)  
*Metriorhynchidae* (KÄLIN, 1955; GASPARINI & DIAZ, 1977)  
*Hylaeochampsia vectiana* (CLARK & NORELL, 1992; ORTEGA *et al.*, 2000)  
*Bernissartia fagessi* (BUSCALIONI & SANZ, 1990; NORELL & CLARK, 1990)  
*Borealosuchus formidabilis* (ERICKSON, 1976; BROCHU, 1997b)  
*Civalis gangeticus* (CLARK, 1994; BROCHU, 1997a)  
*Crocodylus niloticus* (CLARK, 1994; BROCHU, 1997a)  
*Alligator mississippiensis* (CLARK, 1994; BROCHU, 1997a)





*Araripesuchus patagonicus*

201000?1010000?1[01]000101111?0111001022?10100011?12?11?1000??0?1?02?11212?0?011[01]1??1?1?????  
????1000??0111100??01??0?01?01101?010000??100110102?0?01???0??[01]1000111?0100001110?0000000  
0000000010010000?01100?1?111100111210211??01221?

*Baurusuchus pachecoi*

100??0?121??00?1101??111?0110??2?2?10110011112011?1000?10??10??311121010111111?????????????  
?????12103??1??1??1101110101011100110011110110?0111??[01]0[01]1111011101?00001?0001000000000  
0??010000101?01000????????????????????????????

*Stratiotosuchus maxhechti*

100?0??1??0000?11?111101?0??10?11?????????1?1?????????????????130?????????11?????????????????  
?0?2103??1?????????1111?10?1??010001101?10??1?????010??01????1?????10??010?0000??000?0??1?  
1??1????????????????????????????????

*Bretesuchus bonapartei*

1[01]0??01121?000?????????0?????????2??10011????????1011?1?????13?1??1?00?10110?????????????  
??????1100??1??1??1?01??0??0?1?0??0??0?1?0?????????0[01]0[01]?1?10?1??1?001?000?????????0??1?  
?00101?0100????????????????????

*Iberosuchus macrodon*

1?0?00012?0?0011100011111?01?000?02??10100111?12??1?101??10?1??111??10?0?1011011?????[12][12  
34]00?00??000?[12][01]0?2??0000??11001101010?1?0??100?11001?0??101??[01]?0111?001101?0??01?1000  
01000000?0?0?10?00??0100????????????????????

*Lomasuchus palpebrosus*

201????1211?00?11000101111??110001022?1010001??12??1?100??1??1??2?21?????00??0[12]11?????????????  
??????11??00??000?????0?00??1?110?00??00011?0??1?0?0?????010??0?11??10??01?1000??11000?0??01  
?000100??1????????????????????????????

*Peirosaurus torminni*

201?011??1?000?????10?1?????????0??2?10?????????????????????????????1?????????[12]1?????????????????  
?????000?????????????0??1??0?0?????0?1?????????????0[01]?????0?????????????00??1?????????0??000?00  
??1????????????????????????????

*Uberabasuchus terrificus*

201100?1211?00?1100010?1?1?0110101122??0?0001?????????????????????11?131110?11[12]11?????????????  
??????011000??0?0??0101?01?10?00?1?010000101?11?0?0??10010?00?1??1000??100?0?1?000000??0  
?1000100?01001????????????????????????

*Theriosuchus pusillus*

2011011111010011000011011100110011?211010001?11?0111000?????1?20211?410010101011011110001  
1112001001010002?00?10?110110[01]001?1100?00?0?00100?01?0?00??10100000?11?010?01?10000?0000  
??????010?000??1?1?0?0000110??1??0211????????

*Alligatorium*

?0?????1?0000?1000010?111?0?100?1?????0??0??11??1??1000??????20?1??00101?101?01111000??1?0  
0100?????????10??1?????????????????0?????????????????????0?????????????????0?????????????0000??[  
01]?1000?00001??????0211?0????

*Eutretauranosuchus delfsi*

203????1?10010111000100111?00?0001001110?000?112011?1010?0?1?0?121204?00001020111??1?0?0?0?  
1????????0000??000?????0?100????110??????0?000??1?0?0??10?2??001?0?000?1?110?01?0000000??01  
0?00?????????????????????0????? ????

*Goniopholis*

203?121110010111000100111?0010001002?101000?1112011?1010?10?1?021312?4100[01]0[12]02011?1??1??  
0?00?1200?11?000002100010?1101100??101100?000010010001?1??0000110020000011001000011110?01000  
0000000010000??01????0001100?11?0211??0????

*Pholidosaurus decipiens*

212?11101??11?11101100111?00100010?211?100001112111?101??10?100?1311?300??2?0??11?1??0??0?  
2?0?????????????????1??1?110?????0010?????????????????0?1?0001??10?001?100?010?0??0?????010?  
00????01????0001100?11?0211??0????  
00?11?021111030111

*Dyrosaurus phosphaticus*

002??1?101?010?11?00100011?1010011012?10101001112011?1011?10?10101302?3?00??2?000?????????0?00?  
????1?????????????????1?????????????0?0?0?????????????021?0001????0?????00??1?0000000??010?0  
0?11?01????0001100?11?0211??0????





## APPENDIX IV

## ANATOMICAL ABBREVIATIONS

ab: anterior blade; ac.r: acromial ridge; AM: insertion of the *M. ambiens*; as: astragalus; Br: origin for the *M. brachialis*; ca: caudal vertebrae (1 to 5); cap: capitulum; CB: insertion of the *M. coracobrachialis brevis*; ce: cervical vertebrae (4 to 9); DC: insertion of the *M. deltoideus clavicularis*; dci: dorsal crest of ilium; di: diapophysis; dpc: deltopectoral crest; do: dorsal vertebrae (1 to 4); f: femur; ff: fossa flexoria; FT: insertion of the *M. femorotibialis*; FTE: insertion of the *M. flexortibialis externus*; FTI: insertion of the *M. flexortibialis internus*; gc: glenoid cavity; GI: origin for the *M. gastrocnemius internus*; h: humerus; hk: scapular hook; hy: hypapophysis; i: ilium (= il); ip: ischiadic peduncle; is: ischium; it: inner tuber; IT: insertion of the *M. iliobtibialis*; k: keel; lc: lateral condyle; ldr3: third left dorsal rib; lh: left humerus (= lu); lpe: lateroproximal expansion of humerus; lr: left ribs; ls: left scapula; lt2: left tibia (second individual); lf2: left fibula (second individual); mc: medial condyle; mcp.ti: medial condyle process of the femur in the tibia; ne: neural spine; ol: olecranon process; os?: osteoderm?; P: insertion of the *M. pectoralis*; pa: parapophysis; pap: postacetabular process; pb: posterior blade; pdp: postdiapophyseal process; pp: postparapophyseal process; pr: prezygapophysis; pz: postzygapophysis; pu: pubis; r: radius; ra: radial; rh: right humerus; rf: right femur; ri: right ischium; rp: right pubis; rra: right radius; rs: right scapula; rt.f: right tibia and fibula; rul: right ulna; sa: sacral vertebrae (1 to 2); SC: insertion of the *M. scapulocoracoideus*; sr: sacral ribs; tp: transverse processes; Tr: origin for the *M. triceps brevis*; tu: tuberculum; u: ulna; vph: ventroposterior process in caudal vertebrae for hemal arches.

## APPENDIX V

Definitions of the nodes used in the text and the phylogenetic results (figure 15) with the diagnoses character of each node. The definitions are based in SERENO *et al.*, 2001 and *sensu* SERENO *et al.*, 2005:

- 1 – CROCODYLOMORPHA: The most inclusive clade containing *Crocodylus niloticus* but not *Poposarus gracilis*, *Gracilisuchus stipanicorum*, *Prestosuchus chiniquensis*, *Aetosaurus ferratus*.
- 2 – "SPHENOSUCHIA": The most inclusive clade containing *Terrestrisuchus gracilis* but not *Crocodylus niloticus*. Characters 33(1), 105(0), 128(0), 197(1), 220(1).
- 3 – CROCODYLIFORMES: The least inclusive clade containing *Protosuchus richardsoni* and *Crocodylus niloticus*. Characters 1(2), 3(1), 16(1), 24(1), 30(1), 45(1-2), 47(1), 51(1), 65(2), 67(1), 68(1), 80(1), 82(1), 86(1), 95(1), 99(1), 164(1), 166(1), 172(1), 173(1).
- 4 – PROTOSUCHIA: The most inclusive clade containing *Protosuchus richardsoni* but not *Crocodylus niloticus*. Characters 25(0), 55(1), 60(1), 73(2), 140(0), 165(2), 185(1), 215(0).
- 5 – GOBIOSUCHIDAE: The least inclusive clade containing *Gobiosuchus kielanae* and *Zaraasuchus shepardii*. Characters 1(1), 32(1), 75(1), 96(0), 97(1), 174(0), 181(1), 182(1), 183(1), 184(1), 186(1), 187(1), 188(1), 189(1), 190(1), 191(1).
- 6 – PROTOSUCHIDAE: The least inclusive clade containing *Protosuchus richardsoni* and *Hemiprotosuchus leali*. Characters 48(0), 50(1), 74(1), 132(1).
- 7 – MESOEUCROCODYLIA: The most inclusive clade containing *Crocodylus niloticus* but not *Protosuchus richardsoni*. Characters 37(2), 39(1), 41(1), 66(1), 79(1), 84(1), 141(1).
- 8 – Innominated. Characters 31(1), 113(1), 176(1).
- 9 – Innominated. Characters 55(1), 143(2), 163(0), 169(1), 178(1).
- 10 – Innominated. Characters 37(1), 170(1).
- 11 – Innominated. Characters 91(1); 226 (1).
- 12 – *Neuquensuchus universitas*. Characters 173(0), 220(1)
- 13 – "MESOSUCHIA": not defined. Characters 10(1), 29(1), 73(2), 119(1), 171(0), 192(1), 197(1), 221(2).
- 14 – METASUCHIA: The least inclusive clade containing *Notosuchus terrestris* and *Crocodylus niloticus*. Characters 15(1), 17(1), 26(1), 67(2), 83(1), 142(0), 167(1).
- 15 – NEOSUCHIA: The most inclusive clade containing *Crocodylus niloticus* but not *Notosuchus terrestris*. Characters 6(1), 29(0), 36(0), 80(0), 140(0), 166(0), 209(0).
- 16 – EUSUCHIA: The least inclusive clade containing *Hylaeochampsia vectiana* and *Crocodylus niloticus*. Characters 43(1), 44(1), 69(0), 71(3), 76(1), 90(1), 91(3), 92(1), 93(1), 110(1), 126(1), 200(0).
- 17 – PEIROSAURIDAE: The most inclusive clade containing *Peirosaurus torminni* but not *Araripesuchus gomesii*, *Simosuchus clarki*, *Notosuchus terrestris*, *Baurusuchus pachecoi*, *Crocodylus niloticus*. Characters 11(1), 81(1), 105(0), 199(0).
- 18 – Innominated. Characters 32(1), 74(1), 128(0), 139(0), 140(0).
- 19 – Innominated (Originally Peirosauridae *sensu* Gasparini *et al.*, 1991). Characters 120(0).
- 20 – NOTOSUCHIA: The most inclusive clade containing *Notosuchus terrestris* but not *Crocodylus niloticus*. Characters 71(2), 76(1), 90(1), 91(1), 104(2), 123(1), 135(1), 145(0).
- 21 – SEBECOSUCHIA: No definition has been proposed. Characters 1(1), 3(0), 102(0), 118(1), 120(0), 128(0), 130(1), 156(1), 159(1), 160(1).
- 22 – Innominated. Characters 9(0), 67(1), 80(0), 156(1), 202(1).
- 23 – NOTOSUCHIDAE: The most inclusive clade containing *Notosuchus terrestris* but not *Araripesuchus gomesii*, *Comahuesuchus brachybuccalis*, *Simosuchus clarki*, *Baurusuchus pachecoi*, *Crocodylus niloticus*. Characters 45(2), 105(0), 137(1), 156(0), 176(1), 202(0).
- 24 – SPHAGESAURIDAE: The most inclusive clade containing *Sphagesaurus huenei* but not *Baurusuchus pachecoi*, *Sebecus icaeorhinus*, *Araripesuchus gomesii*, *Comahuesuchus brachybuccalis*, *Simosuchus clarki*, *Notosuchus terrestris*, *Crocodylus niloticus*. Characters 105(3), 121(1), 124(1).