



NEW REMAINS OF *NOTOSUCHUS TERRESTRIS* WOODWARD, 1896
(CROCODYLIFORMES: MESOEUCROCODYLIA) FROM LATE CRETACEOUS
OF NEUQUÉN, PATAGONIA, ARGENTINA ¹
(With 17 figures)

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ABSTRACT: New materials of *Notosuchus terrestris* are here described. They were found on Bajo de la Carpa Formation outcrops, near the Universidad Nacional del Comahue, Neuquén City. Descriptions were based on five specimens, one of them the only specimen of *Notosuchus* with postcranial remains articulated to the skull. As in *Sphagesaurus*, it presents triangular teeth in cross-section and oblique molariforms with worn facet surface. As in *Mariliasuchus*, it possesses procumbent mandibular incisiform teeth and, like in other notosuchians and basal crocodyliforms, it was able of proal mandibular movement. The centra of cervical vertebrae possess ventral keel as in *Chimaerasuchus*. Elongated cervical neural spines and suprapostzygapophyseal laminae in cervicodorsal vertebrae are observed. The scapular dorsal end is greatly enlarged, while the coracoid ventromedial process end is moderately developed. The dorsal surface of the ilium is lateromedially wide with a greatly expanded acetabular roof and a prominent anteromedial process in the femoral shaft. Based on diverse cranial and postcranial characters, we infer that *Notosuchus* possessed facial and perioral musculature well developed and an herbivore diet, confirming the suggestions of previous authors. *Notosuchus* represents, based on phylogenetic studies, the sister taxon of *Mariliasuchus* and the monophyly of Notosuchia is demonstrated. Paleobiogeographically, the occurrence of *Chimaerasuchus* in China evidences the faunistic interchange between Gondwana and Central Asia during the Early Cretaceous.

Key words: Mesoeucrocodylia. *Notosuchus terrestris*. Cretaceous. Articulate remains. Functional anatomy.

RESUMO: Novos restos de *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) do Cretáceo Superior de Neuquén, Patagônia, Argentina.

Novos materiais de *Notosuchus terrestris* são aqui descritos. Eles provêm de afloramentos da Formação Bajo de la Carpa, localizados próximos à Universidad Nacional del Comahue, na cidade de Neuquén. As descrições foram baseadas em cinco exemplares, um deles o único espécime de *Notosuchus* com restos pós-cranianos articulados ao crânio. Como em *Sphagesaurus*, *N. terrestris* apresenta dentes triangulares em seção cruzada e molariformes oblíquos com superfície da faceta com desgaste. Como em *Mariliasuchus*, a espécie possui dentes mandibulares incisiformes procumbentes e, como em outros notossúquios e crocodyliformes basais, era possível realizar o movimento antero-posterior mandibular. Os centros das vértebras cervicais possuem uma quilha ventral como em *Chimaerasuchus*. Espinhos neurais cervicais alongados e lâminas suprapóstzigapofiseais em vértebras cérvico-dorsais são observados. A extremidade escapular dorsal é amplamente alargada, enquanto a extremidade do processo ventro-medial do coracóide é pouco desenvolvida. A superfície dorsal do ilium é larga látero-medialmente com um teto acetabular amplamente expandido e processo ântero-medial proeminente na diáfise femoral. Baseado em diversos caracteres cranianos e pós-cranianos, infere-se que *Notosuchus* apresentava grande desenvolvimento da musculatura facial e perioral e tinha uma dieta herbívora, confirmando o que foi sugerido anteriormente por outros autores. *Notosuchus* representa, baseado em estudos filogenéticos, o táxon irmão de *Mariliasuchus* e a monofilia de Notosuchia é demonstrada. Paleobiogeograficamente, a ocorrência de *Chimaerasuchus* na China evidencia o intercâmbio faunístico entre o Gondwana e a Ásia Central durante o Cretáceo Inferior.

Palavras-chave: Mesoeucrocodylia. *Notosuchus terrestris*. Cretáceo. Restos articulados. Anatomia funcional.

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INTRODUCTION

Notosuchia is a clade of small to medium basal brevirostrine Mesoeucrocodylia. Most of their taxa were registered and gathered in regions that were part of the old Gondwana during the Cretaceous. These taxa are represented by several species. *Notosuchus terrestris* Woodward, 1896 and *Comahuesuchus brachybuccalis* Bonaparte, 1991 come from the Upper Cretaceous of Argentina (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991; MARTINELLI, 2003). *Candidodon itapecuruense* Carvalho & Campos, 1988 comes from the Early Cretaceous of Brazil (CARVALHO, 1994; NOBRE & CARVALHO, 2002). *Sphagesaurus huenei* Price, 1950, *Adamantinasuchus navae* Nobre & Carvalho, 2006, and *Mariliasuchus amarali* Carvalho & Bertini, 1999 come from the Upper Cretaceous of Brazil (PRICE, 1950; POL, 2003; NOBRE & CARVALHO, 2006; CARVALHO & BERTINI, 1999). Both species of *Uruguaysuchus*, *U. aznarezi* Rusconi, 1933 and *U. terrai* Rusconi, 1933, come from the Cretaceous of Uruguay (RUSCONI, 1933) and were posteriorly included in the Notosuchia (GASPARINI, 1971). From Africa, there are records of *Malawisuchus mwakasyungutiensis* Gomani, 1997, that comes from the Early Cretaceous of Malawi (CLARK *et al.*, 1989; GOMANI, 1997), *Anatosuchus minor* Sereno, Sidor, Larsson & Gado, 2003, from the Aptian-Albian of the Republic of Niger (SERENO *et al.*, 2003), and *Simosuchus clarki* Buckley, Brochu, Krause & Pol, 2000, from the Upper Cretaceous of Madagascar (BUCKLEY *et al.*, 2000). Finally, *Chimaerasuchus paradoxus* Wu, Sues & Sun, 1995 comes from the Early Cretaceous of China (WU *et al.*, 1995; WU & SUES, 1996). In recent works, other notosuchians forms of different sites from South America have been notified (*e.g.*, NOVAS *et al.*, 2004; ANDRADE & BERTINI, 2005a; GARCIA *et al.*, 2005; MARCONATO, 2006); these forms are still under study but they may indicate a greater diversity of notosuchians in the continent. Phylogenetic relationships of Notosuchia have been discussed by many authors (CLARK, 1994; WU & SUES, 1996; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; MARTINELLI, 2003; SERENO *et al.*, 2003; POL, 2003; ANDRADE, 2005; POL & APESTEGUIA, 2005; FIORELLI, 2005; ZAHER *et al.*, 2006). However, there is not a common agreement about them.

Notosuchus terrestris is a Crocodyliform with terrestrial and cursorial habits, with a short and relatively high skull, presenting plesiomorphic and derived characteristics (GASPARINI, 1971;

BONAPARTE, 1991; POL, 2005; FIORELLI, 2005). For instance, in the rostral region of the muzzle, teeth and articular region, that present characteristics only developed in other notosuchians (GASPARINI, 1971; BONAPARTE, 1991; WU & SUES, 1996; GOMANI, 1997; CARVALHO & BERTINI, 1999; POL, 2003; FIORELLI, 2005; ANDRADE, 2005; NOBRE & CARVALHO, 2006; ZAHER *et al.*, 2006).

The first remains of *Notosuchus* were found in Neuquén Province at the end of the XIX century and WOODWARD (1896) was the one who carried out the first publication. Later, GASPARINI (1971) and BONAPARTE (1991), restudied the material described by Woodward together with new cranial materials, reaching important conclusions regarding their anatomy and phylogenetic relationships. Recently, new postcranial materials of *Notosuchus* were described in detail (POL, 2005). Due to the strong association with cranial remains, they were assigned to the taxon.

Since the first publication of Woodward, more than 50 skulls were recovered, some of them complete, collected in different paleosites of Bajo de la Carpa Formation. Few remains of postcranial materials were found associated, but not articulated to these skulls (WOODWARD, 1896; POL, 1999, 2005), being a limiting factor to certify these studies. Here we describe new cranial materials associated and articulated to postcranial pieces of *Notosuchus terrestris*.

MATERIAL AND METHODS

Abbreviations: Institutional. MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP: Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MUCP: Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina.

MATERIAL

All the remains of *Notosuchus terrestris* described in the present work were collected in the south hill of the Neuquén River and in the current university campus of the Universidad Nacional del Comahue, located in North of Neuquén City (Fig.1). Outcrops belong to Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (DIGREGORIO, 1972; CAZAU & ULIANA, 1973; RAMOS, 1981; LEANZA *et al.*, 2004) (Fig.1).

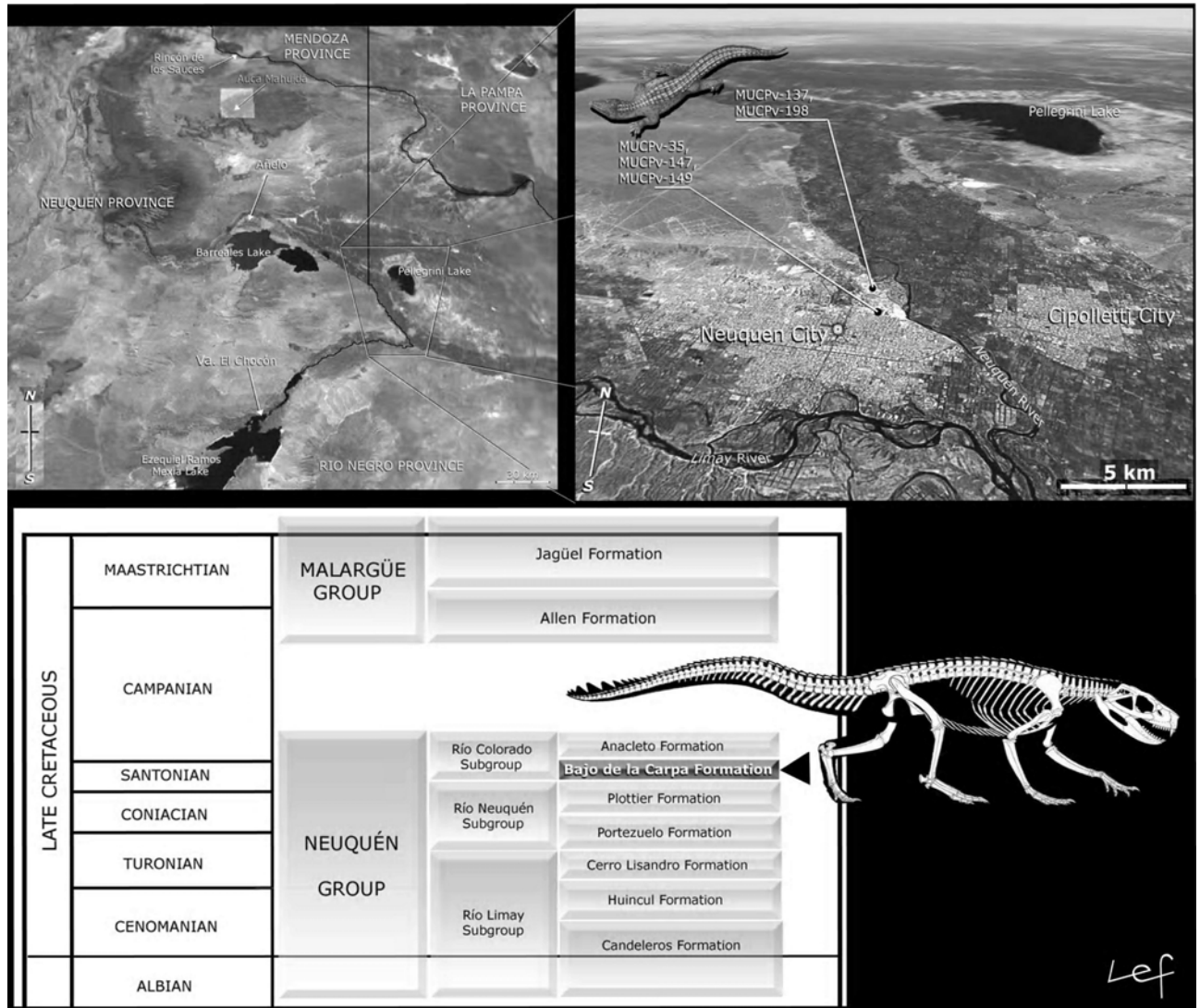


Fig.1- Up left: satellite map of Northern Patagonia region showing the location of the Neuquén Province and Comahue region. Up right: area of the Comahue and Neuquén City where were found and collected the materials of *Notosuchus terrestris* (MUCPV-35, 137, 147, 149 and 198). Below: stratigraphy of the Cretaceous of Neuquén Basin and stratigraphic column of the Neuquén Group (modified from LEANZA *et al.*, 2004).

GEOLOGICAL SETTINGS

Bajo de la Carpa Formation is one of the most homogeneous units in the Neuquén Group widely distributed with outcrops on the north, center and east of Neuquén Province, as well as towards the northwest of Río Negro Province. This Formation is composed of coarse-grained, light violet and pink sandstones of fluvial origin and it is Santonian in age (LEANZA *et al.*, 2004).

This formation is registered in the paleontological site in the campus of the Universidad Nacional del Comahue. Besides *Notosuchus* remains, a wide variety of other crocodyliforms such as *Cynodontosuchus rothi* Woodward, 1896, *Comahuesuchus brachybuccalis*, *Neuquensuchus universitas* FIORELLI & CALVO, 2007, and considerable remains of a new peirosaurid crocodyliform (FIORELLI *et al.*, 2007); dinosaurs: *Alvarezsaurus calvoi* Bonaparte, 1991, *Velocisaurus*

unicus Bonaparte, 1991, *Neuquenornis volans* Chiappe & Calvo, 1994, *Patagopteryx deferrariisi* Alvarenga & Bonaparte, 1992, cf. *Laplatasaurus* (LEANZA *et al.*, 2004), Titanosauridae indet. (CHIAPPE & CALVO, 1994; pers. obs.), *Neuquensaurus* sp. (pers. obs.), *Antarctosaurus* Huene, 1929, and *Bonitasaura salgadoi* Apesteguiá, 2004 (BONAPARTE, 1991; CHIAPPE & CALVO, 1994; ALVARENGA & BONAPARTE, 1992; BONAPARTE, 1992; APESTEGUIÁ, 2004); snakes: *Dinilysia patagonica* Woodward, 1901 (WOODWARD, 1901); a countless nests of birds containing small eggs with embryos (SCHWEITZER *et al.*, 2002), and dinosaur egg shells of *Megaloolithus patagonicus* Calvo, England, Heredia & Salgado, 1997 (CALVO *et al.*, 1997).

The remains of the peirosaurids *Lomasuchus palpebrosus* Gasparini, Chiappe & Fernandez, 1991 and *Peirosaurus tormini* Price, 1955 together with the remains of the turtle *Lomalatachelys* Broin & De La Fuente, 2001 coming from outcrops on the North Coast of Barreales Lake were assigned by LEANZA *et al.* (2004) to the Bajo de la Carpa Formation. However, recent works show that the patagonian *L. palpebrosus* comes from the Portezuelo Formation (Upper Turonian – Lower Coniacian).

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Walker, 1970
 Crocodyliformes Hay, 1930
 (*sensu* Benton & Clark, 1988)
 Mesoeucrocodylia Whetstone & Whybrow, 1983
 Metasuchia Benton & Clark, 1988
 Notosuchia Gasparini, 1971
 Notosuchidae Dollo, 1914
Notosuchus Woodward, 1896

Type-species – *Notosuchus terrestris* Woodward, 1896.

Junior synonym *Notosuchus lepidus* Saez, 1957 (GASPARINI, 1971)

Lectotype – MLP 64-IV-16-5, skull and jaw designated by GASPARINI (1971).

Referred specimens – MUCPv-35: skull and anterior part of jaw (Fig.2); MUCPv-137: skull and incompletely articulated postcranial, together with associated postcranial remains (Fig.3); MUCPv-147: complete and articulated skull and jaw with associated postcranial remains (Fig.4); MUCPv-149: associated postcranial remains (Fig.5); MUCPv-198: cranial and disarticulated fragmentary postcranial associated materials (Fig.6).

Type-locality – The specimens MUCPv-35, MUCPv-147 and MUCPv-149 were found in the campus of the Universidad Nacional del Comahue, while MUCPv-137 and MUCPv-198 were found on the south hill of the Neuquén River, Neuquén Province, Argentina (Fig.1).

Type-horizon – Bajo de la Carpa Formation (RAMOS, 1981), Río Colorado Subgroup, Neuquén Group (Santonian; LEANZA *et al.*, 2004) (Fig.1).

Diagnosis (modified from WOODWARD, 1896 and GASPARINI, 1971) – Extremely short and relatively high skull, with confluent and terminal external nares, vertical and anteriorly positioned, without nasal sept. Big orbit laterodorsally directed, covered partial and dorsally with anterior and posterior palpebrals. Rostrum lightly higher than wide. The premaxilla presents two (or three) incisiforms, a hipertrophied caniniform tooth, and a postcaniniform tooth (first molariform); each maxilla possesses 6 molariform teeth, depending on the specimen. The jaw exhibits a great lateral fenestra, anteroposteriorly lengthened. The occipital condyle is posteroventrally directed. Cervical vertebrae have slightly amphicoelous centra with a ventral kell and relatively high neural spines. Zygapophyses are width from the fourth to the eighth cervical vertebra and the cervical parapophyses are low. Presence of suprapostzygapophyseal lamina in cervicodorsal vertebrae. Presence of three sacral vertebrae fused between the second and third. Dorsal end of the scapula greatly enlarged. Distal end of the ventromedial process of the coracoid poor developed. Dorsal surface of the ilium lateromedially and acetabular roof both width. Femoral shaft with a well developed anteromedially directed process on the distal end.

RESULTS

DESCRIPTION OF THE MATERIAL

We describe novel information about the cranial and postcranial anatomy of *Notosuchus*. Further data must be remitted to previous published references (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991, 1996; POL, 1999, 2005; MARTINELLI, 2003; ANDRADE, 2005; ANDRADE & BERTINI, 2005a; FIORELLI, 2005).

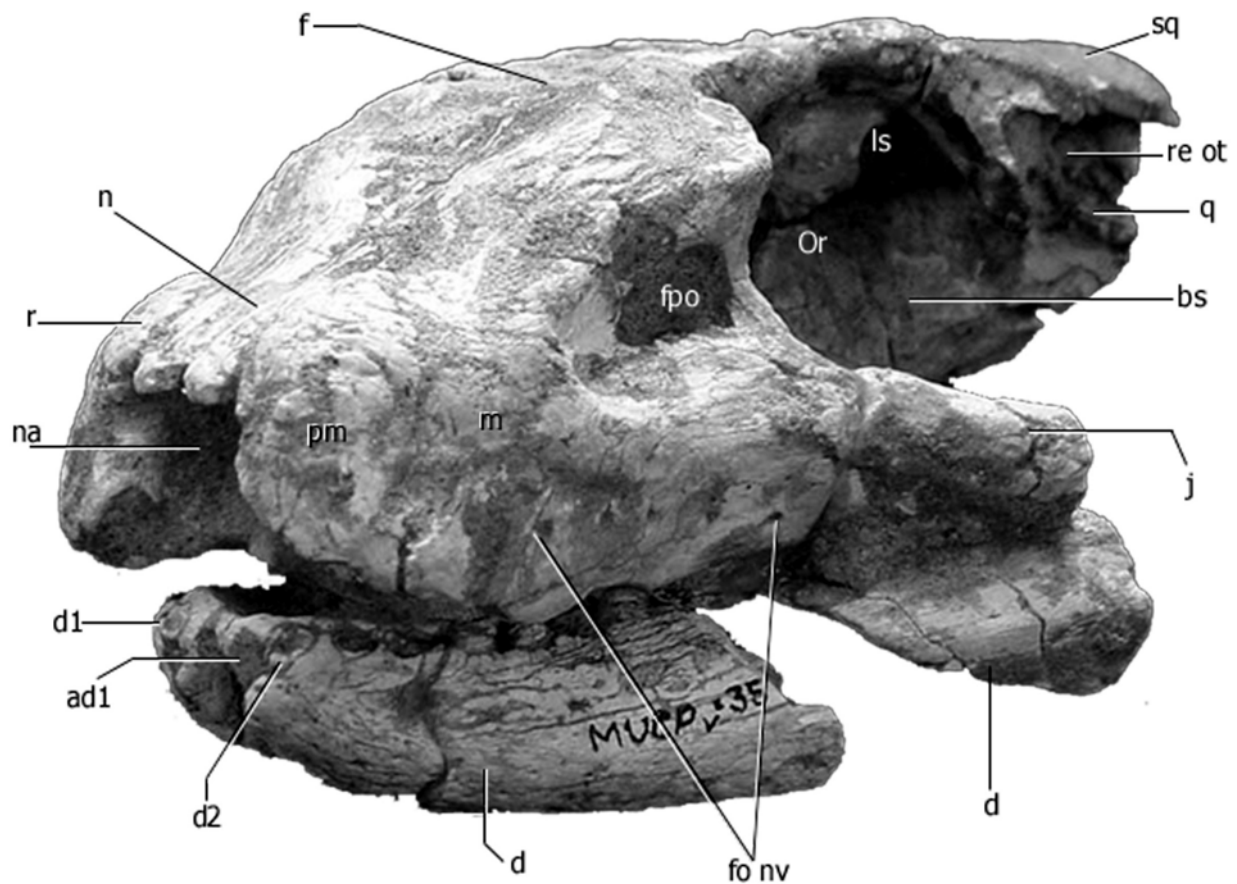


Fig.2- *Notosuchus terrestris*, MUCPv-35, referred materials. Skull and jaw in left anterolateral view. Abbreviations: (ad1) first dentary alveolus, (bs) basisphenoid, (d) dentary, (d1) first dentary tooth, (d2) second dentary tooth, (f) frontal, (fo nv.) neurovascular foramina, (fpo) anteorbital fenestra, (j) jugal, (ls) laterosphenoid, (m) maxilla, (n) nasal, (na) external nares, (Or) orbita, (pm) premaxilla, (q) quadrate, (r) protuberances and ruggedness, (re ot) otic region - otic groove, (sq) squamosal.

Skull – Cranial remains of specimens studied possess slight variations in sizes and longitude, due probably to ontogenetic and/or sexual differences (e.g., the anteroposterior length – MUCPv-35: 142mm; MUCPv-137: 123mm; MUCPv-147: 137,9mm). The robustness as well as the ornamentations and ruggedness in the surface of the cranial bones varieties depend on the specimen. (MUCPv-35 is the most robust with much ruggedness and ornamentations).

Each premaxilla (Fig.7) is high, lateral and vertically exposed and unfused in ventral view with two incisiform teeth. However, it is probable that in between another smaller incisiform tooth is located between them, although in the specimen studied here these structures are not present. Contrary to notosuchians like *Sphagesaurus* (POL, 2003) and

Chimaerasuchus (WU & SUES, 1996), *Notosuchus* and *Comahuesuchus* do not have a foramen incisivum in the premaxilla-maxilla suture (BONAPARTE, 1991; MARTINELLI, 2003). Possibly, this suture would have been constituted by a delicate bony lamina, supporting the third incisiform (Figs.7C, 8A). The lack of bony nasal sept indicates the presence of cartilaginous conjunctive tissues corroborating therefore the observed and conjectured by other authors (BONAPARTE, 1991; ANDRADE, 2005; FIORELLI, 2005; FIORELLI & CALVO, 2005).

The hiperatrophied caniniform implanted in the premaxilla is vertically directed with its root slightly curved posteriorly (Figs.7, 8). A premaxillary tooth near to this caniniform (BONAPARTE, 1991) represents the first molariform tooth of the series (seen in MUCPv-35 and MUCPv-147) (ANDRADE *et al.*, 2006).

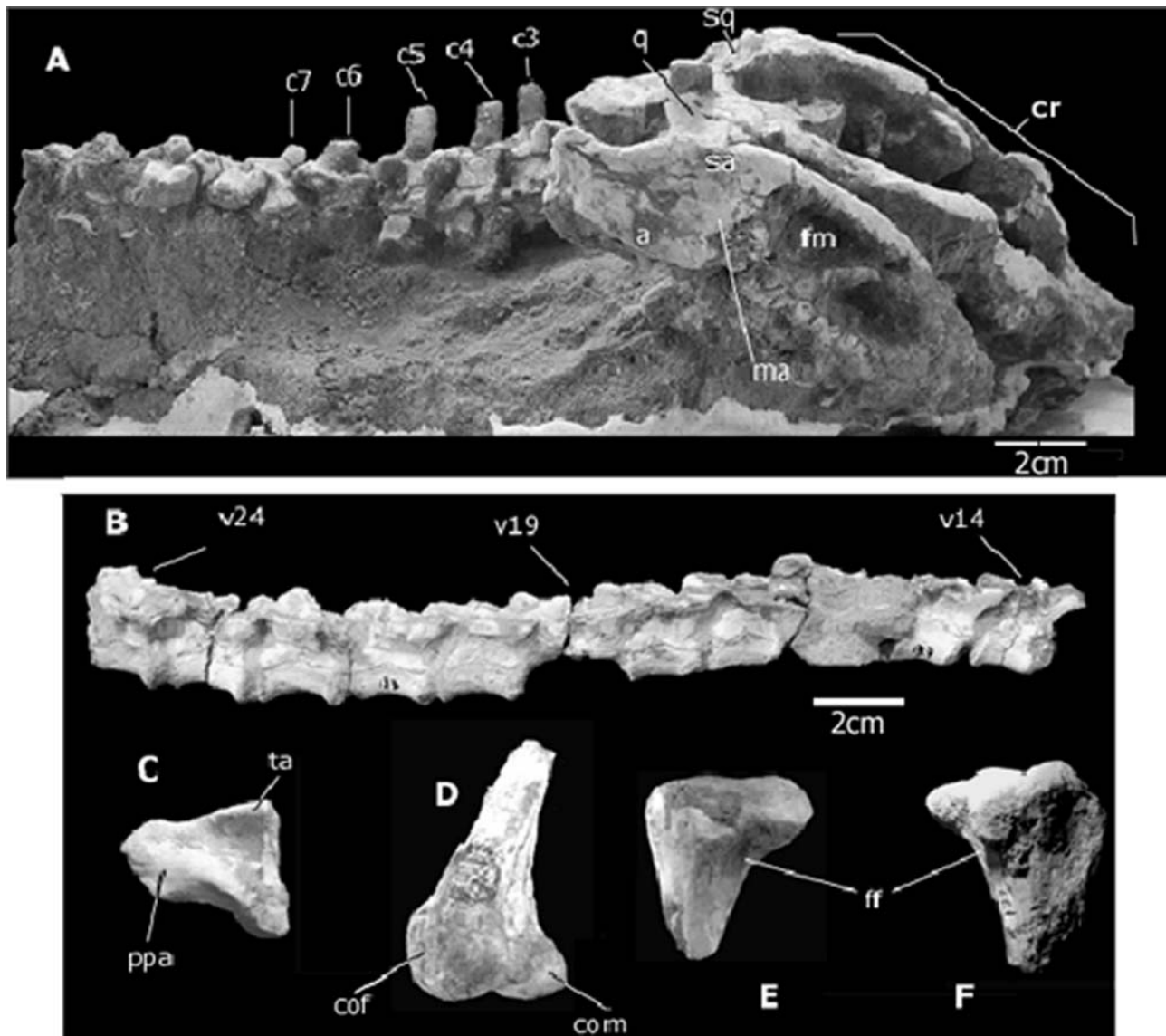


Fig.3- *Notosuchus terrestris*, MUCPv-137, referred materials. A, skull and articulated postcraneal in right lateral view. B, anterior and medial dorsal vertebrae in right lateral view. C, posterior fragment of the right ilium in lateral view. D, distal fragment of the left femur in lateral view. E and F, proximal fragments of both tibiae in posterolateral view (E, left tibia; F, right tibia). Abbreviations: (a) angular, (c) caniniform, (cof) fibular condyle, (com) medial condyle, (cr) cranium, (ff) fossa flexoria, (fm) mandibular fenestra, (ma) mandible, (ppa) postacetabular process, (q) quadrate, (sa) surangular, (sq) squamosal, (ta) acetabular roof, (v) vertebra.

Nasals are elongated and wide posteriorly. They form the dorsal end of the nares (Figs.7A, D). At the level of the antorbital fenestra, nasals are narrowed abruptly, forming a “V-shaped” contact surfaces with the lacrimals and prefrontals. On the nasals medial contact a longitudinal concavity with striations posteroanteriorly directed is developed (deeper in MUCPv-35 and MUCPv-147 but practically null in MUCPv-137).

A deep study of maxilla was done by BONAPARTE (1991); however, new data can be added. There is a longitudinal edge that defines the boundaries between the upper (rugged) and the lower (smooth) surfaces, due to the presence of strongly marked striations above the alveolar zone (Figs.7A, B). Below the alveolar zone and posteriorly, the maxilla possesses a relatively large foramen not seen in other specimens (MUCPv-35 and MUCPv-147).

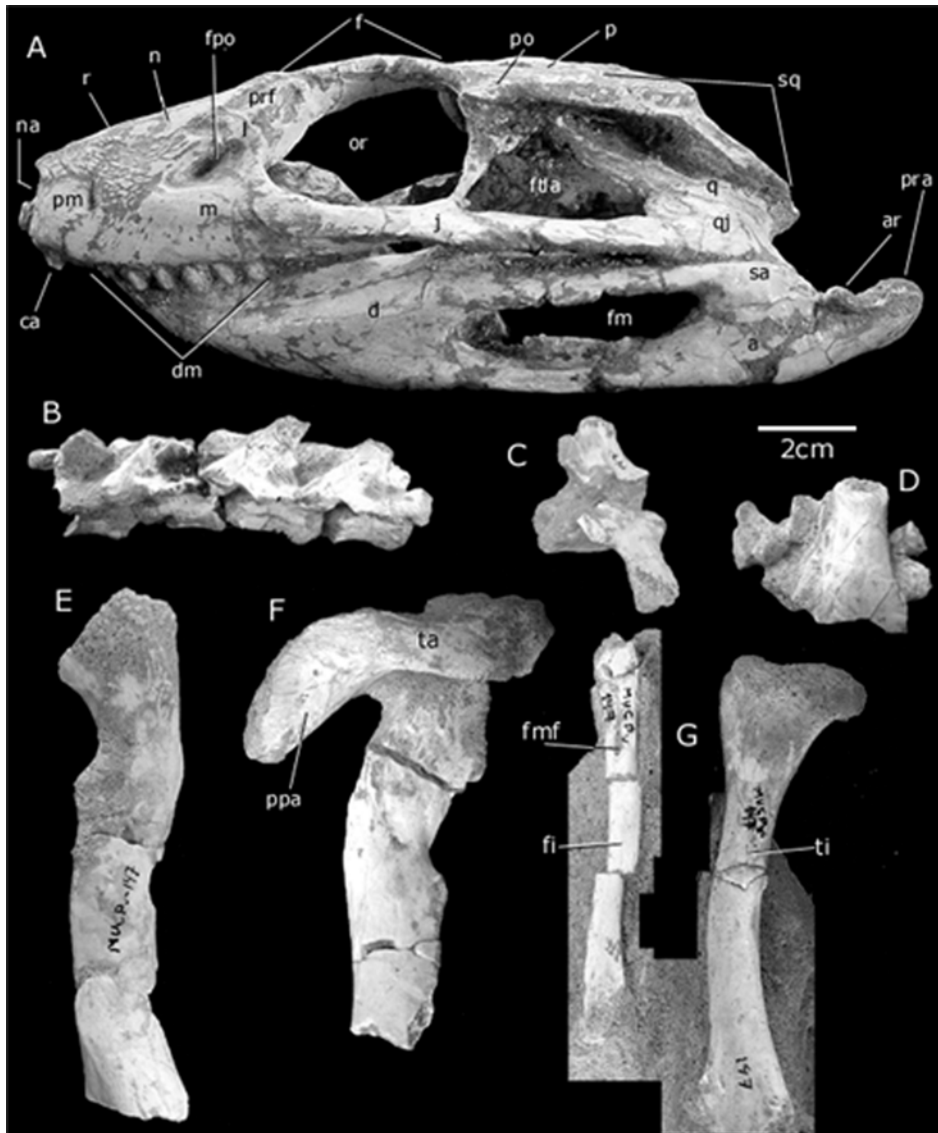


Fig.4- *Notosuchus terrestris*, MUCPv-147, referred materials. A, complete skull in left lateral view. B, posterior dorsal vertebrae in right lateral view. C, medial dorsal vertebra in right lateral view. D, distal end of the right tibia in anterior view. E, left femur in anterior view. F, right ilium in dorsal view and right femur in anterior view. G, left tibia and fibula in posterior view. Abbreviations: (a) angular, (ar) articular, (ca) caniniform, (d) dentary, (dm) maxillary teeth, (f) frontal, (fi) fibula, (fm) mandibular fenestra, (fmf) fossa medial fibular, (fpo) anteorbital fenestra, (ftla) infratemporal fenestra, (m) maxilla, (n) nasal, (na) external nares, (or) orbita, (p) parietal, (pm) premaxilla, (po) postorbital, (ppa) postacetabular process, (pra) retroarticular process, (prf) prefrontal, (q) quadrate, (qj) quadratojugal, (r) protuberances and ruggedness, (sa) surangular, (sq) squamosal, (ti) tibia.

The presence of dorsoventrally lineal striations associated to foramens indicates the presence of soft tissues to avoid food loss during the mastication (BONAPARTE, 1991; 1996; GOMANI, 1997; FIORELLI, 2005).

The features most remarkable in the maxilla are the teeth (Figs.7A, B, C, 8). Each maxilla possesses six

molariform teeth. The first maxillary tooth is the second molariform in the series. Many authors proposed this kind of teeth as being of the zipodont type, which would imply carnivore habits for *Notosuchus* and other notosuchians (PRICE, 1959; GASPARINI, 1971; BENTON & CLARK, 1988; CLARK *et al.*, 1989; WU *et al.*, 1995; WU & SUES, 1996; BUCKLEY *et*

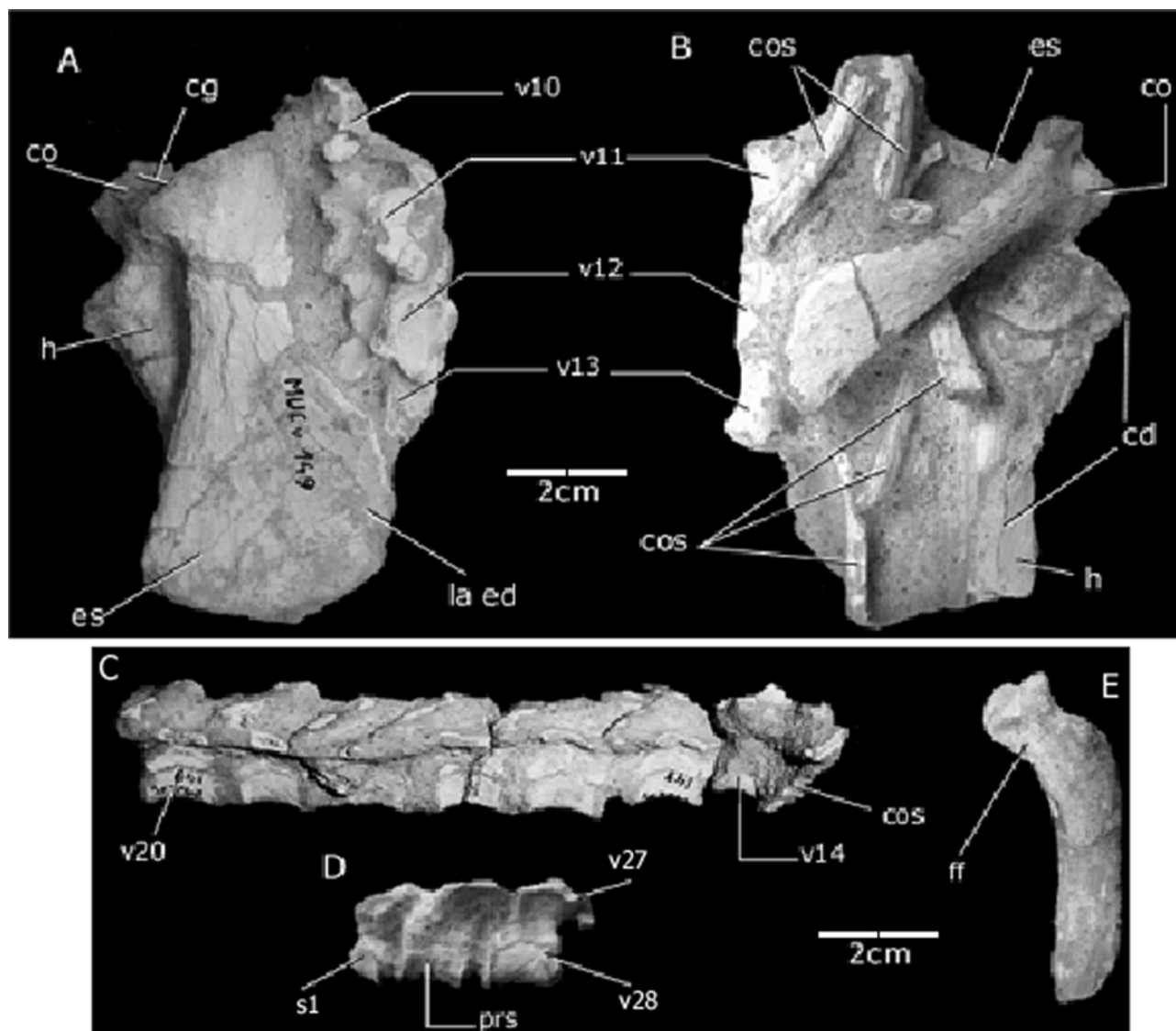


Fig.5- *Notosuchus terrestris*, MUCPv-149, referred materials. A and B, block containing the last cervical -10- and first dorsal vertebrae, left scapula, left coracoid, left humerus and ribs (A, in dorsal view and B, in ventral view). C, anterior and medial dorsal vertebrae in right lateral view. D, posterior dorsal vertebrae and fragment of the first sacral vertebra in right lateral view. E, fragment of the right tibia in posterolateral view. Abbreviations: (cd) deltoid crest, (cg) glenoid cavity, (co) coracoid, (cos) ribs, (es) scapula, (ff) fossa flexoria, (h) humerus, (la ed) anterior scapular lamina, (prs) presacral vertebra, (s1) first sacral vertebra, (v) vertebra.

al., 2000; ORTEGA *et al.*, 2000). Other authors suggested a similar situation in *Mariliasuchus*, a *Notosuchia* very related with *Notosuchus*, which also could be considered a ziphodont crocodyliform (ANDRADE, 2005; ANDRADE & BERTINI, 2005b). By definition, there are two ziphodont teeth types: “true ziphodont”, that possess laterally compressed crown with posteriorly recurved apex, anterior and

posterior carinae bearing a number of isolated festoon-like denticles (serrations) (Fig.8D); and “false ziphodont”, that possesses the anterior and posterior carinae relatively coarse and bear crenulations generally formed by anastomosing, irregular ridges issued from the main body of the crown (Fig.8E) (LANGSTON, 1975; PRASAD & BROIN, 2002). Molariform teeth of *Notosuchus* possess blunt apices and they

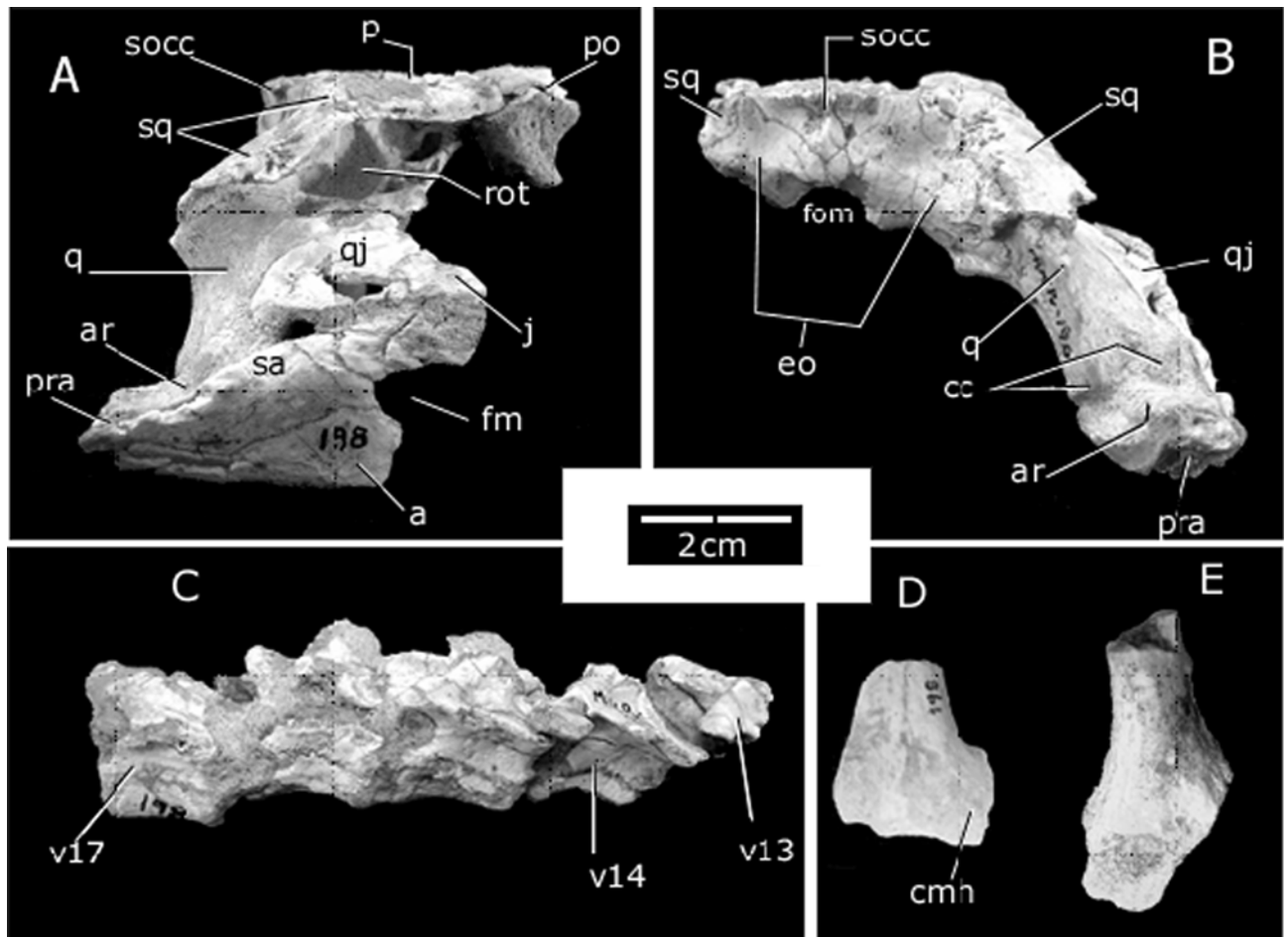


Fig.6- *Notosuchus terrestris*, MUCPv-198, referred materials. A and B, posterior section of the skull and mandible in right lateral view (A) and occipital view (B). C, anterior dorsal vertebrae in right lateral view. D, distal fragment of the left humerus in anterior view. E, distal fragment of the left tibia in anterior view. Abbreviations: (a) angular, (ar) articular, (cc) quadrate condyles, (cmh) medial condyle of humerus, (eo) exoccipital, (fm) mandibular fenestra, (fom) foramen magnum, (j) jugal, (p) parietal, (po) postorbital, (pra) retroarticular process, (q) quadrate, (qj) quadratojugal, (rot) semilunar otic groove, (sa) surangular, (socc) supraoccipital, (sq) squamosal, (v) vertebra.

are implanted obliquely to the longitudinal axis (BONAPARTE, 1991; FIORELLI, 2005) (Figs.7C, 8A) with the sharpened border posterolingually located and triangular in traverse section, similar to *Sphagesaurus* (POL, 2003), *Mariliasuchus* (ANDRADE & BERTINI, 2005b; ZAHER *et al.*, 2006), *Adamantinasuchus navae* (NOBRE & CARVALHO, 2006), and clearly visible in MUCPv-35 (Figs.8B, C). The diameter increases from the middle of the maxillary sequence and decreases anterior and posteriorly. By contrast, in *Sphagesaurus*, the diameters of the teeth decrease from the anterior to posterior ones. Although there is some matrix covering over the skull and jaw, the molariforms of MUCPv-147 have several spaced

longitudinal carinae, as in *Sphagesaurus* (POL, 2003) and *Mariliasuchus* (ANDRADE & BERTINI, 2005b; ZAHER *et al.*, 2006). The carinae can also be seen over the sixth left molariform of MUCPv-35. There are neither denticles on these carinae, nor the sharp posterolingual border. The anterolingual internal surface of the molariform presents, as in *Sphagesaurus* (POL, 2003) and *Mariliasuchus* (ANDRADE & BERTINI, 2005b; ZAHER *et al.*, 2006), a worn surface extending from the apex until the lingual border of the tooth, near the alveolar border (Figs.7C, 8A). These anatomical-structural characteristics of the molariform teeth of *Notosuchus* are not framed inside the definition of “typical teeth ziphodonts true or false”.

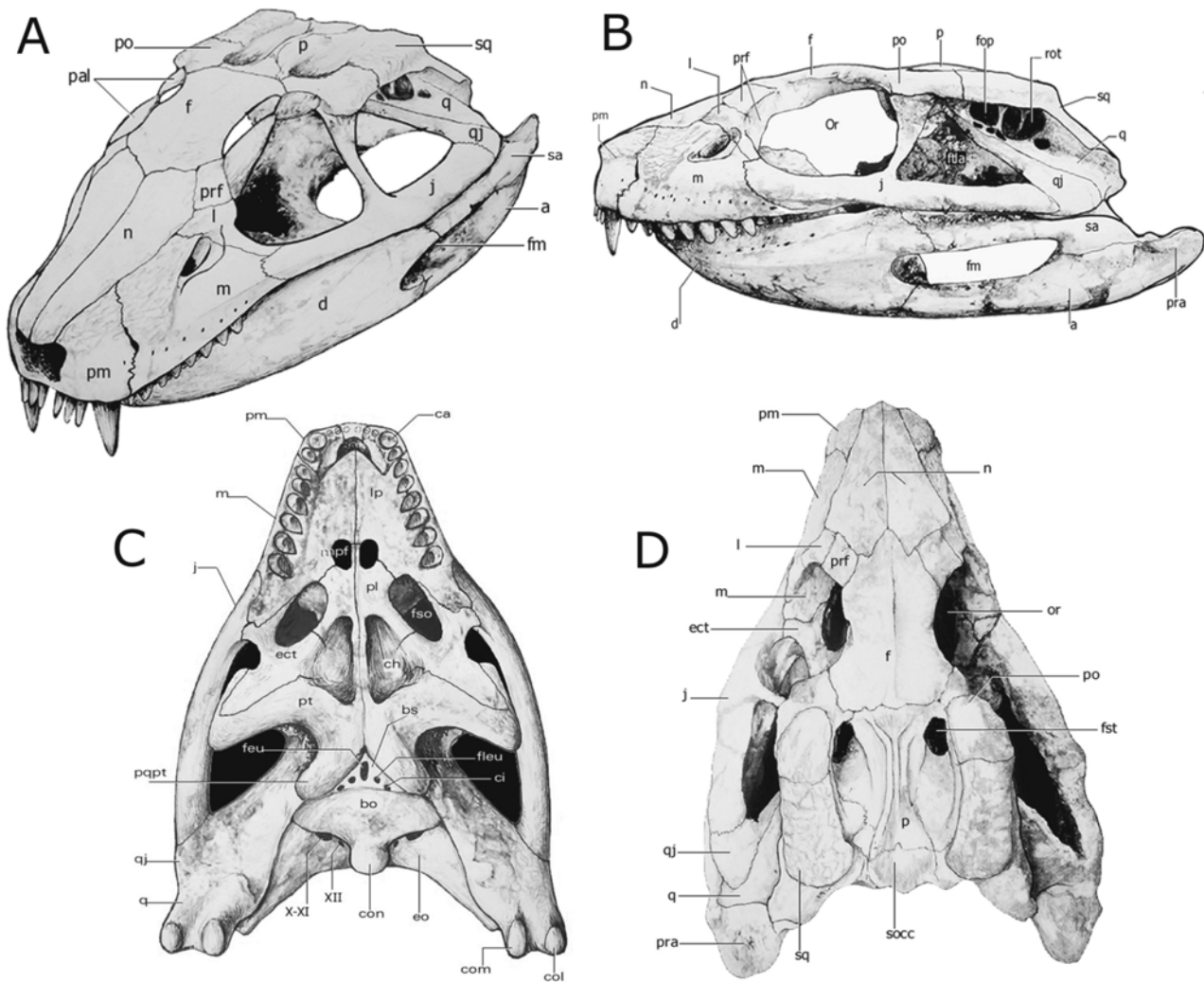


Fig.7- *Notosuchus terrestris*. Skull and jaw restoration based on the specimens MUCPv-35, MUCPv-137 and MUCPv-147. A: in left dorso-anterolateral view. B: in left lateral view. C: in palato-occipital view, without the mandible. D: in dorsal view. Abbreviations: (a) angular, (bo) basioccipital, (bs) basisphenoid, (ca) caniniform, (ch) choanal passage, (ci) internal carotide, (col) lateral condyle, (com) medial condyle, (con) occipital condyle, (d) dentary, (ect) ectopterigid, (eo) exoccipital, (f) frontal, (feu) eustachian foramen, (fleu) lateral eustachian foramen, (fm) mandibular fenestra, (fop) preotic foramen, (ftla) infratemporal fenestra, (fso) suborbital fenestra, (fst) supratemporal fenestra, (j) jugal, (l) lacrimal, (lp) maxillo-palatal lamina, (m) maxilla, (mpf) maxilopalatal fenestra, (n) nasal, (Or, or) orbita, (p) parietal, (pal) palpebral, (pl) palatine, (pm) premaxilla, (po) postorbital, (pqpt) quadrate process of pterigid, (pra) retroarticular process, (prf) prefrontal, (pt) pterigid, (q) quadrate, (qj) quadratojugal, (rot) semilunar otic groove, (sa) surangular, (sq) squamosal, (x) vague nerve, (xi) spinal accessory nerve, (xii) hypoglose nerve.

For this reason, it is not appropriate the designation of the molariform teeth of *Notosuchus* as typical ziphodont teeth, made by other authors (ORTEGA *et al.*, 2000). The molariform teeth of *Notosuchus* clearly resemble a mammal molar, with which they have a high morphologic convergence and in some way with those observed

in ornithischians dinosaurs too (BONAPARTE, 1991). In ventral view (Figs.7C, 8A), the maxilla expands medially forming a flat and horizontal surface of the palatal lamina (secondary palate). Posteriorly, each palatal lamina surrounds and embraces the maxillo-palatal fenestrae, which is in contact with the anterior projections of the palatine.

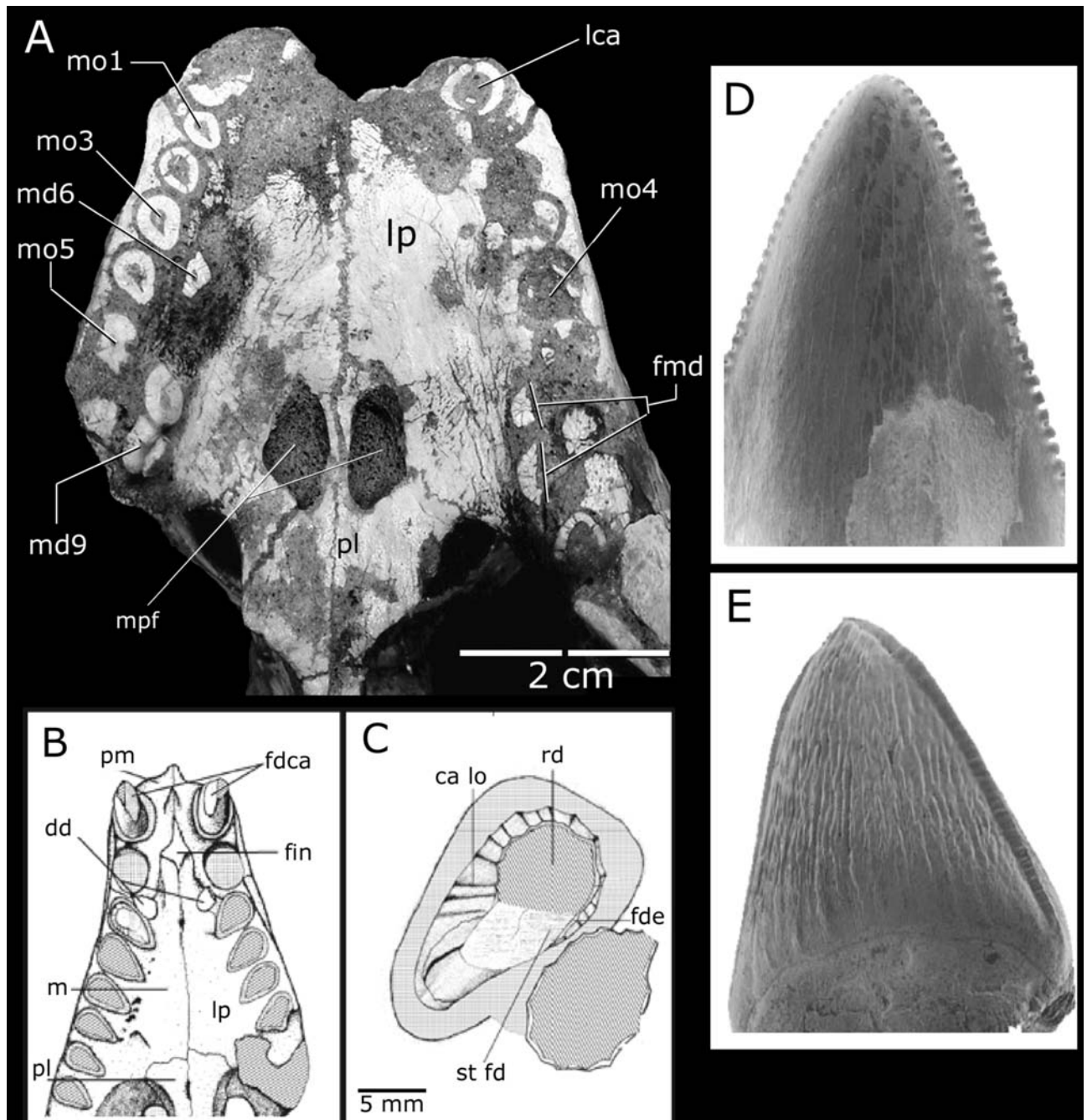


Fig.8- A, *Notosuchus terrestris*, MUCPv-35. Anterior extreme of the skull in palatal view. B and C, *Sphagesaurus huenei* (modified from POL, 2003); B, Anterior extreme of the skull in palatal view; C, first tooth of the right maxillary. D, tooth of the “true ziphodont” type of cf. *Iberosuchus* sp. E, tooth of the “false ziphodont” type of a juvenile of *Trematochampsia taqueti* (modified from PRASAD & BROIN, 2002). Abbreviations: (ca lo) longitudinal carina, (dd) dentary tooth, (fd ca) waste facet of caniniform, (fde) worn surface of enamel, (fin) foramen incisivum, (fmd) waste facet of mandibular tooth, (lca) left caniniform, (lp) maxilo-palatal lamina, (m) maxilla, (md) dentary molariform, (mo) maxillary molariform, (mpf) maxilopalatal fenestra, (pl) palatine, (pm) premaxilla, (rd) broken surface of dentine, (st fd) striae on dentine worn surface.

Separating both maxillo-palatal fenestrae, there is a thin lamina formed by the union of the posterior and medial palatal projections of the maxilla. The maxillo-palatal fenestrae are exclusive of *Notosuchus* and *Mariliasuchus* (FIORELLI, 2005; ANDRADE, 2005; ANDRADE & BERTINI, 2005a; ANDRADE *et al.*, 2006; ZAHER *et al.*, 2006).

In MUCPV-35 it is possible to observe the posterior limits of the palatal lamina that form the anterior border of the suborbital fenestra (Fig.8A). At this point, the maxilla rises vertically, internally to the cavity of the orbit and, as in *Sphagesaurus* (POL, 2003), it articulates with the jugal, lacrimal, prefrontal, the anterior process of the pterygoids, palatines, and ectopterygoids. Anteriorly, the palatal laminae possess appropriate morphology for the existence of cartilaginous conjunctive tissues embracing to the ventral premaxillary lamina in the proximal end of the snout. Considering that recently a highly descriptive work on the palate structures in Mesoeucrocodylia has been published (see ANDRADE *et al.*, 2006), we think that it is not necessary greater explanations in this section.

MUCPV-137 possesses both anterior and posterior palpebrals. Frontals are wide and relatively flat. The frontal does not participate of the supratemporal fenestra.

The morphology of the lacrimal, prefrontal, jugal, postorbital as well as the bones that conform the cranial roof, supraoccipital, squamosal, basioccipital and basisphenoid, have been well described in other works (GASPARINI, 1971; BONAPARTE, 1991; FIORELLI, 2005).

The quadrate possesses two lobular condyles, being the internal (medial condyle) slightly bigger than the lateral one (Fig.6). In *Notosuchia*, these condyles fit on the anteroposterior elongated channel-like of the articular. Moreover, the quadrate has a wide ventral projection that articulates with the pterygoids, basisphenoid and medially with the basioccipital (BONAPARTE, 1991). The otic region is exquisitely preserved in the cranial fragment of the specimen MUCPV-198 (Fig.6) and it is possible to observe more than five fenestrae.

The unique parietal bone is narrow and possesses a longitudinal crest among both supratemporal fenestrae (Figs.7A, D); it is bifurcated posteriorly and forms an acute angle depending on the specimen (ANDRADE, 2005; FIORELLI, 2005). The supratemporal

fenestrae do not possess an anteriorly located foramen. In occipital view (see Fig.6), the supraoccipital supports a vertical medial crest (or supraoccipital nape central crest), decreasing in height near to the foramen magnum. This crest is laterally limited by deep cavities for musculary inserts (branchiomic muscles). The exoccipital possesses a crest laterally directed that limits the dorsal area from the ventral one. It covers the foramen magnum and the occipital condyle, separated by a greatly defined neck (BONAPARTE, 1991); therefore, allowing wide cranial movements. Exoccipital possesses a large foramina of combined exits for the nerves motors and sensorial X (vague nerve) –which keeps relationship with the mouth, the pharynx, and most of the organs –, and XI (spinal accessory nerve) related with the branchiomic muscles of the neck (Fig.7C). On the other hand, between this foramina and the foramen magnum there is a small foramen belonging to the nerve XII, the visceral motor (hypoglose nerve). The morphology of the laterosphenoid is not clear due to the state of the materials. Possibly, the foramina for the exit of nerves IV (troclear) and V (trigeminal) are in the lateral inferior of the temporary and orbital faces of the laterosphenoid (FIORELLI, 2005); only the nerves II and III would occupy a previous wide opening, axially below the olfactory nerve (BONAPARTE, 1991). As in basal Crocodylomorpha, the foramen of the main branch of the trigeminal – maxillary and mandibular – would be between the union of the laterosphenoid and the prootic; meanwhile, the foramen for the exit of the ophthalmic branch of this nerve would be located ventrally in the orbital face of the laterosphenoid, above the basisphenoid (see BUSBEY & GOW, 1984; WALKER, 1990; GOWER & WEBER, 1998). These characteristics of nerves IV and V are important because they are related to the facial musculature, what is extremely outstanding in *Notosuchus* and it will be discussed posteriorly.

Mandible – Splenials and dentarys on the symphysis are projected anterodorsally approximately 45° (Figs.9A, 10A). Therefore, when the mandibular occlusion takes place, the end of the jaw inserts between both superior caniniforms and the first two incisiforms in each hemimandible. This feature is present in *Chimaerasuchus*, *Sphagesaurus*, and *Mariliasuchus* (ANDRADE, 2005; ANDRADE & BERTINI, 2005a; FIORELLI, 2005; ZAHER *et al.*, 2006) and maybe in *Adamantinasuchus navae* (NOBRE & CARVALHO, 2006). In ventral view the opening of the Meckelian channel can be seen (Fig.9A). On

the dentary, there is a lateral rim that separates an alveolar area from the ventral one. In both areas there are numerous aligned neurovascular foramina (even in the symphyseal region), clearly observable in MUCPv-35. This morphology agrees with the existence of thick soft muscular tissues like cheeks to avoid loss of food. The anterior 6 teeth of each hemimandible possess their alveoli on the dorsal surface of the dentary, while the posterior four teeth are implanted between the dentary and the splenial (Fig.10A).

The first incisiform of each hemimandible is implanted to 45° as that of symphysis. The crown is anterodorsally directed with the same angle, similar to that of *Mariliasuchus* (ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b), *Chimaerasuchus* (WU & SUES, 1996), and possibly other notosuchians

(*Sphagesaurus* and *Adamantinasuchus*). The second tooth possesses a similar characteristic but its alveolus and its crown is placed more vertical. Mandibular teeth cross-section gets progressively less circular and more triangular, from the first to the fourth teeth (Fig.10A). Middle and posterior teeth are completely vertical and they are implanted obliquely to the longitudinal axis, with the sharpest border located anterolabially.

During occlusion, inferior teeth fit in the triangular space present in between superior molariforms in MUCPv-35 and in *Sphagesaurus* (POL, 2003). In MUCPv-35, the mandibular molariform teeth possess a worn surface on their labial face and the upper molariform teeth on the lingual face (BONAPARTE, 1991).

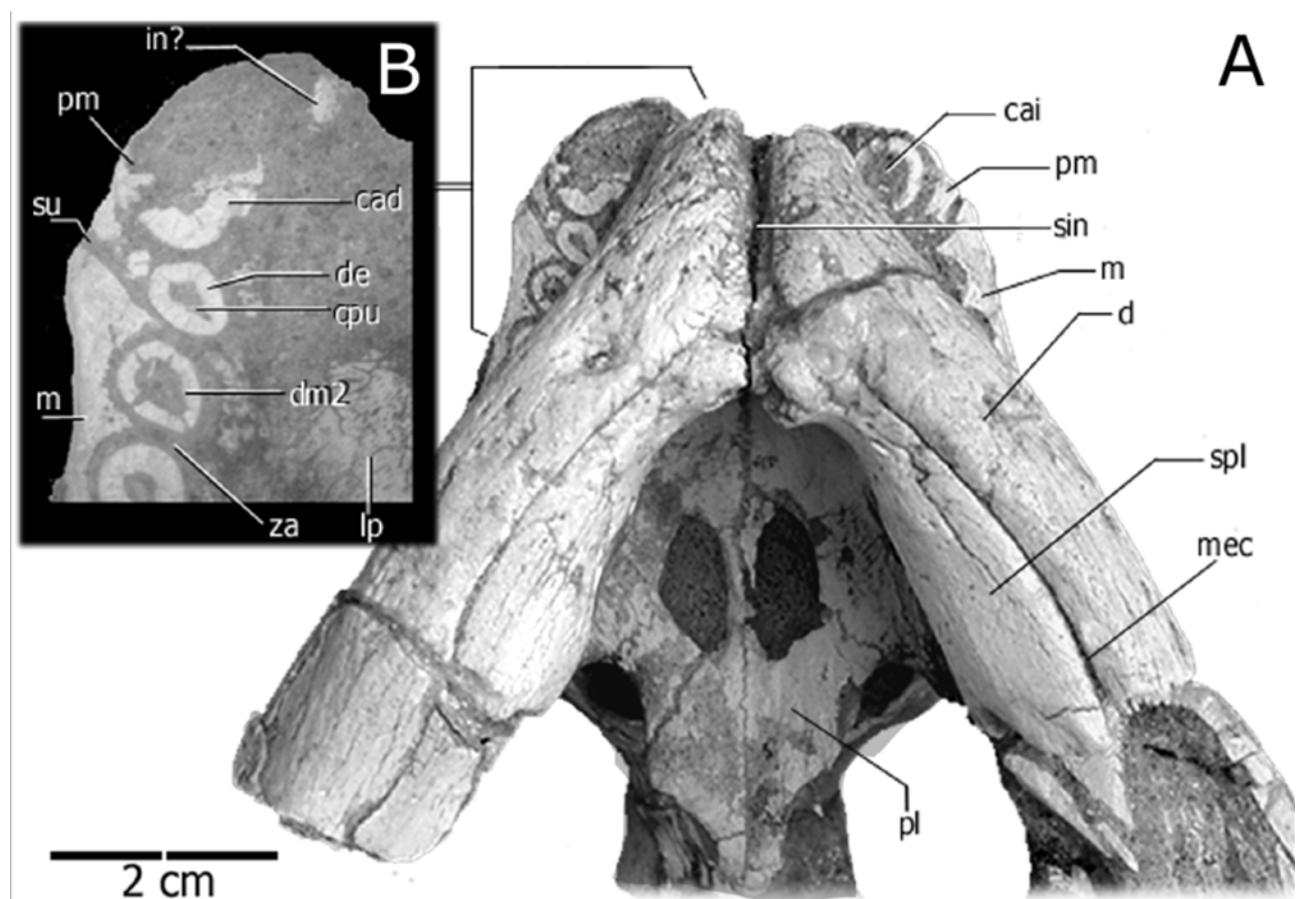


Fig.9- *Notosuchus terrestris*, MUCPv-35. A: anterior extreme of the skull and jaw in ventral view. B: right maxilla-premaxilla in alveolar view. Abbreviations: (cad) right caniniform, (cai) left caniniform, (cpu) pulpar cavity, (d) dentary, (de) dentine, (dm) maxillary teeth, (in) incisiform, (lp) maxillopalatal lamina, (m) maxilla, (mec) Meckelian groove, (pl) palatine, (pm) premaxilla, (sin) symphysis, (su) premaxilla-maxilla suture, (spl) splenial, (za) alveolar zone.

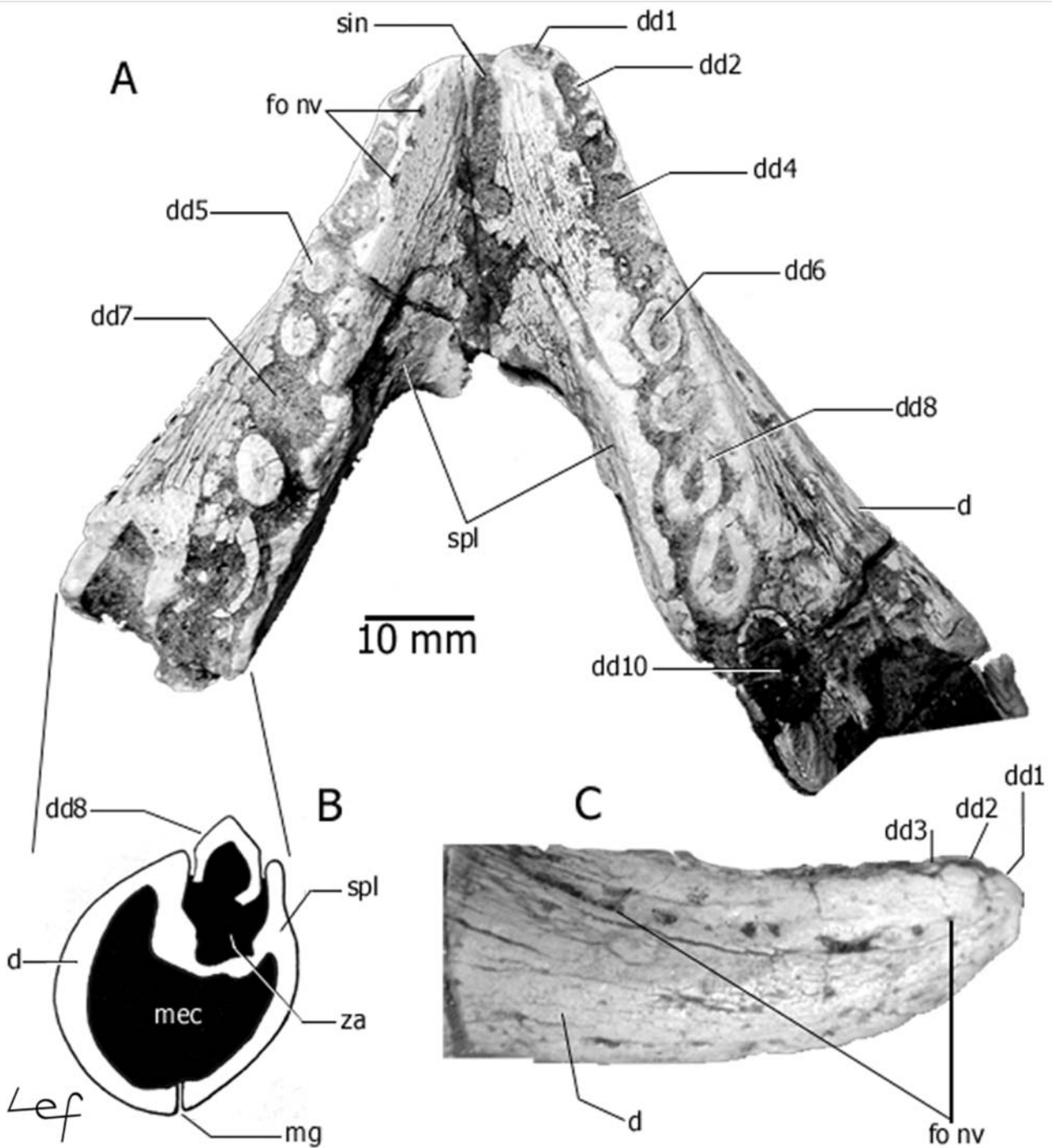


Fig.10- Jaw of *Notosuchus terrestris*, MUCPv-35. A: in alveolar (dorsal) view. B: transverse section through the left jaw. C: right jaw in lateral view. Abbreviations: (d) dentary, (dd) dentary tooth, (fo nv) neurovascular foramina, (mg) Meckelian groove, (sin) symphysis, (spl) splenial, (za) alveolar zone.

The articulate structure between the skull and the lower jaw is clearly visible and exquisitely preserved in the described specimens that conserve this structure. The angular supports the surangular and expands forming the ventral surface of the posterior retroarticular process. The surangular expands posterodorsally forming a fine thorn for the angular. In the posterior internal face of the mandibular branch, there is a clearly visible suture among the angular and articular, from where a shelf of this bone is projected medially. The articular projects posteromedially and forms the shelf for the quadrate process articulation. Condyles insert in two shallow channels directed anteroposteriorly and located in the glenoid fossa of the articular (Fig.6). The articular also lacks a posterior buttress. This morphology is clearly visible in MUCPv-198, *Araripesuchus* (ORTEGA *et al.*, 2000), *Malawisuchus* (CLARK *et al.*, 1989; GOMANI, 1997), *Sphagesaurus* (POL, 2003), *Chimaerasuchus* (WU & SUES, 1996), *Mariliasuchus* (CARVALHO & BERTINI, 1999; ANDRADE & BERTINI, 2005a; ZAHER *et al.*, 2006), and some few basal crocodylomorphs (HARRIS *et al.*, 2000). This is ambiguous in *Candidodon* (NOBRE & CARVALHO, 2002) but the quadrate characteristics and the condyles of the same one would indicate something similar. By contrast, in other Crocodyliformes the glenoid fossa is much wider than long. It is deeply concave without central crest and with a great posterior buttress. In *Notosuchus* this combination of structures indicates clearly a proal movement of the jaw during the mastication for the prosecution of the food. Posteriorly to the glenoid fossa, the articular expands and forms the “tablespoon” or dorsal face of the width retroarticular process (Figs.3, 7B) suturing toward ventral with the angular, similar to that of *Malawisuchus*, *Chimaerasuchus*, and *Mariliasuchus* (FIORELLI, 2005; ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b; ZAHER *et al.*, 2006).

Postcranial Axial Skeleton – An excellent postcranial study of *Notosuchus terrestris* has been published recently by POL (2005) but new observations that increase knowledge of this species contributes to give new anatomical and phylogenetic data. This is possible due to the specimen MUCPv-137, which represents the first and only record of *Notosuchus* with postcranial remains articulate to the skull (FIORELLI, 2005).

Between the skull and the first preserved cervical vertebra (axis), there were many tiny dispersed bony fragments in the matrix. They could be attributed to atlas and parts of the axis. In fact, the whole articulate cervical sequence was quite damaged and fragile preserved, hindering its description. Probably, the

skull-neck articulation was located ventrally and, for this reason, the snout of *Notosuchus* is anteroventrally directed, contrary to the current Crocodyliformes.

An important morphology in *Notosuchus* opposing to other crocodyliforms is the presence of 10 cervical vertebrae (FIORELLI, 2005). All cervical vertebrae possess lightly amphicoelous centra with anteroposteriorly short and ventral keel (Fig.11). Between the keel and the parapophysis there is a shallow cavity. The diapophyses are located in the pedicelous, anteroventrally to the neurocentral suture of the anterior cervicals. Posteriorly they change being located more dorsally reaching the same level that the zygapophyses.

The curved suprapostzygapophyseal lamina extends from half of the height of the neural spines until the posterior end of the postzygapophysis.

The neural spines are high and located in a central position in the vertebra. They are rectangular in lateral view; wider in the base than in the apex.

As it was described by POL (2005), starting from the contact between the fourth and fifth vertebrae, the width at level of its zygapophysis increases notably, increasing the development of its articular surfaces (Fig.11A). It increases in the fifth-sixth and sixth-seventh vertebrae, and decreases in the seventh and eighth vertebrae. The angle formed between the right and left postzygapophysis of the posterior cervical is smaller than 90°.

The cervical centra are abnormally heptagonal, with one of its vertex developed ventrally forming a keel all along the ventral surface (Figs.11D-F). At last, pedicelous of the neural arch are placed laterodorsally to the centrum, as a consequence of this heptagonal shape. Starting from the tenth vertebra, the centrum progressively loses the heptagonal form and takes a more rounded and circular form.

The specimen MUCPv-149 possesses a very well preserved cervicodorsal sequence and the anterior to middle dorsal vertebrae (Figs.5, 12). This material presents a total of eleven articulated vertebrae; the first preserves part of the pedicelous and the zygapophysis.

POL (2005; MACN-RN 1037) described three dorsal vertebrae from the eleven to thirteen. However, their descriptions correspond from the twelve to fourteen vertebrae. They are characterized by having the tenth cervical vertebra (MUCPv-137) with a relatively short and wide center, with transitional characteristics between the ninth vertebra (MUCPv-137) and the eleventh (second vertebra in MUCPv-149 because the first vertebra of this specimen – tenth – only preserves the left superior part).

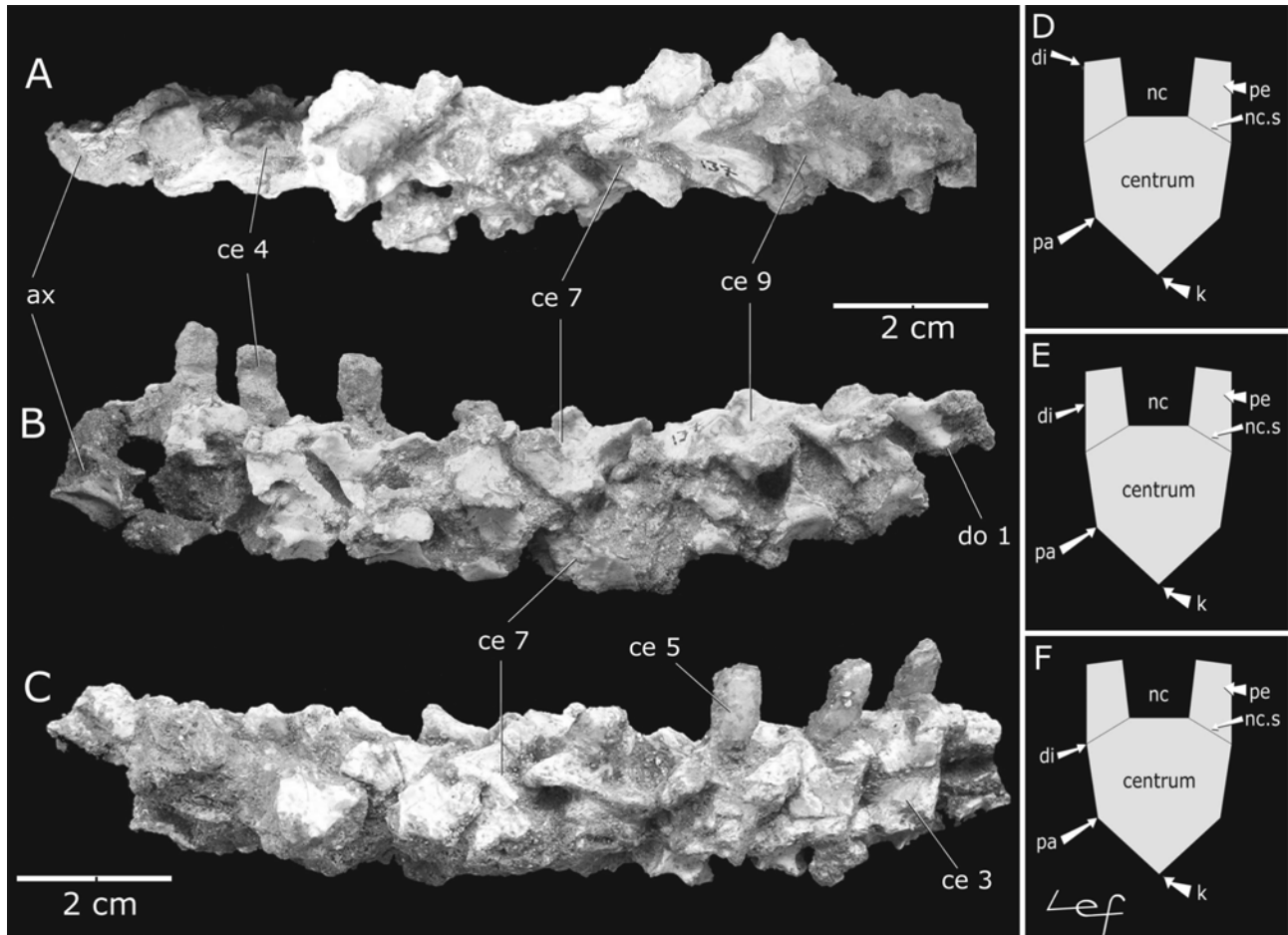


Fig.11- Cervical vertebrae of *Notosuchus terrestris*, MUCPv-137. A, in dorsal view; B, in left lateral view; C, in right lateral view. D, E and F, structures of the cervical centra in anterior view showing the variation in the position of diapophysis on de pedicelous; D, cervical III; E, cervical VII; F, cervical IX and X. Abbreviations: (ax) axis - second vertebra, (ce) cervical vertebra, (di) diapophysis, (do) dorsal vertebra, (k) ventral keel, (nc) neural channel, (nc.s) neurocentral suture, (pa) parapophysis, (pe) pedicelous.

The centrum of the tenth vertebra is longer than the ninth (MUCPv-137) but shorter than the eleventh (of MUCPv-149). The tenth vertebra possesses a similar width to the ninth cervical, and also a posterior articular face diameter similar to the anterior articular face of the eleventh in MUCPv-149. The posterior articular diameter of the centrum in relation to the anterior one is more elongated (Fig.12).

The prezygapophyseal and postzygapophyseal articulations are horizontal and are placed practically at the same level than the diapophysis. Postzygapophysis are posterolaterally curved. Diapophysis on the 14th vertebra is robust and born at the same level that the zygapophysis, with a wide surface in dorsal view, and expands toward

anterior. All characteristics of the cervicodorsal vertebrae are very similar to those present in *Chimaerasuchus* and *Marliasuchus*.

In the last cervicodorsal vertebra (13) and in the first three dorsal vertebrae (14, 15, and 16), the pedicelous of the neural arches are lightly inclined anteriorly (more marked in 14 and 15). It is also present in dorsals 19 and 20 (Figs.3B, 5C, 6C).

On the specimens available, combining the specimens studied here and the specimen MUCPv-287 studied by Pol (1999, 2005), there is a complete vertebral sequence until the caudal vertebrae (except for the atlas). *Notosuchus* possessed a total of 29 presacral vertebrae (10 cervical, 3 cervicodorsal, and 16 dorsal vertebrae), 3 sacral (MUCPv-287), and the first 13 caudal vertebrae (MUCPv-287).

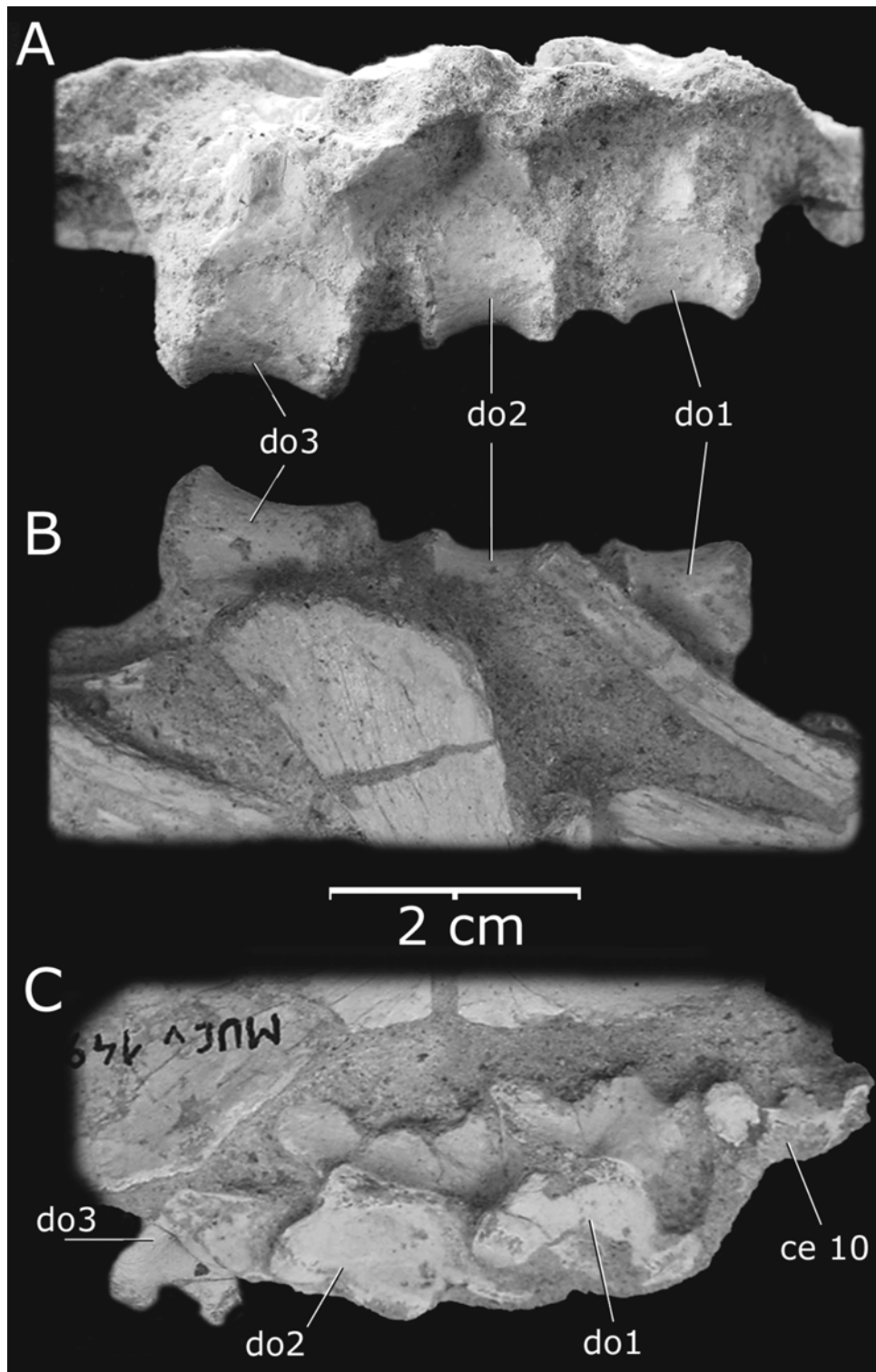


Fig.12- Cervicodorsal vertebrae of *Notosuchus terrestris*, MUCPv-149. A, in right lateral view; B, in ventral view; C, in dorsal view. Observe the size change and the longitude of the centra starting from the dorsal vertebra III. Abbreviations: (ce) cervical vertebra, (do) dorsal vertebra.

The centra of anterior dorsal vertebrae increase the length and they stay practically constant through the sequence. In posterior dorsals, the diameter of the centra increases gradually until the vertebra 28 and the presacral (29), which is wider and shorter (Fig.13). The centra are amphicoelous and they do not present hypapophysis.

Appendicular skeleton – Of the appendicular skeleton of *Notosuchus* only novel and outstanding characters are denoted because they were described minutely in previous works (POL, 1999, 2005; FIORELLI, 2005).

The left scapula of MUCPv-149 is very well preserved (Figs.5A, 14A). A half constriction separates the dorsal expansion of the scapula of the opposed ventral expansion. This material lacks the anterior lamina of the dorsal expansion, but it possesses a great expansion backward generating a great concavity in relation to the convexity of the posterior border. This morphology is seen in *Chimaerasuchus* (WU & SUES, 1996), *Araripesuchus* (ORTEGA *et al.*, 2000; TURNER, 2006) and other basal crocodyliforms as *Sichuanosuchus* (WU *et al.*, 1997). In the anterior margin it is concave while in the posterior one it is convex. The ventral expansion is shorter (practically half of the dorsal expansion) than in most crocodyliforms. The anterior border of the ventral expansion possesses a small acromial crest (acromial process), which is poor developed and located more ventrally than in other crocodyliforms (POL, 2005).

The left coracoid is less robust than the specimen MACN-RN-1037 described by POL (2005). The coracoid is slightly curved in all its longitude from the dorsal expansion until the ventral one (Figs.5B, 14B), contrary to other crocodyliforms that present an angular coracoid in the constriction (POL, 2005). The great foramen of the coracoid is placed in a deep lateral cavity between the glenoid fossa and the border of the scapular process of the coracoid. As in *Chimaerasuchus*, the articular surface for the scapula is perpendicular to the surface of the glenoid cavity. It is formed by a small crest that separates the surfaces for insertion of the *M. supracoracoideus longus* and *M. s. brevis* from the insertion of the *M. biceps brachii*.

The humerus of MUCPv-149 is more gracil than the humerus of Crocodylia, but is slightly more robust and more massive than in other Notosuchia. The deltoid crest of MUCPv-149 is relatively thick and more extensive than in *Chimaerasuchus* and other protosuchians (FIORELLI, 2005).

The preacetabular process of the ilium (Fig.4F) is

small and it possesses a light development (POL, 2005), a character state that is shared with *Chimaerasuchus* (WU & SUES, 1996), *Araripesuchus* (ORTEGA *et al.*, 2000; TURNER, 2006), *Uruguaysuchus* (RUSCONI, 1933), and *Theriosuchus* (WU *et al.*, 1996). As it was noticed in *Chimaerasuchus* (WU & SUES, 1996) and in the material described by POL (2005), the specimens MUCPv-137 and MUCPv-147 lack the iliac blade present in most of the crocodyliforms, pterosaurs, and dinosaurs (inclusive in birds), related with the *M. ilitibialis*. Therefore, this muscle in *Notosuchus* is more reduced than in other crocodyliforms. The dorsal crest of the ilium is greatly expanded forming a laterally extensive acetabular roof and produce a deep acetabular cavity. The surface for insertion of the *M. iliofemoralis* is wide and horizontal in the acetabular roof of the cavity, showing that this muscle ran vertical and ventrally. It possesses a great development of the postacetabular iliac process; this goes posteriorly with the distal end directed ventrally.

The femur (Figs.4E, F) is much more robust than in other notosuchians (*i.e.*, *Chimaerasuchus*, *Malawisuchus*, *Marilyasuchus*, and *Adamantinasuchus*). In anterolateral view, it possesses a slightly sigmoid shape and is twisted. The proximal end directs anterodorsally, while the distal end does posteroventral with the shaft that is slightly curved. The fourth trochanter is wide, rounded, and located on the posteromedial surface of the proximal end of the femoral shaft. The distal end of the left femur of the specimen MUCPv-137 does not possess the condylar expansions so marked as the condition presents in *Malawisuchus* (GOMANI, 1997). The fibular condyle (lateral c.) is markedly bigger than the tibial condyle (medial c.) and possesses a more ventral development. Both condyles are posteroventrally directed and possess long processes or supracondylar crests.

The tibia (Fig.4G) is also more robust than in other notosuchians and possesses a slightly smaller longitude in relation to the femur. It possesses a great expansion of the proximal end and a lateromedial expansion of the distal end. The tibial head expands excessively back and possesses a characteristic notch that separates the great process for the medial condyle of the femur; ventrally to the notch is the deep fossa flexoria. It lacks fibular crest. On the distal end, the medial maleolus is more robust and developed ventrally than the lateral maleolus. The fibula is long and smooth (Fig.4G). It possesses a porous area in the proximal portion for muscles attach and distally it is clearly visible with a deep and long medial fibular fossa.

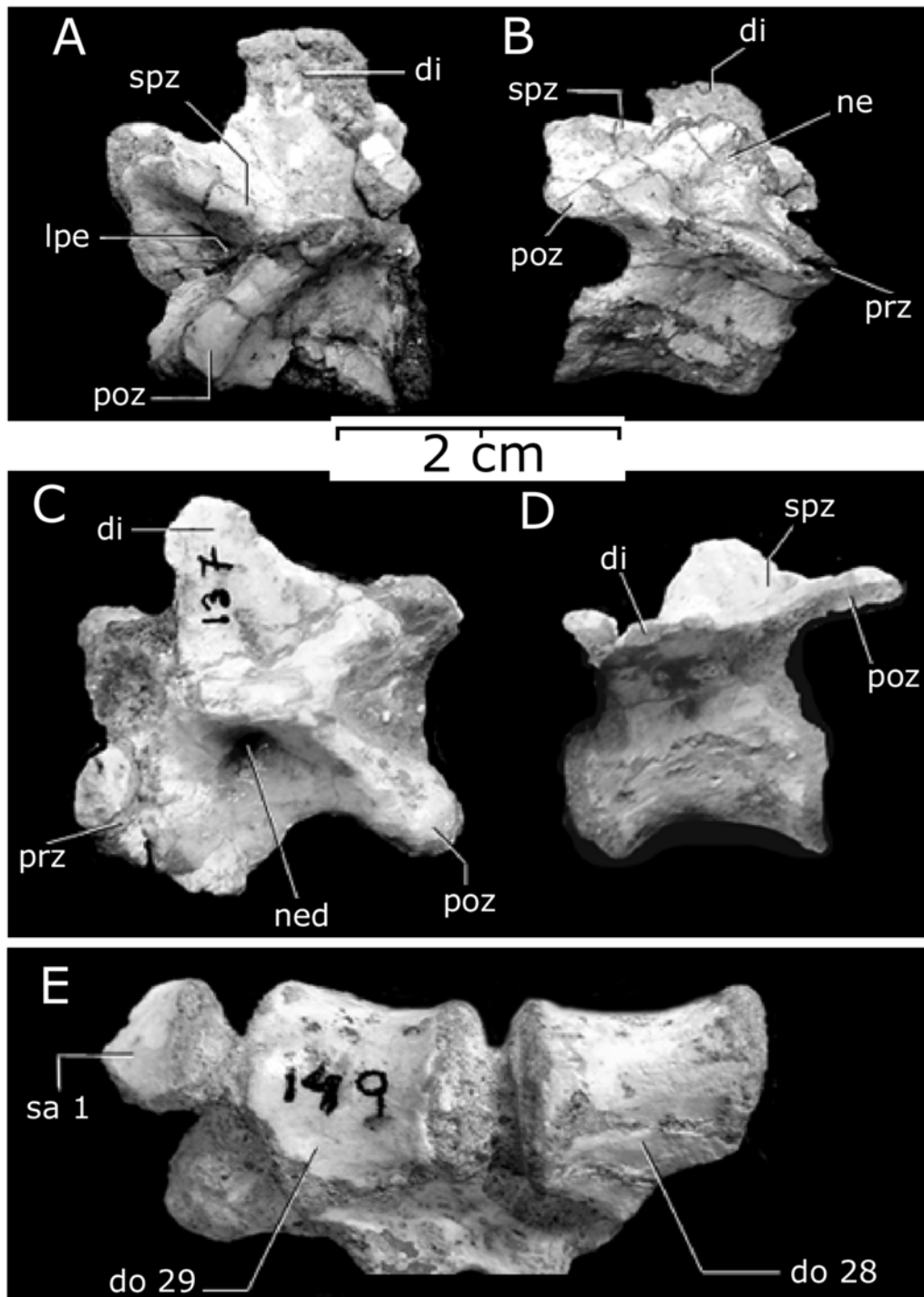


Fig.13- Dorsal vertebrae of *Notosuchus terrestris*. A and B, anterior dorsal vertebra (vertebra XV), MUCPv-198; A, in dorsal view; B, in right lateral view. C and D, medial dorsal vertebra (v. XXII), MUCPv-137; C, in dorsal view; D, in left lateral view. E, MUCPv-149; posterior dorsal vertebrae (v. XXVIII and v. XXIX -presacral) and fragment of the first sacral vertebra (v. XXX), in ventral view. Abbreviations: (di) dyapophysis, (do) dorsal vertebra, (lpe) postspinal lamina, (ne) neural spine, (ned) depression in the base of the spine, (poz) postzygapophysis, (prz) prezygapophysis, (sa) surangular, (spz) suprapostzygapophyseal lamina.

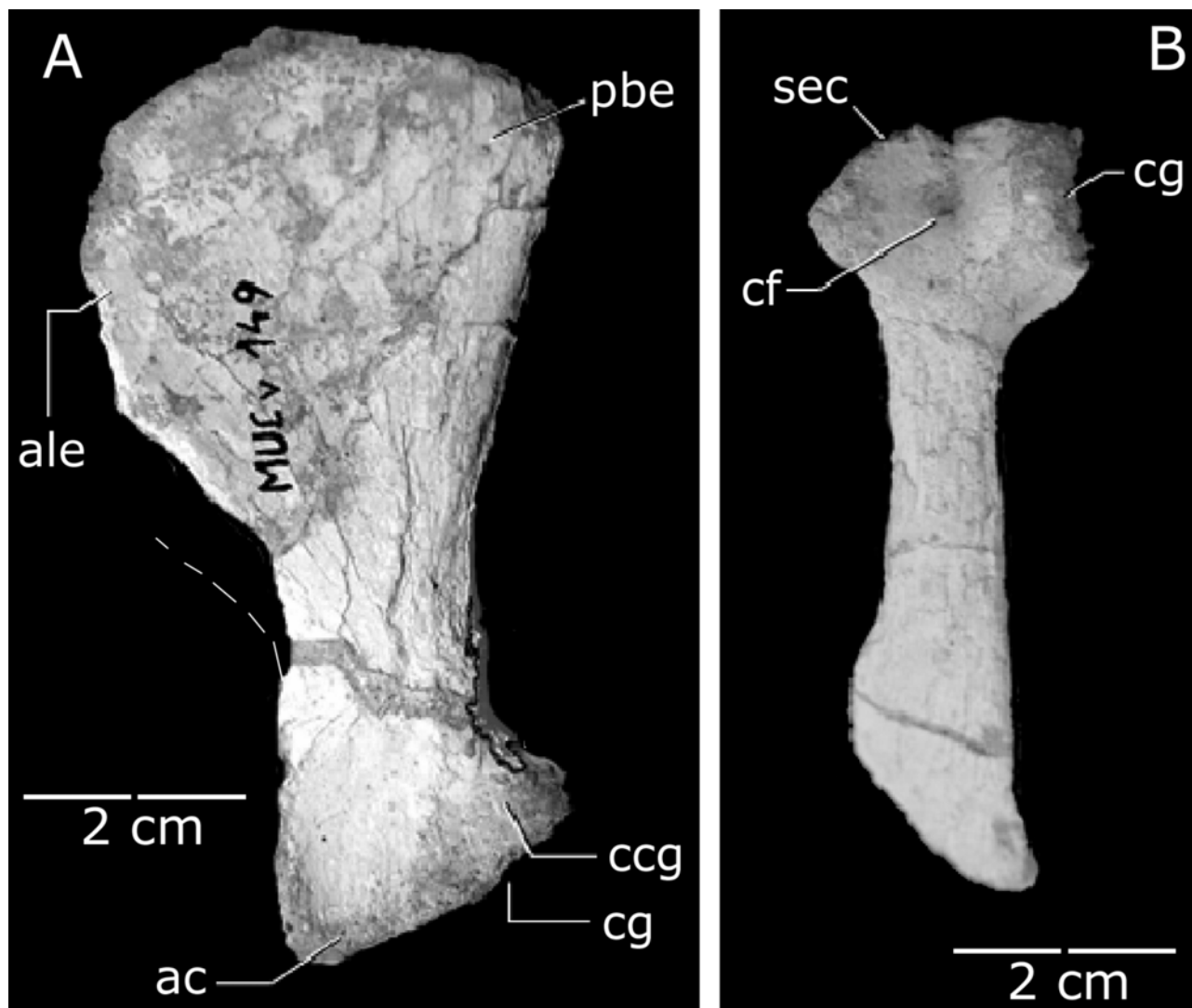


Fig.14- Pectoral girdle of *Notosuchus terrestris*, MUCPv-149. A, left scapula in laterodorsal view; B, left coracoid in ventrolateral view. Abbreviations: (ac) acromium, (ale) anterior scapular lamina, (ccg) glenoid cavity crest, (cg) glenoid cavity, (cf) coracoid foramen, (pbe) posterior scapular blade, (sec) scapulocoracoid articulation.

DISCUSSION

FORM AND FUNCTION OF THE ANATOMY OF *NOTOSUCHUS TERRESTRIS*: FUNCTIONAL ASPECTS OF THEIR TEETH AND SPECIALIZATION IN THE FEEDING

Many published works about the anatomical and functional aspects of Mesoeucrocodylia members have been done (BONAPARTE, 1991, 1996; CLARK *et al.*, 1989; WU *et al.*, 1995; WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; POL, 2003). However, few works have been dedicated to the feeding mechanism of *Notosuchus* (BONAPARTE, 1991, 1996)

and other notosuchian (ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b). In general they support an herbivore habit. Specializations regarding teeth and feeding are diverse on basal Crocodylomorpha. For instance, *Phyllodontosuchus lufengensis* Harris, Lucas, Estep & Li, 2000 (HARRIS *et al.*, 2000) and *Edentosuchus tienshanensis* Young, 1973 (POL *et al.*, 2004), present a heterodont dentition and a complex jag suggesting that both species had a diet not limited to meat (HARRIS *et al.*, 2000).

Notosuchia were perhaps the crocodyliforms that developed more variability in relation to teeth and

feeding aspects. *Chimaerasuchus paradoxus* possessed very specialized teeth, with wide molariforms and three lines of longitudinal cusps, similar to the molars of tritylodontoid sinapsids (WU *et al.*, 1995; WU & SUES, 1996). Moreover, the mandible possessed a proal movement and “lips” to avoid the loss of food. *Simosuchus clarki* (BUCKLEY *et al.*, 2000) has their teeth more smoothed in lingual-labial sense but they also possessed multiple cusps in the apical border. As it was suggested, *Chimaerasuchus* and *Simosuchus* were crocodyliforms highly specialized for an herbivore diet. Multicuspid teeth have also been reported in *Candidodon* (CARVALHO, 1994; NOBRE & CARVALHO, 2002), *Malawisuchus* (GOMANI, 1997), *Uruguaysuchus* (RUSCONI, 1933), and *Adamantinasuchus* (NOBRE & CARVALHO, 2006). In the case of *Malawisuchus*, it probably fed on small sized preys (*i.e.*, insects, amphibians, gastropods), captured by the caniniforms and processed by with multicuspid molariforms (GOMANI, 1997).

Undoubtedly, the dentary morphology present in *Notosuchus* indicates a feeding mechanism different to that of the other crocodyliforms, only comparable with that of *Sphagesaurus* and *Mariliasuchus* (FIORELLI, 2005; ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b; ZAHER *et al.*, 2006).

The first incisiform mandibular teeth of *Notosuchus* present a forward direction approximately at 45°. Teeth have circular section and their apexes rest on the ventral face of premaxillae when the jaw is closed. But during opening the fore and aft movement of the lower jaw made these teeth surpasses the premaxillary incisiform, producing “shovel” movement. These movements are present in varied herbivorous and insectivorous mammals such as in marsupials (Polydolopidae or Caenolestidae), in some Xenarthra, rodents, suids, camelids, notoungulans, ruminant, and lemurs. The caniniform presents a great development, with a deep root and a crown with the apex subcircular in traverse section (worn surface sensu BONAPARTE, 1991).

The molariform have triangular section, oblique to the parasagittal axis and worn surface similar to *Sphagesaurus* (POL, 2003). The worn surface of molariform teeth in *Notosuchus* would also be produced by the tooth-to-tooth contact and fore and after movement of the jaw (proal movement). In *Sphagesaurus* when the jaw is closed, each tooth occluded with a single tooth of the maxilla, while the same tooth of the other hemimandible

didn't reach to occlude with its corresponding one in the maxilla, being a space between them (POL, 2003:821). In *Notosuchus* something similar is observed. The molariform increases the diameter at level of the alveolus toward posterior in the maxilla and the mandible: the first molariform possesses a diameter that oscillates, depending on the specimen, among 2.9 to 4.5mm while the diameter of the posterior molariform is 4.5 to 6.5mm. When being implanted very near to each other, the distance that occupy two teeth sum easily the longitude of mobility of the quadrate in the articular shelf, with the difference that each tooth is implanted more internally than the following one located toward posterior (FIORELLI, 2005). So, when the jaw carried out the proal movement, the waste facet was not due to the occlusion of complementary maxilla-jaw teeth, but to the friction contact of a maxillary tooth with the posterior tooth to its complementary tooth of the jaw and, in this point, a perfect occlusion tooth-tooth took place of both hemimandibles with the maxillary ones (FIORELLI, 2005). For this reason, the waste facets of the teeth not necessarily have to be explained by means of alternative hypothesis, as for example cranial kinesis or lateral mandibular movements, but to the same “proal” movement carried out by the jaw.

As it was mentioned previously, it is not appropriate the assignment of “ziphodont teeth” to the molariform or postcanines present in the maxilla or dentary of *Notosuchus* (ORTEGA *et al.*, 2000). The molariform teeth clearly are not ziphodont, neither “false”, nor “true” (see PRASAD & BROIN, 2002). The characteristic aligned neurovascular foramina present in the alveolar region of the maxillary and in the surface of dentary indicate that *Notosuchus* possessed wide soft tissues like thick lips and facial and perioral musculature (*e.g.*, *m. orbicularis oris*), to maintain oral food during mastication (BONAPARTE, 1991, 1996; ANDRADE, 2005; FIORELLI, 2005).

On the nasal surface the presence of a wide central depression, with lineal striations and similar ruggedness possibly indicate the presence of nasolabial muscles (as the *m. levator nasolabialis* in mammals) that elevates the lip or the nose. In the area of articulation of the maxillar and the nasal, another smaller depression with grooves indicates also a possible analogy with the *m. caninus*. On the lower jaw, some striations, ruggedness and numerous foramina in the base at level of the symphysis, indicates the action of a depressor muscle of the lips (FIORELLI, 2005).

On the other hand, the external nares are directed forward and they do not possess nasal sept. For this reason, at the end of the muzzle, cartilaginous tissues could exist and, together with the lips and the muscles, they will form a short trunk or “hog’s snout”, similar to the characteristic muzzle of the suids (pigs) or tayassuids (pecaris), which use it for sniffing or smelling the land in food search (FIORELLI, 2005).

Notosuchus possessed a strong musculature of the neck, evidenced by the occipital inserts and very high neural spines of the cervical vertebrae. It possessed also a big suborbital fenestra for a great *m. pterygoideus anterior* (indicating a proal movement of the jaw). *Notosuchus* possessed a reduced *m. pseudotemporalis* characterized by the small size of the supratemporal fenestra, as well as a great development of the pterygoid wings for the *m. pterygoideus posterior* and a wide ventral margin of the mandibular fenestra, all evidences of a strong mandibular adduction.

Unlike other crocodyliforms, *Notosuchus* possessed a well developed and long *m. depressor mandibulae*, evidenced by the wide surface of the retroarticular process and its lack of a dorsal projection. It also possesses a good development of the posterior crests of the squamosal, suggested for *Malawisuchus* (GOMANI, 1997), *Mariliasuchus* (ANDRADE & BERTINI, 2005a; ZAHER *et al.*, 2006), *Squamata*, and *Sphenodon* Gray, 1831 (WU & SUES, 1996:695), as related to the control of the proal movements of the jaw and their adduction.

The cervical vertebrae of *Notosuchus* possessed diverse characteristic as for example elongated spines, wide zygapophysis, a depression among prezygapophysis, etc. It demonstrates the existence of marked arched dorsally movement on the vertebral region (POL, 2005). *Notosuchus* possessed

the head above that the neck and directed down, allowing wide cervico-cranial movements. Therefore, according to the evidence showed, *Notosuchus* distant too much of having a strict carnivore or scavenging habits. Probably, it will fit inside a description of a Suidae and Tayassuidae (Fig.15) or South American Caviidae as for example Dolichotinae (mara). These extant species have herbivore habits (or occasionally omnivorous), feeding a diverse vegetation mainly bulbs and roots, and in such case of fruits, seeds, annelids, and other worms (helped by the “hog’s snout” and incisiform) and possibly also arthropods (FIORELLI, 2005). Anyway, we do not discard the use of robust forelimb to dig and so obtain its food.

PHYLOGENETIC ANALYSIS: INTRA AND INTER NOTOSUCHIAN RELATIONSHIPS

In the last years several works that include analysis of the phylogenetic relationships within Notosuchia and related groups of crocodyliforms have been published (*i.e.*, CLARK, 1994; WU & SUES, 1996; GOMANI, 1997; WU *et al.*, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; MARTINELLI, 2003; SERENO *et al.*, 2003; POL, 2005; POL & APESTEGUIA, 2005; POL & NORELL, 2004a, 2004b; ANDRADE, 2005; FIORELLI, 2005; TURNER, 2006; TURNER & CALVO, 2005; ZAHER *et al.*, 2006). In any case, and although in practically all recent analyzes, *Notosuchus terrestris* is located relatively derived within the clade, the relationships of many of his taxa are quite conflicting, and these works do not show a consensus in their results.

According to this necessity, numerous phylogenetic studies that were realized focused mainly in the relationships of Notosuchia in a general context within Paracrocodylomorpha (*sensu* PARRISH, 1993; SERENO, 2005; SERENO *et al.*, 2005) and in direct

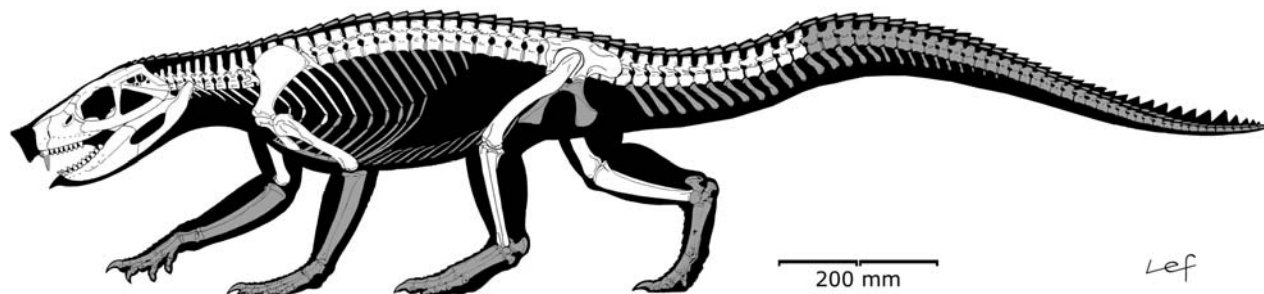


Fig.15- Skeleton restoration of *Notosuchus terrestris* based on the specimens contained in the Museum of Geology and Paleontology of the Universidad Nacional del Comahue located in the Centro Paleontológico Lago Barreales (included the specimen MUCPv-287, studied by POL, 2005). Lacking parts in gray color.

correlation with the more influential groups of Mesoeucrocodylia. The original differences in the diverse analyses were based mainly on the number of taxa included in the different matrixes. It is interesting to observe that to incorporate different basal taxa (variant between sphenosuchians and protosuchians), the results are extremely dissimilar. Thus, the variation, inclusion and/or extraction of basal groups of Crocodylimorpha, influence markedly in the possible topology within notosuchian and neosuchian clades (see Appendix I).

The cladistic analysis by which it was chosen was lead using a modified dataset of 264 characters scored for 66 taxa of Paracrocodylomorpha plus *Gracilisuchus stipanicorum* Romer, 1972 as outgroup. This dataset is an extension of the used by FIORELLI & CALVO (2007) which is based in previous publications and new definitions.

Additionally, in the present work new characters were incorporated (232 to 245; see Appendix II) taken from POL & APESTEGUIA (2005) and new taxa included (see Appendix III). In the present analysis, this dataset was analyzed with equally weighted parsimony through of TNT (GOLOBOFF *et al.*, 2003). A heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult*1000; max*), holding 10 trees per replication (hold/10), followed by a final round of TBR branch swapping and zero-length branches were collapsed. The analysis resulted in ten most parsimonious trees of 1089 steps (CI: 0.278; RI: 0.636) found in all replicates. An alternative phylogeny is presented (Fig.17, see Appendix IV).

In all most parsimonious hypotheses group we observe that *Notosuchus terrestris* represents the sister taxon of the clade forming by [*Mariliasuchus amarali* + *Adamantinasuchus navae*] both from the Upper Cretaceous of Brazil. This South American clade (Fig.16, stem 11 – Notosuchidae) possesses a derived localization inside the Notosuchia clade and is diagnosed by five unambiguous synapomorphies (Character 45[2]: quadrate with three or more fenestrae on dorsal and posteromedial surfaces; Character 103[2]: articular facet for quadrate condyle close to three times the length of the quadrate condyles; Character 160[1]: forked ectopterygoid medial process; Character 176[1]: maxillopalatal fenestrae present; Character 202[0]: postcanines teeth (molariforms) triangular in traverse section). Also, the node 12 [*Mariliasuchus amarali* + *Adamantinasuchus navae*] is diagnosed by four unambiguous synapomorphies (Character 120[0]: tooth margins with denticulate carinae;

Character 241[1]: ventral half of the lacrymal tapers posteroventrally, not contacting or contacting slightly the jugal; Character 242[1]: large foramen on lateral surface of anterior jugal; Character 243[1]: procumbent premaxillary –incisiform– in anterior dentary alveoli).

On the other hand, Notosuchidae (stem 11) represents the sister clade of the node conformed by *Comahuesuchus brachybuccalis* + [*Sphagesaurus huenei* + *Chimaerasuchus paradoxus*]. This node, *Notosuchus* more *Chimaerasuchus* and all his descendants (node 10, Fig.17), is diagnosed by six unambiguous synapomorphies (Character 111[1]: short and broad prefrontals anterior to orbits and oriented posteromedially-anterolaterally; Character 198[1]: ectopterygoid contact palatine excluding the pterygoid of the posterior edge of the fenestra palatina; Character 199[1]: nasal-frontal suture obliquely oriented; Character 232[1]: transversal splenial-dentary suture at symphysis on ventral surface; Character 244[1]: rodlike posterolateral palatine bar present; Character 245[1]: ectopterygoid projecting medially on ventral surface of pterygoid flanges widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges). In other phylogenetic results in which they were, extracted/included some taxa (excluding poposaurids, some “sphenosuchians” or gobiosuchids; including the *Sarcosuchus-Terminonaris* clade), *Comahuesuchus* is shared like a Notosuchidae, forming a trichotomy with *Mariliasuchus* and *Adamantinasuchus*.

Also, when excluding or including some basal taxa, the *Araripesuchus*-clade shared is paraphyletic with *A. buitreaensis* more basal within notosuchians than the other araripesuchids. Another important aspect that is derived from the present study is the intimate relationship between *Araripesuchus* with the rest of the notosuchians, occupying a relative basal place inside the notosuchian. The relationships of *Araripesuchus* are concordant with some recent publications (POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006) and in turn different from others which present its relation with the neosuchian clade (CLARK, 1994; BUCKLEY & BROCHU, 1999; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; ANDRADE, 2005; TURNER & CALVO, 2005; TURNER, 2006).

Anatosuchus minor was described as a “notosuchian” from the Late Aptian or Early Albian, Republic of Niger. Originally it was closely related to *Comahuesuchus brachybuccalis* integrating the monophyletic Comahuesuchidae clade (*sensu* BONAPARTE, 1991).

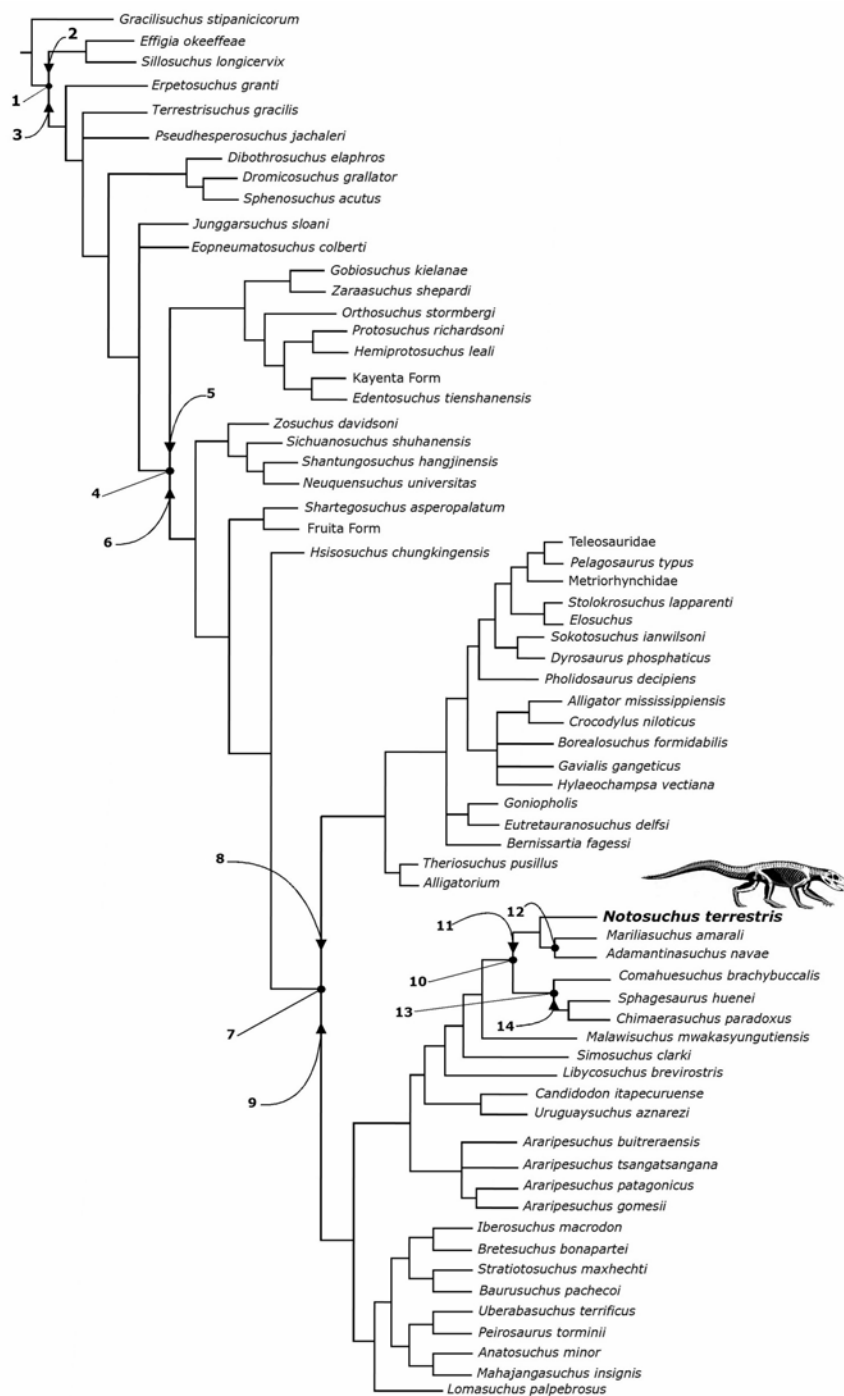


Fig.16- Strict consensus of the 10 most parsimonious topologies that resulted from a strict parsimony analysis obtained through of TNT (GOLOBOFF *et al.*, 2003). Tree length is 1089 with a CI of 0.278 and a RI of 0.636. 1: Paracrocodylomorpha; 2: Poposauridae; 3: Crocodylomorpha; 4: Crocodyliformes; 5: Protosuchia; 6: Mesoeucrocodylia; 7: Metasuchia; 8: Neosuchia; 9: Notosuchia; Node 10, 12 and 13: Innominate. 11: Notosuchidae. 14: Sphagesauridae. Unambiguous synapomorphies for the labeled nodes 10-14: Node 10: 111(1), 198(1), 199(1), 232(1), 244(1), 245(1). Stem 11 – Notosuchidae–: 45(2), 103(2), 160(1), 176(1), 202(0). Node 12: 120(0), 241(1), 242(1), 243(1). Node 13: 11(1), 154(1). Stem 14 –Sphagesauridae–: 105(3), 121(1), 124(1).

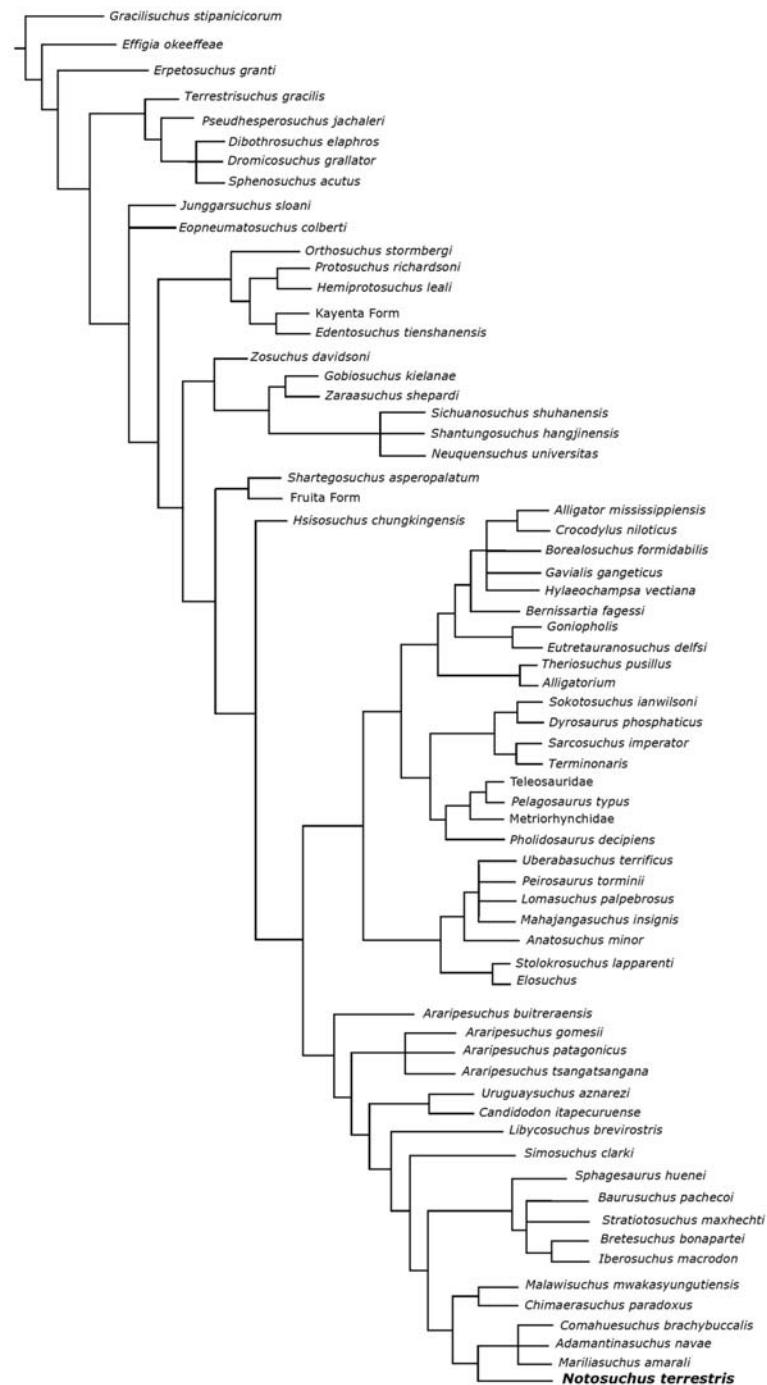


Fig. 17- (Alternative phylogeny for the appendix IV): Strict consensus of the 10 most parsimonious topologies that resulted from a strict parsimony analysis obtained through of TNT (GOLOBOFF *et al.*, 2003). Tree length is 1108 with a CI of 0.274 and a RI of 0.636. This analysis result shared the different topology obtained from the exclusion of *Sillosuchus* and the inclusion of *Sarcosuchus* (BROIN & TAQUET, 1966; SERENO *et al.*, 2001; GASPARINI *et al.*, 2006) and *Terminonaris* (MOOK, 1934; WU *et al.*, 2001; GASPARINI *et al.*, 2006).

Contrary to this, in recent phylogenetic analyses carried out in another works (*e.g.*, MARTINELLI, 2003; FIORELLI, 2005; FIORELLI *et al.*, 2007) *Anatosuchus* is relocated outside of Notosuchia, and therefore from Comahuesuchidae, and related to peirosaurids which is similar to the present result. However, other authors related this bizarre crocodyliform to different mesoeucrocodylian or neosuchian forms (ANDRADE, 2005; JOUVE *et al.*, 2006) which make evident that a more carefully analysis is necessary.

The notosuchian relationships presented here, especially in relation to the more derived forms, raise important paleobiogeographic questions. In fact, Notosuchia offers evidence in favor to the hypothesis of a dispersion event among Gondwana and Central Asia during the Early Cretaceous (Berriasiano–Aptiano), which took to important faunistic interchanges (JUÁREZ VALIERI & FIORELLI, 2002, 2003; JUÁREZ VALIERI *et al.*, 2004; FIORELLI, 2005; FIORELLI & CALVO, 2005). This fact is mainly demonstrated by the derived Notosuchia *Chimaerasuchus paradoxus*, of uncertain Cretaceous age of China, which represents in all parsimonious hypotheses the sister taxon of *Sphagesaurus huenei* from the Upper Cretaceous of Brazil. Such results are concordant with recent phylogenies presented by diverse authors whom they include to *Chimaerasuchus* inside his analyses (WU & SUES, 1996; WU *et al.*, 1995; POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; ANDRADE, 2005; FIORELLI, 2005; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006).

An interesting consequence from the phylogenetic result is the important relationships between peirosaurid and sebecosuchian crocodyliforms. This particularity, although different from the recent phylogenetic results (POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; FIORELLI, 2005; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006), is partially similar to the analysis carried out by JOUVE *et al.* (2006) and LARSSON & SUES (2007), in which these crocodyliforms represent sister groups. However, it is important to observe that in another heuristic search (excluding some sphenosuchians or the poposaurid clade) both group did not share sister relationships; thus, the sebecosuchian clade is more related to notosuchians (or inside them) and the peirosaurid clade as sister group of neosuchian crocodyliform (POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006), inside them as sister group of the [*Elosuchus* + *Stolokrosuchus*] clade or related to trematochampsid crocodyliforms (BUCKLEY & BROCHU, 1999; BUCKLEY

et al., 2000; TURNER, 2006; TURNER & CALVO, 2005).

On the other hand, and although this does not have direct relevance with the present study, from the phylogenetic analysis derive other two very interesting aspects. First, the results confirm the position of the new basal Mesoeucrocodylia *Neuquensuchus universitas* FIORELLI & CALVO, 2007, from the same Cretaceous locality and levels of *Notosuchus*, as the sister taxon of *Shantungosuchus hangjinensis* Wu, Brinkman & Lu, 1994, from the early Cretaceous of China. However, the most parsimonious tree that depicts *Neuquensuchus* in other position, for example together with notosuchians, requires nine extra steps. Secondly, this result shared a clear paraphyly of “sphenosuchians” ratifying therefore the results offered recently by CLARK *et al.* (2004). In any case, this is not confirmed since if other sphenosuchian taxa are gotten up to the analysis, like *Hesperosuchus*, *Kayentasuchus*, *Litargosuchus*, and *Macelognathus*, the monophyly of the group is guaranteed with the difference that *Junggarsuchus* would not represent a sphenosuchia. This rather represent the sister taxon of Crocodyliformes together to *Eopneumatosuchus*.

CONCLUSIONS

The new *Notosuchus* remains reported and described here increase the knowledge about the species and its characteristics. The study of the cranial and postcranial offers new information that allows understanding and confirming its relationships with the notosuchian members and the remaining crocodyliform groups. The phylogenetic analysis results demonstrate the monophyly of Notosuchia reinforcing the previous studies realized on the group (WU *et al.*, 1995; GOMANI, 1997; POL, 2003; POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; FIORELLI, 2005; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006). In addition, it confirms the close existing relationships between the Argentine, Brazilian, and Chinese taxa.

This work, together with the last works on Crocodyliformes, clarifies that the heterodonty in basal crocodylomorph members (HARRIS *et al.*, 2000; POL *et al.*, 2004) and Mesoeucrocodylia was not the exception but the rule, the most habitual in the mesozoic crocodyliforms. These display a great variety and dentary morphologies, doubtlessly related to its different functions, nutritional strategies, and dietary types. In

addition and as it were noticed by POL *et al.* (2004) and ÖSI *et al.* (2007), the present analysis demonstrates that the heterodonty evolved independently in the different Crocodylomorpha groups (Sphenosuchia, Protosuchia, “protosuchians”, Notosuchia and Eusuchia).

In the present work and on the basis of the diverse anatomical characteristics in the skull, jaw and postcranium of *Notosuchus*, it is clear the possible herbivores habits inferred for the species and other notosuchian groups.

Notosuchia would have been a remarkable group in Gondwana, very important within the faunal diversity of the Upper Mesozoic, mainly in South America. However, the presence of it outside Gondwana (*Chimaerasuchus*) during the Cretaceous demonstrates the occurrence of a paleobiogeographic land connection between Gondwana and Central Asia, by which a great migration of faunas occurred towards both continents, demonstrated by diverse vertebrate groups.

Without doubts, the least inclusive clade containing *Araripesuchus* and *Chimaerasuchus* (Fig.16) shows a great morphological diversity. It is evidenced mainly in the rostral region and in the snout, likewise on the tooth morphology and their possible nutritious specializations. Definitely, none of these taxa possesses ziphodont-like teeth (“true or false”); therefore, we do not think that the name Ziphosuchia is appropriated for this mesoeucrocodylians group (*sensu* ORTEGA *et al.*, 2000).

Notosuchia had to represent a great and much more diverse group than it is known at the moment, partly by the disparity of forms and the different morphotype. The recent new notosuchian notifications (*e.g.*, NOVAS *et al.*, 2004; ANDRADE & BERTINI, 2005a; GARCIA *et al.*, 2005; MARCONATO, 2006) not only confirm this hypothesis but extend the knowledge of the group and help to strengthen its phylogenetic relationships.

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A P P E N D I X

APPENDIX I

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Gracilisuchus stipanicorum

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Effigia okeeffeae

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Sillosuchus longicervix

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Erpetosuchus granti

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Terrestrisuchus gracilis

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Pseudhesperosuchus jachaleri

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Dromicosuchus grillator

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Sphenosuchus acutus

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Dibothrosuchus elaphros

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Junggarsuchus sloani

000?00?11??00001?0001?0?0?00100?10?????????1????????????????1?0??11?01?1101001?10???????411?????0?101
100?0?000??000000000?11?00??000?010?1?0??0?0??0??0000?000?1????00??100?0?0?1?0?0?00000?100101101???0
00??[01]1?1????????????010??0??0??000?0??

Eopneumatosuchus colberti

20????????????000100????0?01102?10?0000201001111100?0?0110??0?0?????????????????????????????????
?????00????????????????????0??
????????????????????0?0??0??0??
1??0000?0000000

Protosuchus richardsoni

21000001201000011010002100000100010001010?002010011111001010102011?110210001010100011100[1234]00
?120011010111021001010000[01]000000?01?0?01?10010[01]0101000000?0?010000000120000011110?0?0100?010?
000000100001201100???10111011122011100030011?00?1?0000??

Hemiprotosuchus leali

?00?00?10?????10010?0?00?0010?11?0?01??0020?00?11?1100101??1?2?11??1?21??01??????0??1200?1?10
1??0????????000?000??10?00??00000??10????00??????000?12??001??10?0?00?01??00??00000000?01?00?
??????0????????????????????????????????

Kayenta Form

[12]01110?1200000?10010?0?00?0?0?0??11110?002010011111100001011?2011?0102100?1010??0??00?0?1200
101101112????0????01100?00?01000111?101001?01?1000000011?0??40012??00011?0?00??00??????011100??
?01????????????????????????????????001?00?????

Edentosuchus tienshanensis

201????[12]????0??[01]0??1?0100?0?0??02?110?00????????????????????[12]311????10?01010????????[234]????
?????????1[23]????????00110??1?01?1???1000110?11?1????????011????4?0??1????11??0????0100?????00111000?
?01100??10110????????????????????01?0?0???

Orthosuchus stormbergi

21100001201?0001001000[01]10000010001000?000?002011001111100??1?1?02011?0?0?0?001000100011100000?12
0010010211421001?10010?100000001?01010000000000?0??00001??000000?12?000011110000100000?000?00000
10001?01?00??10?1?00??3?0?1??0?????????00?0?0?0??

Gobiosuchus kielanae

101000?110000011001?01[01][01]?1?00001?10?0201000?0020112011111000?1????201??1?20100[01]010?0?0??????0?
1010110[01]012002??0000??0010[01]00001000000?00001001211?0000??110000000?121000011?00?0?00111111111
11000100?1?01?0????100??0000??0100000??00??0?1?00000?0

Zaraasuchus shepardii

10????????????1?01?01?1000001?10?02????????????????????????????????2?????1??010??????????????[1234]0??1010?0?
????????0????????????????????????0????1??1????????1?00????????1?00??0??????111111111?00????00??000???
?001??0??1????????????????1???????

Shantungosuchus hanqinensis

2?1????1?0?0?0?1??1????11????????2?1[01]100020?1?011?1100?10??????101?1?000??10??????0?1??????????
1??????1?????0010??????00??10?00??111211?0001?????0?0?00??10111111?0?110?0??1????00[01]1000?201??
0??10001?00?0?0100001??0?0??0??0???

Neuquensuchus universitas

??1?0111?11000????????????
0??1?0??0????????????2?????0??000111003
0110000102100????????????

Sichuanosuchus shuhanensis

[12]01??0?1200[01]00?1001011?110??1?00?021?10?00020?1?011?1100??????2?11??1?000011?1?01?1??000?????
??1?11?0?1??0??100100??1??10?0??00111[01]1210??00??01????01011101111100?110000100?1??00?01000
1201000?00?0?0111002001?00?0210????001?0?00?0

Zosuchus davidsoni

201??0?1200000??001010[01]110?001110?02211010012?1??011?11000?0?1?0211110????0?0111????????????????
?1?12?3???1????00100011011?0001?0?0010112?[01]0001??0?00??010111?1011?1011100000100??000010001
?011?0????????????????????????00?0?00?0000

Shartegosuchus asperopalatum

201?12?1?00100??0?101011???1010?01121?11?111????????????????????20312101010?10110?????????????????1?
1?01??1?????01000?01001000??0100?11011?1??0????10010?0011?0010001?011?0?0?00000??000010101?010?
????????????????????????1000??0100010

Fruita Form

201??001200100010000100100000110010221?11?0020112?1??0?0?0?0?1?2?31????1?0111101011?1?00011112?0??
1??[01]00??1?1001?001?0?0100100??101?0011?01110??0?00?10?0000?1??000????101?0?00000?000?0?0?0????
?1????????????????????????????1?00??00

Hsisosuchus chungkingensis

211?????1??00000010000110001000?0221101000[12]??12?11?10000?0?1?0?11?4?00[01]02?1??10??????000?100
0??101?0021??1?????01001??????0000?000?1?11?1?000??????0?0?0??10?0?0111[01]000?00?0?1000?01?00010
12?1?0?????????????02?????2121????0?????0??0

Mahajangasuchus insignis

203110?12?1?00?110001011?1?0110?0101??????1????????????????????11?121110??[01]111?1110?1220001110??
0112?00?100?0000101001001?11?1?????010011001?1??0????200101?00?1??1?00?0100?010?00000000?0?0011?110
1001010011100111220201110122101001?0?0000??

Anatosuchus minor

203?10?1011?001?1?00101111?0010101022?1010?01?????????0?????????1212131110?10101????????????????????11
1000??0??0??0?01101001?11?00??000?10011?00?0?0??20020?0111?1?000??100??0?000000??010001000??1?00
????????????????????100100??000001

Lomasuchus palpebrosus

201??0?1211?00?1100010111?0110001022?1010001??121?1?1001?1??1?121211????00??[01]11?????????????????
?1?2?00??000??0?00?0?010110000??000011?01?1??00????010??0?11??10?01?10000111000?0??010000100??1
????????????????????????00?0?0?00

Peirosaurus torminni

201?0011211?00?????010?1??????01?2?10??0????????????????????31?131110?11[01]11????????????1120????1
2000?????????10010?01?0?????0?001????????????[01]0?????0????????????00??1?????????0??00?00?01001??
????????????????????0000?0?0?00??

Uberabasuchus terrificus

20110011211?00?1100010111?0110101022??0?00011??2????????????????1111131110?11[01]11????????2200011201
?0012000??0?0??01001001?11?00?1?00001[01]101?11??0??10010?0011??1000??100?011100000000?0?00010
010100101??1100????????????????000000?0000??

Bretesuchus bonapartei

1[01]0??011211??00????????????0?????????2??10011????????1011?1??????13?1??1?00?10110????????????????????
100????1??????01?0?0??01?0?0??0??1?0????????[01]0[01]1?10?1??1?001?000?????????0??1?00101?0100?
????????????????????00?0?1?01?

Iberosuchus macrodon

1?0?00012?0?0011100011111?01?000?02??10100111?12??1?101??10?1??111?10?0?1011011????[12][1234]00??
00??00?[12][01]0?2??0000??11001101010?1?0??100?11001?0??101??[01]0111?001101?0?01?100001000000?0??
010?00??0100????????????????000000?21000??

Baurusuchus pachecoi

100?0?121?00?1101????11?0110????2?1011001112011?1000?10??10?31112101011111????????????????????
12103?????1????110111010101110011001110110?0111??[01]0[01]111011101?00001?0001000000000??0100001
11?01000??????011220211?0?0??100000?0000011

Stratiotosuchus maxhechti

100?0??1?0000?11?11101?0??10?11?????????1?1?????????????????131?????????11?????????????????0?210
3??1?????????1111?10?1??010001101?10?1?????010?01????1?????10?010?0000??00?0?0?1?1?1?????????
????????????????????0000??

Uruguaysuchus aznarezi

201?001101??00??10??1??1????1??01022?101?0011????1?????0??0??0111[12]??000110100??1?1????0000?0??0
1?21002100?00?000?[01]??01?1?00??1?0111?11????11????1?0001??????0??10????00??????01?001101?01
100?11111?00111120211?0?0??01??????????

Candidodon itapecuruense

201?00??1?00??110010????0010101022?111?00????????????????????11212????????11????????????????????1?
01????????????1011010?00??0100111011????11?????1?0?21?1?1??????1?0??00?000????01101?000??1???????
????????????????????1????000010

Arapesuchus gomesii

20100011010000111000101111011[01]00102211010001112011?10000?0?110201121210001101[01][01]11111?
1[234]000100000111002100100100100100100000010011000210000110?0011[01]0000111101000011100?0000
000000000010010000?01?0?0??110011121021111012211001?101?000000

Araripesuchus patagonicus

201000?1010000?1[01]000101111?0111001022?10100011?12?11?1000??0?1?02?1 1212?0?011[01]1??1?1?????????10
000?0111100??01??0?01?01101?010000??100110102?0?01??0?0?0[01]1000111?0100001110?000000000000000100
10000?01100?1?111100111210211??01221?01?01?1?0?0000

Araripesuchus buitreaensis

[12]01????1?1??0??10001?0111?0110?0??2?1010001????????????????[12]??12??0?0?1?100??????????????????[
01]??0[0123]??0?????11??1?10?100??0??0?10?02??0??01??000?1??110?01?0?0??00?0??0?010?1[01]1
01?010?0????????????????????[01]1?0100?0?000

Araripesuchus tsangatsangana

201101?1211?0011101010111100110001012110100011112?11?1000??0?1101021102100011010111111?001000???
??1110002100?0000101?01001?01000001110110102?0?001?110011[01]0000111?0100001100000100000000?000100
111?02011101111110011121?2001100211101?010?000000

Libycosuchus brevirostris

201000?101?00??10?010?1??011000?0?2?101??0?11120?1?10?0??0??0?011??210001?1000????????????????1[
01]2010?????????01?011????????????011000??1??01??????00000110????001?100?01?????00??0100100??01???
????????????????????00?1?00?????

Simosuchus clarki

10301011000000100010111110?0110001021?10100011?11011?1000010?1?020112121010110000??????02100?2010?
10002010??01?????11011012120000101001110021100120??211[12]0001111011001[01]1?1000000000010000010
110100001100????110?????202????????[01]1001100000000

Malawisuchus mwakasyungutiensis

101?00?1110000?01]10001[01][01]1100?110001?22110100011??20??1000?10?1?02?111[01]2?0101110001????1??21
000[02]010?0?1[12]2111??01?0??01100101?11000??110110101?0?0001??0?100??21110?10000111000000000000
??0100110002?1110101??11001112?0211??01221?00?001??0?000

Notosuchus terrestris

101000110101001110001111100110011022110110021112011?1000010?110211111210101110001[01]11101?210001
000??0122011??01100101[01]1101[01]01001000000111111011000001100100001011101100001110110000000000
0001001111121011011111100111120211??01221?110001?0000011

Mariliasuchus amarali

101000?10100001110001[01]111100011001022110100021?12011?1000010?1?0213011210[01]0111000??1?0?2?000
????0??22111?011?010?0[01]001101001001100[01]0011110110?0011??0110001001100100001?1010000000000?0
00100111?1?10110?11?1??????0211??01221?110001?0?11111

Adamantinasuchus navae

101000?1010?00?110001??11?011????????????????????????????????13??1??00??10????????????????????1??21
1??1?????01000101?01?0??111110?02?0?0?0??01100?211????0??10??010?000000??01?01?0?1?1[01]10???
????????????????????0?1?0111??

Comahuesuchus brachybuccalis

103??0?1011?00????0112??????0010?2????1??11?1????????????????131?????0?10101????????????????????[0
1]13??1?????0?10?101201?01????011?0?1??11??11?00100?1?0?000??100??0?000??0??0?0?11?11?111???
????????????????????1100?1?011111

Sphagesaurus huenei

1010000101?00??100????110??????21101?00????011?1000??????13?2??????100??????1??????????????3
12??0?0?????111110111111111110011101011?0?11?0?011?0?10?0?1?000000?00?????01001?1????0?????
????????????????????0?01?00000??

Chimaeresuchus paradoxus

101?0001111?00????????????????????????????????????12?0110?01010??1?1?????2100?00????11[01]?
314210??00?010011111011?????0?0110?????????10?11????3?????????1?00??0?????????0??111?1211?10111
1?110011?1202????01221??0????0000??

Elosuchus

202?111110000111001001?1?1010111012?101000?1?12111?1000?11????1202?3??00?21100????????????1110?0?
0?0000??01?????011010110[01]1010?00000010001?1?101??00011?0001?1?0000??10000[01]??0000?0??0110001
01?010????????????????001000?1000000

Stelokrosuchus lapparenti

2020000010000?111001001?1?0010111012?1?0?011?1211??1000?11?1??020?1??0?21100?????????????????1
 ?0000??01?????01?010110[01]1010?00000010001????101??000111?00?0?00000??1000011?0000??0?0001?0?0
 10????????????????????????????????0010?0?00000??

Pholidosaurus decipiens

212?111101??11?11101100111?00100010?211?100001112111?101??10?100?1311?300??2?0???11?1??0??0??2?0???
 ??????????????????1????1?110?????0010?????????????????1?0001??10?001?100?010??0?????010?00????01?????
 0001100?11??0211??0?????0?????0????0??

Dyrosaurus phosphaticus

002??1?101?010?11?00100011?1010011012?10101001112011?1011?10?1010101302?3?00??2?000?????????0?00?????1?
 ??????????????????1?????????????????0?0?0?????????????????021?0001?????0?????00??1?0000000??010?00?01?0100100
 00011001112?021111012101??0000?0?000

Sokotosuchus ianwilsoni

2?2??1101??10??001001??101001?012?1?????1112?11?1?11?0??0?1?1?0??????01?????????????????????????
 ??????????????????1?????????????????0?0?0?????????????????0?????????????????0?????????????????00?????????????????
 ??????????????????0?????????????????

Teleosauridae

[02]02?111110011020100100000000000110021?01000?001101111001011?1?00120003?000?20000210111?0000?12
 000101011?0???10??01001101??1011000011000010100?0??0000??10001000011?010?0111000101000000000001000
 01?1201000000011000110?0211??0??????00?0?00??000

Metriorhynchidae

[02]02?12110100111201011000?0000000110021?0?000?001101111001011?1?001200?300010200002101?11?0000???
 ???0?012?0??100?01001101??1011?000??000010102?0??000??001000011?01000?1100000100000000??010000
 1?1?01000000011000110?0211??0??????00?0?000?000

Pelagosaurus typus

202?111111001102010100000000000[01]100211010000001101111001001?10001200?30000020000110111?0000001
 200011101?00???10??????1?1?????0000?010010?0010??00??0001000011201000011000001?0000000??010000
 ???0?1?0???000????????????????????????000?0?000

Theriosuchus pusillus

20110111110100110000110111100110011?211010001?11?01111000?????1?20211?4100101010110111110001111200
 1001010002?00?10?110110[01]001?1100?00?0?00100??01??0?00??1010000?11?010?01?10000?00000?????010?00
 0??1?1?0?0000110??1??0211??????0[01]?00?0?0??0

Alligatorium

?0?????1?0000?1000010?111?0?100?1????0?00??11?1??1000??????20?1??00101?101?01111000??1?00100??
 ?????????10?1?????????????????0?????????????????0?????????????????0?????????????????0000??[01]?1000?000
 01??????0211?0???????????????????

Eutretauranosuchus delfsi

203??1?10010111000100111?00?0001001110?000?1112011?1010?0?1?0?121204?00001020111??1?0?0?0?1?????
 ???000??000??0?100????110?????0?00??1?0?0??10?2??001?0?000?1?110?01?0000000??010?00?????????
 ?????????????0????????????0000?00?00?0

Goniopholis

203?1211110010111000100111?0010001002?101000?1112011?1010?10?1?021312?4100[01]0[01]02011?1??1?0?00?1
 200?11?000002100010?1101100??101100?000010010001?1??0000110020000011001000011110?010000000000010
 000????01????0001100?11??0211??0??????0000?0000000

Bernissartia fagessi

203??21111?00111000?00111?001000?002????00001112?11?10100?0?1??1?1??410010102011?1?11??02002111011
 0100000?000??????1????1????????0?0?10??01??0????1?12000001????0?????00??10000?????0?01??????1?1?0?
 ?0001100?11??????0?????0?????0??0

Hylaeochampsia vectiana

00?????11??11?????1?01?????0?002?1?1011?????????101?1?1?1?????10?????????????????????????????????
 ?????0??????10????????????0?????????0?????????2?00????????????????????????????????01?????????1?0??000?????
 ?????????????????????????0?

Gavialis gangeticus

212?121111001111110110111110010001002110101101112011110110101110[01]131003100012000001111110131112
111100?000002110?100100?101??121100?00000001000101?1?00001?0?20?00011001000011100001?0000000000010
000001001001000001100?11??021111030111??00?0?00??000

Borealosuchus formidabilis

203?1211110010111000100111?00100010021101011111211111010010?110?1310031000110?011111111113111?11
0?00?000002110?100100?101??11110??000000010001?1??0000110?20?000110010000111000010000000000001000
0001001001000001100?11??0211110??????00?0?00??00

Crocodylus niloticus

203012111100[01]011100010211110010001002110?0111112011110100101110[01]1310031000100101211111101311
12021100?0000021100100100?101??121100?0000000100110101100001?0?2000001100100001110000100000000000
10000001001001000001100?1112021111030111??0000?0000000

Alligator mississippiensis

203112?101?0001110001021111001000?002110101111112011110100101110[01]03120310001002012111111131112
0211?0?00000211001001001101??111000?00000001001[12]01011000011[01]120000011001000011100001000000000
00010000001001001000001100?111202111103011

APPENDIX II

LISTS OF CHARACTERS CORRESPONDING TO THE DATA MATRIX USED IN THE PHYLOGENETIC ANALYSES

Characters 1-231, not cited here, were taken and are the same from FIORELLI & CALVO (2007). The following ones, 232 to 245 characters, were taken from POL & APESTEGUIA (2005) that originally corresponded to the characters listed in the contiguous reference.

Character 232 (POL & APESTEGUIA, 2005: character 180): Splenial-dentary suture at symphysis on ventral surface: V-shaped (0), or transversal (1).

Character 233 (POL & APESTEGUIA, 2005: character 181): Posterior peg at symphysis: absent (0), or present (1).

Character 234 (POL & APESTEGUIA, 2005: character 184): Dorsal surface of mandibular symphysis: flat or slightly concave (0), or strongly concave and narrow, trough-shaped (1).

Character 235 (POL & APESTEGUIA, 2005: character 185): Medial surface of splenials posterior to symphysis: flat or slightly convex (0), or markedly concave (1).

Character 236 (POL & APESTEGUIA, 2005: character 186): Choanal septum shape: narrow vertical bony sheet (0), or T-shaped bar expanded ventrally (1).

Character 237 (POL & APESTEGUIA, 2005: character 188): Lateral surface of dentaries below alveolar margin, at middle to posterior region of toothrow: vertically oriented, continuous with the rest of lateral surface of the dentaries (0), or flat surface exposed laterodorsally, divided by a ridge from the rest of the lateral surface of the dentaries (1).

Character 238 (POL & APESTEGUIA, 2005: character 220): Flat ventral surface of internal nares septum: anteriorly broad (0), or tapering anteriorly (1).

Character 239 (modified from SERENO *et al.*, 2001: character 67 by POL & APESTEGUIA, 2005: character 222): Premaxillary palate circular paramedian depressions: absent (0), present located anteriorly on the premaxilla (1), or present located at the premaxilla-maxilla suture (2).

Character 240 (POL & APESTEGUIA, 2005: character 223): Posterolateral region of nasals: flat surface facing dorsally (0), or lateral region deflected ventrally, forming part of the lateral surface of the snout (1).

Character 241 (defined by ZAHER *et al.*, 2006: character 192 and taken by POL & APESTEGUIA, 2005: character 224): Ventral half of the lacrymal: extending ventroposteriorly widely contacting the jugal (0), or tapers posteroventrally, not contacting or contacting slightly the jugal (1).

Character 242 (defined by ZAHER *et al.*, 2006: character 193 and taken by POL & APESTEGUIA, 2005: character 225): Large foramen on lateral surface of anterior jugal: absent (0), or present (1).

Character 243 (modified from ZAHER *et al.*, 2006: character 194 and POL & APESTEGUIA, 2005: character 226). Procumbent premaxillary –incisiform– anterior dentary alveoli: absent (0), or present (1).

Character 244 (defined by ZAHER *et al.*, 2006: character 195 and taken by POL & APESTEGUIA, 2005: character 227): Rodlike posterolateral palatine bar: absent (0), or present (1).

Character 245 (defined by ZAHER *et al.*, 2006: character 198 and taken by POL & APESTEGUIA, 2005: character 230): Ectopterygoid projecting medially on ventral surface of pterygoid flanges: barely extended (0), or widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges (1).

APPENDIX III

LIST OF THE 67 TAXA USED IN THE PHYLOGENETIC ANALYSIS (TAKEN FROM FIORELLI & CALVO, THIS VOLUME).

Effigia, *Sillosuchus*, *Erpetosuchus*, *Pseudhesperosuchus*, *Dromicosuchus*, *Sphenosuchus*, *Junggarsuchus*, *Eopneumatosuchus*, *Shartegosuchus*, *Mahajangasuchus*, *Araripesuchus buitrraensis* and *A. tsangatsangana*, *Libycosuchus*, *Adamantinasuchus*, *Stolokrosuchus* and *Elosuchus*, are new taxa included by the authors for this analysis.

Gracilisuchus stipanicorum (ROMER, 1972)
Effigia okeeffeae (NESBITT & NORELL, 2006; NESBITT, 2007)
Sillosuchus longicervix (ALCOBER & PARRISH, 1997)
Erpetosuchus granti (NEWTON, 1894; OLSEN *et al.*, 2000; BENTON & WALKER, 2002)
Pseudhesperosuchus jachaleri (BONAPARTE, 1971, 1978; CLARK *et al.*, 2000)
Terrestriusuchus gracilis (CRUSH, 1984)
Dromicosuchus grillator (SUES *et al.*, 2003)
Sphenosuchus acutus (HAUGHTON, 1915; WALKER, 1990)
Dibothrosuchus elaphros (WU & CHATTERJEE, 1993)
Junggarsuchus sloani (CLARK *et al.*, 2004)
Eopneumatosuchus colberti (CROMPTON & SMITH, 1980)
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 (FIORELLI & CALVO, 2007)
Sichuanosuchus shuhanensis (WU *et al.*, 1997)
Zosuchus davidsoni (POL & NORELL, 2004a)
Shartegosuchus asperopalatum (EFIMOV, 1988)
 Fruita Form (CLARK, 1985, 1994)
Hsisosuchus chungkingensis (YOUNG & CHOW, 1953; LI *et al.*, 1994; WU *et al.*, 1994)
Uruguaysuchus aznarezzi (RUSCONI, 1933)
Candidodon itapecuruense (CARVALHO, 1994; NOBRE & CARVALHO, 2002)
Araripesuchus gomesii (PRICE, 1959)
Araripesuchus patagonicus (ORTEGA *et al.*, 2000)
Araripesuchus buitrraensis (POL & APESTEGUIA, 2005)
Araripesuchus tsangatsangana (TURNER, 2006)
Libycosuchus brevirostris (STROMER, 1914)
Simosuchus clarki (BUCKLEY *et al.*, 2000)
Malawisuchus mwakasyungutiensis (CLARK *et al.*, 1989; GOMANI, 1997)
Notosuchus terrestris (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991, 1996; FIORELLI, 2005; POL, 2005)
Mariliasuchus amarali (CARVALHO & BERTINI, 1999; ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b; ZAHER *et al.*, 2006)
Adamantinasuchus navae (NOBRE & CARVALHO, 2006)
Comahuesuchus brachybuccalis (BONAPARTE, 1991; MARTINELLI, 2003)
Chimaeresuchus paradoxus (WU & SUES, 1996)
Sphagesaurus huenei (PRICE, 1950; POL, 2003)
Baurusuchus pachecoi (PRICE, 1945)
Stratiotosuchus 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)
Mahajangasuchus insignis (BUCKLEY & BROCHU, 1999)
Anatosuchus minor (SERENO *et al.*, 2003)
Elosuchus (BROIN, 2002)
Stolokrosuchus lapparenti (LARSSON, 2000; LARSSON & GADO, 2000)
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 (EUDÉS-DESLONGCHAMPS, 1863)
Teleosauridae (BUFFETAUT, 1982; CLARK, 1986, 1994)
Metriorhynchidae (KÄLIN, 1955; GASPARINI & DIAZ, 1977)
Theriosuchus pusillus (OWEN, 1879; CLARK, 1986, 1994; ORTEGA *et al.*, 2000)
Alligatorium (WELLNHOFER, 1971; CLARK, 1986, 1994)
Eutretauranosuchus delfsi (MOOK, 1967; CLARK, 1986, 1994)
Goniopholis (MOOK, 1942; CLARK, 1986, 1994; SALISBURY *et al.*, 1999)
Hylaeochampsa vectiana (CLARK & NORELL, 1992; ORTEGA *et al.*, 2000)
Bernissartia fagessi (BUSCALIONI & SANZ, 1990; NORELL & CLARK, 1990)
Borealosuchus formidabilis (ERICKSON, 1976; BROCHU, 1997b)
Gavialis gangeticus (CLARK, 1994; BROCHU, 1997a)
Crocodylus niloticus (CLARK, 1994; BROCHU, 1997a)
Alligator mississippiensis (CLARK, 1994; BROCHU, 1997a)

APPENDIX IV

ALTERNATIVE PHYLOGENY (FIG. 17)

Sarcosuchus imperator

203?12?10100101?100010011001010001012?10101[01]01?12?1??10100?0?100?131213??00021[01]101?112????[01]00
?1200?00?010[01]0??000[01]001?0?101??121100??00000010010?1??00??110210000?1001000?1?100?010?00000000
?0100001011010010010011000?????1?110????10000?0?0000000

Terminonaris

202?[01]2?1010010?11??01001???1010001012?1010[01]1?????11?1010??0??0??13[01][12]13?000?2100011112??0000
0?1200?10?0?0102100?1001001101??1??10??0??0?0010??1??0000111?[12]?000??00?0?0?11100?0?0??00??00?0
100001011010010000011000112202111102220100?000??000000