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Postcranial remains of *Notosuchus terrestris* Woodward (Archosauria: Crocodyliformes) from the upper Cretaceous of Patagonia, Argentina

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Abstract. Postcranial remains of *Notosuchus terrestris* are described here in detail for the first time. Comparison of these remains with other crocodyliform taxa revealed that *Notosuchus* bears numerous postcranial characters previously unknown for this group (*e.g.*, axial prezygapophyses arising from the anterior half of the neural arch pedicels, disconnected from the neural spine; well developed suprapostzygapophyseal laminae on cervicodorsal vertebrae; poorly expanded end of ventromedial process of the coracoid; presence of a posterior process on proximal end of radiale; presence of three sacral vertebrae, being the second and third vertebrae completely fused to each other; dorsal surface of ilium flat, rugose, and lateromedially wide, lacking an iliac blade and forming a markedly extensive acetabular roof). The postcranial morphology of *Notosuchus* also sheds light on some paleobiological aspects of this Cretaceous crocodyliform. These include the presence of an erect hindlimb posture for this basal mesoeucrocodylian, suggesting that the sprawling locomotion appeared late during the evolution of Crocodylomorpha. Furthermore, comparisons with other forms suggest that postcranial morphology of Crocodyliformes is not as conservative as previously thought, providing a source of phylogenetic information usually overlooked in previous approaches to crocodyliform systematics.

Resumen. RESTOS POSTCRANEANOS DE *NOTOSUCHUS TERRESTRIS* WOODWARD (ARCHOSAURIA: CROCODYLIFORMES) DEL CRETÁCICO SUPERIOR DE PATAGONIA, ARGENTINA. Se describen aquí en detalle por primera vez restos postcraneanos de *Notosuchus terrestris*. Las comparaciones de estos restos con otros crocodyliformes revelan que *Notosuchus* posee numerosos caracteres postcraneanos hasta ahora desconocidos para este grupo (*e.g.*, prezygapófisis del axis originadas en la mitad anterior de los pedicelos de los arcos neurales, desconectadas de la espina neural; láminas suprapostzygapopfiseales en vértebras cervicodorsales; extremo del proceso ventromedial del coracoides pobremente desarrollado; presencia de un proceso posterior en el extremo proximal del radial; presencia de tres vértebras sacras, presentando una fusión completa de la segunda y tercer vértebra; superficie dorsal del ilium plana, rugosa, y lateromedialmente ancha, estando ausente la lámina ilíaca y formando un techo acetabular notablemente extenso). La morfología postcraneana de *Notosuchus* provee también información sobre algunos aspectos paleobiológicos de este crocodyliforme cretácico. En éstos se incluye la presencia de una postura erecta en su miembro posterior, sugiriendo que la condición semierecta apareció tardíamente en la historia evolutiva de los Crocodylomorpha. Las comparaciones con otras formas sugieren también que la morfología postcraneana de Crocodyliformes no es tan conservativa como había sido sugerido previamente, proveyendo una fuente de información filogenética comúnmente ignorada en trabajos previos de la sistemática de Crocodyliformes.

Key words. Notosuchia. Crocodyliformes. Postcranial morphology. Cretaceous.

Palabras clave. Notosuchia. Crocodyliformes. Morfología postcraneana. Cretácico.

Introduction

During the Mesozoic crocodyliforms, a large clade of archosaur reptiles that includes extant crocodiles and several fossil relatives, achieved a wide morphological disparity, including terrestrial, marine, and amphibious taxa. Several terrestrial crocodyliforms are known from Cretaceous beds of Gondwana, particularly in South America. One of these forms, discovered in northwestern Patagonia in the XIXth century, is *Notosuchus terrestris* (Woodward, 1896), a bizarre form found in Bajo de la Carpa Formation (?Coniacian-Santonian; Hugo and Leanza, 2001). This taxon draw the attention of many researchers mainly because of the presence of plesiomorphic characters in conjunction with a large number of autapomorphies, depicting *Notosuchus* as a distinctive form within Crocodyliformes (Gasparini, 1971). *Notosuchus* is currently known from numerous additional skulls found during the XXth century in outcrops of the Bajo de la Carpa Formation in Neuquén and Rio Negro Provinces. However, post-

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cranial remains undoubtedly associated with *Notosuchus* skulls were unknown until now. Here, postcranial remains found in close association with skulls are described for the first time. The study of postcranial remains associated with skulls allows us to improve the knowledge of this crocodyliform's morphology, bearing important features for the analysis of its mode of life, and additionally offers a novel source of phylogenetic information for this taxon.

Material and methods

The postcranial remains were described following the osteological nomenclature proposed by Romer (1956) and Mook (1921). The counting of cervical vertebrae was done considering the atlas as the first vertebrae. Previous studies suggested that basal crocodyliforms had their hindlimbs oriented in a parasagittal position (Parrish, 1987; Whetstone and Whybrow, 1983; Carrier, 1987). Following these suggestions, the positional terms used in limb descriptions refer to a vertical orientation of limb elements. This terminology was also applied to sprawling forms such as extant crocodiles for uniformity of terms for comparisons. The nomenclature used for axial muscles and ligaments was taken from Frey (1988), while the appendicular muscle nomenclature follows Romer (1923), Nash (1975), and Rowe (1986).

The postcranial remains of *Notosuchus* were compared within the context of crocodyliform diversity, although special attention was paid to the morphology of some taxa with known postcranial remains that were postulated as closely related to this taxon. In the text, when a taxon is mentioned for the first time, the original description of that taxon will be cited. Further mention to a particular feature of a taxon will include the reference if the information was gathered from the literature, or the specimen collection number if the comparison was based on personal observations.

Some clades of fossil crocodile relatives are mentioned in the following sections such as Crocodylomorpha, Crocodyliformes, Mesoeucrocodylia, Neosuchia, and Crocodylia. These were recognized as successively less inclusive taxonomic groups by Clark (Benton and Clark, 1988; Clark, 1994) based on cladistic analyses.

The remains described here were collected by expeditions of the Museo Argentino de Ciencias Naturales (MACN), Museo Provincial Carlos Ameghino (MPCA), and Museo de Geología y Paleontología de la Universidad Nacional del Comahue (MUC) and are housed at these institutions. The descriptions are largely based on the information gathered from the four best-preserved specimens (MACN-RN 1037, MUC-PV 287, MPCA-Pv 249 , and MPCA-PV 250). Some fragmentary and isolated postcranial materials housed at the Museo de La Plata were figured by Woodward (1896), who identified them as possibly belonging to *Notosuchus*. The identity of some of these fragmentary remains is also discussed here (e.g., MLP 215).

The following abbreviations of institutions are used in the text: AMNH American Museum of Natural History, New York, USA; IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; MACN-RN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, Rio Negro Collection; MPEF Museo Paleontológico Egidio Feruglio; MLP Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MPCA Museo Provincial 'Carlos Ameghino', Cippoletti, Argentina; MUC-PV Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; PVL Instituto Miguel Lillo, Tucumán, Argentina; RCL Museo de Ciencias Naturales, Pontificia Universidade Catolica de Minas Gerais, Brazil; SAM South African Museum, Cape Town, South Africa; UFRJ Unversidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; ZPAL Instytut Paleobiologii PAN, Warszawa, Poland.

Systematic paleontology

CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIDAE Dollo, 1914

Genus ***Notosuchus*** Woodard, 1896

Type species. *Notosuchus terrestris* (Woodward, 1896).

Notosuchus terrestris Woodward, 189´
Figuras 1-19

Lectotype. MLP 64-IV-16-5, Skull and mandible, designated by Gasparini (1971).

Referred specimens studied here. MACN-RN 1037 skull associated with cervical and dorsal vertebrae, pectoral girdle, and forelimb; MACN-RN 1042 humerus proximal end, radius distal end; MACN-RN 1043 isolated osteoderms; MACN-RN 1044 fragmentary skull associated to cervicodorsal vertebrae, scapulae, and pelvic girdle elements; MACN-RN 1027 fragmentary skull associated to osteoderms; MACN-RN 1024 coracoid proximal end MPCA-PV 249 dorsolumbar, sacral, and caudal vertebrae in articulation with right ilium, femur and proximal end of tibia; MPCA-PV250 forelimb associated with skull and lower jaws; MUC-PV 287 associated postcranial remains including vertebral series, scapular girdle, forelimb, pelvis, and hindlimb; MLP 64-IV-16-27 isolated dorsal vertebrae.

Horizon and locality. The lectotype and referred material described by Woodward (1896) and Gasparini (1971) was reported by Gasparini (1971) to be found on the left margin of the Pichi Picún Leufú river, at its contact with the Limay river, but some elements of this material are from the locality Boca del Sapo according to the MLP collection information. The referred specimens described here come from two different outcrops of the Bajo de la Carpa Formation, Rio Colorado Subgroup (?Coniacian-Santonian; Hugo and Leanza, 2001). The specimens housed at the MACN and MPCA collections were collected from outcrops west of Paso Cordova, Río Negro Province, northern Patagonia, Argentina. The MUC-PV specimens were found near Neuquén city, Neuquén Province, northern Patagonia, Argentina.

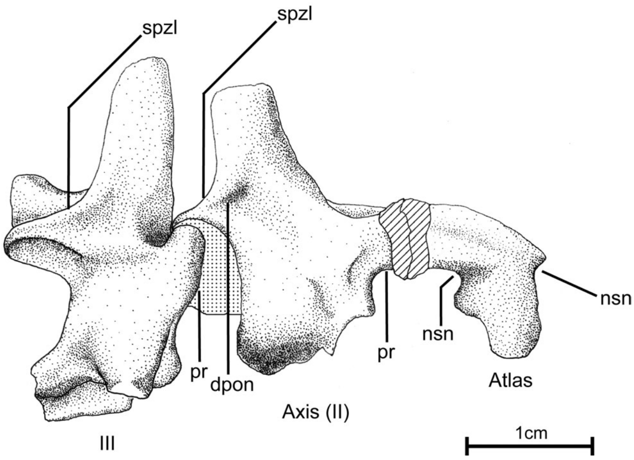

Figure 1. Neural arches of anterior cervical vertebrae of ***Notosuchus terrestris*** (MACN-RN 1037) in lateral view. Abbreviations: **dpon,** triangular depression between the neural spine and the postzygapophysis, **nsn,** notch for spinal nerves I and II; **pr**, prezygapophyseal process; **spzl,** suprapostzygapophyseal lamina./ *Arcos neurales de las vértebras cervicales anteriores de* Notosuchus terrestris (MACN-RN 1037) *en vista lateral. Abreviaturas:* **dpon,** *depresión triangular entre la espina neural y la postzigapófisis;* **nsn,** *escotadura para los nervios espinales I y II;* **pr,** *proceso prezigapofiseal;* **spzl,** *lámina suprapostzigapofiseal.*

Description and comparisons

Axial skeleton

In the specimen MACN-RN 1037 the neural arches of the first ten vertebrae were articulated with the skull. Only one of them is attached to its vertebral centrum. Associated with these remains, three complete vertebrae, possibly the following ones, were also found. The description of the cervicodorsal vertebrae is based on this specimen. Several posterior dorsal and caudal vertebrae are preserved in the specimens MUC-PV 287 and MPCA-PV 249, upon which the description of these vertebrae is based.

Atlas. Both halves of the neural arch of this vertebra are preserved. As in Crocodylia, the neural arches do not contact dorsally and the pedicels have a notch in the anterior and posterior margin where the spinal nerves I and II passed through (Mook, 1921; Hoffstetter and Gasc, 1973). The anterior notch is delimited dorsally by an anterior process and ventrally by the articular facet for the occipital condyle (figure 1). The posterior notch is dorsoventrally higher than the anterior one and is bordered dorsally by the postzygapophyses. The postzygapophyses are short and dorsoventrally deeper than in Crocodylia. Details of contact between the atlas postzygapophyses and the axis prezygapophyses cannot be observed due to the poor preservation of that area (figure 1). The right neural arch bears a medially oriented process on its dorsal surface that could be the contact surface for the non-preserved proatlas.

Axis. The neural spine of axis of most crocodyliforms presents a large anteroposterior development, forming a wide surface in lateral view for the attachment of axial musculature (Frey, 1988). However, in *Notosuchus terrestris* the axial neural spine is triangular in lateral view and its lateral surface is not as broad as in other forms, due to the short anteroposterior development of its base (figure 1). At the moment, this condition is only known to be present in *Sphagesaurus huenei* (Price, 1950; RCL-100) and *Chimaerasuchus paradoxus* (Wu *et al.*, 1995; IVPP V8274). In the latter, however, the axial neural spine is broken but its base is anteroposteriorly short and, as in *Notosuchus*, is located posteriorly on the neural arch.

The axial neural spine is lateromedially broader than the neural spine of the following cervical vertebrae, especially at the base of the spine. On the posterior margin there is a medial thin lamina located on the sagittal plane, similar to the laminae present in cervical vertebrae of Crocodylia for the attachment of the intervertebral elastic ligament (Frey, 1988).

In contrast to most crocodyliforms, in which the prezygapophyseal processes merge from the anterior margin of the neural spine, in *Notosuchus terrestris* they arise from the anterior half of the neural arch pedicels, disconnected from the neural spine. The prezygapophyseal processes are more robust, dorsoventrally higher, and more elongated than in other crocodyliform taxa (figure 1). The postzygapophyses are curved laterally as seen in dorsal view, and its articular surfaces face lateroventrally on a plane inclined 40 degrees from the sagittal plane. There is a suprapostzygapophyseal lamina merging from the dorsal surface of the postzygapophysis up to the posterior margin of the neural spine. In the lateral surface of this lamina, between the base of the neural spine and the postzygapophysis, there is a triangular shaped depression (figure 1).

The pedicels of the neural arch are anteroposteriorly longer than those of the posterior cervicals and bear a bulge in their ventrolateral corner, the area of contact with the odontoid process (missing in MACN-RN 1037).

Vertebra III. The neural arch of this anterior cervical vertebra resembles that of the posterior cervical vertebrae of Crocodylia. The neural spine is anteroposteriorly shorter in its base in comparison to that of the axis, and is anteroposteriorly centered on the pedicels of the neural arch, instead of being located posteriorly as in the third vertebra of extant crocodiles. Consequently, there is a reduction in the area of attachment of the posterior end of the intervertebral elastic ligament located anteriorly to the base of the neural spine in Crocodylia (Frey, 1988). The neural spine of the third vertebra in *Notosuchus terrestris* has a greater anteroposterior length at the base than at the dorsal end, being thus triangular shaped in lateral view (figure 1). In contrast, most crocodyliforms have a rectangular neural spine in this vertebra.

As in the axis, there is a sagittal thin lamina located on the posterior edge of the neural spine, between the suprapostzygapophyseal laminae (figure 2). Frey (1988) noted the presence of similar laminae in Crocodylia, however, in extant forms the lamina is continuous with the lateral surface of the neural spine, differing in this respect from *Notosuchus*.

At the base of the posterior medial thin lamina, between the postzygapophyses, there is a deep, narrow, and rectangular shaped *incisura vertebralis caudalis* (figure 2). In Crocodylia, this is the area of attachment of the interarticular ligament coming from the prezygapophyses of the following vertebra (Frey, 1988).

The prezygapophyseal process of this vertebra is directed forward at the beginning and then curves strongly upwards (figure 1), in contrast to the condition of most neosuchians in which it is directed anterodorsally along most of its length. The *Notosuchus* morphology is also observed in the fourth cervical vertebrae of *Chimaerasuchus* (IVPP V8274). As said before, this kind of prezygapophyseal process resembles those of the posterior cervical vertebrae of Crocodylia.

The postzygapophyseal process is similar to that of the axis, even though is more developed and its articular face is more vertically oriented. Additionally, there is an increase in the development of the suprapostzygapophyseal lamina relative to that of the axis. Similar laminae are absent in derived neosuchians, but commonly present in cervicodorsal vertebrae of other basal mesoeucrocodylians, such as *Malawisuchus* (Gomani, 1997), *Uruguaysuchus* (Rusconi, 1933), *Mariliasuchus* (Carvalho and Bertini, 1999; UFRJ 50-R), and *Araripesuchus* (Price, 1959; AMNH 24450). In this vertebra, the depression located on the lateral surface of the suprapostzygapophyseal lamina also is more developed in comparison to that of the axis.

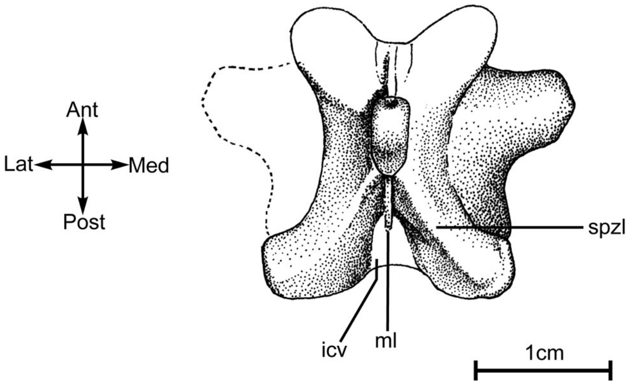

Figure 2. Cervical vertebra III of ***Notosuchus terrestris*** (MACN-RN 1037) in dorsal view. Abbreviations (see also previous figure): **ml**, medial lamina; **ivc**, *incisura vertebralis caudalis./ Vértebra cervical de* Notosuchus terrestris *(MACN-RN 1037) en vista dorsal. Abreviaturas (véase también figura anterior):* **ml**, *lámina media;* **ivc**, incisura vertebralis caudalis.

The pedicels of the neural arch are anteroposteriorly shorter relative to their height and are attached to the vertebral centrum by a suture that is straighter than in Crocodylia. The diapophyses are directed more laterally than in anterior cervical vertebra of other crocodyliforms.

Vertebra IV-IX. The neural spines of vertebrae four and nine are not preserved, so that the transformations described below for this vertebral series are based on the neural spines of the fifth through the eighth vertebrae (figure 3). These neural spines are higher, more elongated, and more posteriorly curved than the corresponding cervical vertebrae of Crocodylia, resembling the shape present only in the eighth or ninth vertebrae of Crocodylia. The presence of elongated neural spines in cervical vertebrae is also present in *Malawisuchus* (Gomani, 1997) and *Mariliasuchus* (UFRJ 50-R). In *Notosuchus* the neural spines are anteroposteriorly centered on the pedicels of the neural arch, as in the third vertebra. However, in other crocodyliforms there is a gradual transition in the position of the neural spine, from the posterior half of the neural arch in the fourth vertebra to a centered position in the ninth vertebra. Along this sequence, there is an increase of the anteroposterior length of the base of the neural spines of *Notosuchus*. The anterior edge of the neural spine of the eighth vertebrae exceeds anteriorly the neural arch margin.

The posterior edge of the neural spines of these vertebrae is formed by the two suprapostzyga-

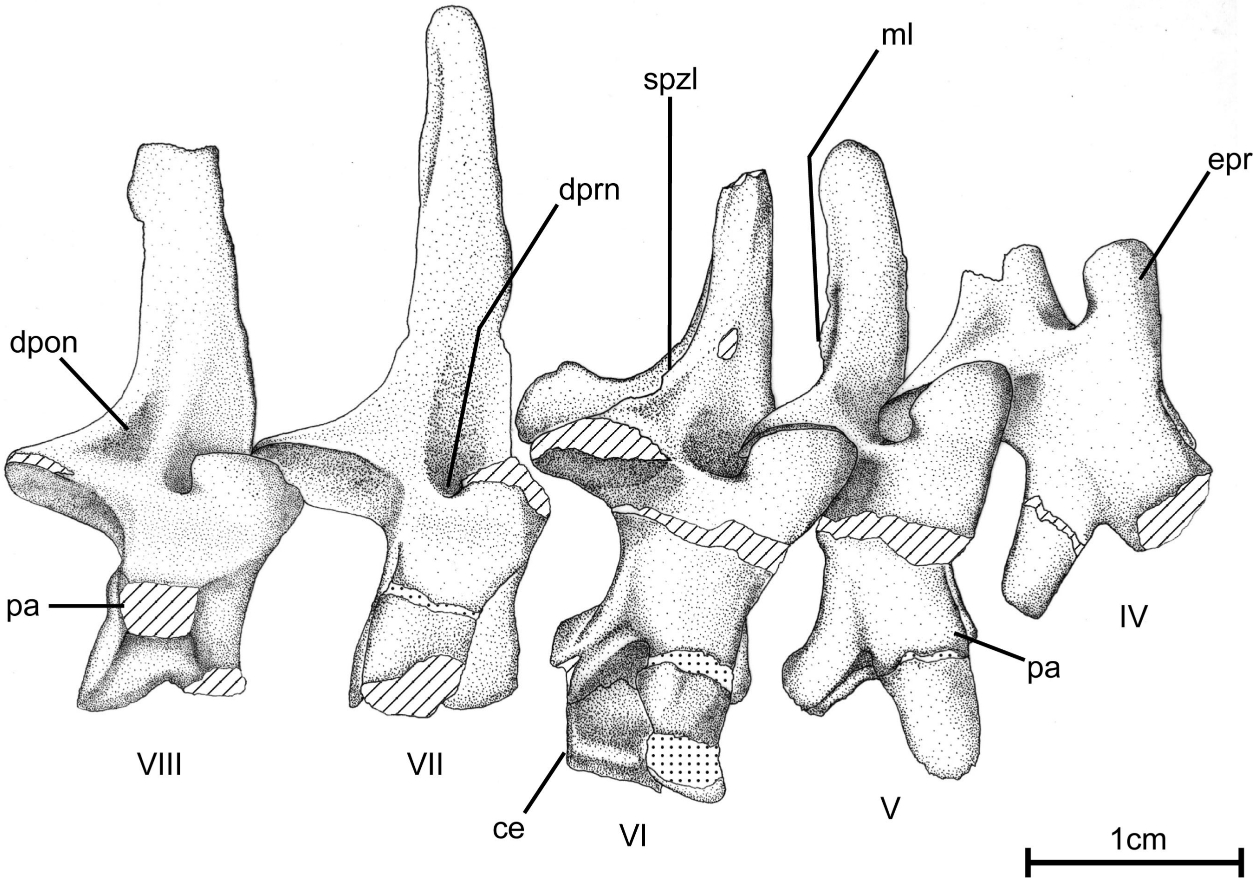

Figure 3. Posterior cervical vertebrae (IV to VIII) of ***Notosuchus terrestris*** (MACN-RN 1037) in lateral view. Abbreviations (see also previous figures): **ce,** vertebral centrum; **dprn,** deep depression between the prezygapophysis and neural spines, **epr**, sharp edge on lateral surface of prezygapophysis; **pa,** parapophysis./ *Vértebras cervicales posteriores (IV a VIII) de* Notosuchus terrestris *(MACN-RN 1037) en vista lateral. Abreviaturas (véanse también figuras anteriores):* **ce,** *centro vertebral;* **dprn,** *depresión profunda entre la prezigapófisis y las espinas neurales;* **epr,** *borde agudo en la cara lateral de la prezigapófisis;* **pa,** *parapófisis.*

pophyseal laminae, which join at half the height of the neural spine. In Crocodylia, two laminae are present on the posterior edge of the neural spine only in posteriormost cervicals. However, in Crocodylia, those laminae do not originate from the postzygapophyses, but from the base of the spine, at the *incisura vertebralis caudalis* between the postzygapophyses.

As in the anterior cervicals, a medial thin lamina is developed on the posterior edge of the neural spine of *Notosuchus*, between the postzygapophyseal laminae (being better preserved in the seventh and eighth vertebrae of MACN-RN 1037). In contrast, in extant crocodylians these medial thin laminae are increasingly reduced in posterior cervicals, which is correlated with a decrease in the development of the interspinal elastic ligament (Frey, 1988).

The zygapophyses augment noticeably in size from the contact of vertebrae four and five, increasing the development of both their articular surfaces and the supporting process (figure 3). Such development is greatest at the contact of the sixth and seventh vertebrae, decreasing in the posterior vertebrae.

The prezygapophyseal process has a sharp edge between its lateral and anterior faces, in contrast with other crocodyliforms, in which the process presents a cylindrical cross section. Between the base of the neural spine and the medial surface of each prezygapophysis there is a deep depression, which varies in size according to the development of the postzygapophyses of the preceding vertebra. The eighth vertebra of some crocodylians (*e.g.*, *Caiman*) presents a similar, though less developed feature. In these vertebrae, the depression located in the lateral surface of the suprapostzygapophyseal lamina, described above in anterior cervicals, presents variations in its development (figure 3), being present in some vertebrae (*e.g.*, fourth, sixth, and eighth) but absent in others (fifth and seventh).

The pedicels of the neural arches become shorter anteroposteriorly along this vertebral series. This shortening, together with the elongation of the neural spines, give an elongated appearance to the neural arches (figure 3). Due to the decrease in neural arch anteroposterior length and the enlargement of the zygapophyses, the origin of the prezygapophyseal and postzygapophyseal processes of these vertebrae are close to each other on the lateral surface of the neural arch (approximately 0.3 mm in the fifth to eighth vertebrae).

The diapophyses changes gradually along this series in four main aspects, the first one is a modification in the orientation of its major axis, from lateroventral in the fourth vertebra to lateral in the eighth and ninth vertebrae (figure 3). The second one, also present in Crocodylia (Hoffstetter and Gasc, 1973), is a change in the dorsoventral position of the diapophysis. In the fourth vertebra it is located slightly above the neurocentral suture, while in the eighth vertebra it is located above it, at the midpoint between that suture and the origin of the neural spine (figure 3). The third modification is a posteriorly increasing development in the dorsoventral height of the diapophysis. In the fourth vertebrae it is a flat lamina, while in the eighth vertebra it is quadrangular in cross-section. The fourth transformation is the anteroposterior location of the diapophysis, close to the anterior margin of the neural arch in the fourth vertebra, and anteroposteriorly centered in the subsequent vertebrae (figure 3).

Only the sixth centrum of the cervical region has been preserved. As in the fourth vertebra of *Chimaerasuchus* (Wu and Sues, 1996; IVPP V8274), this centrum is much shorter anteroposteriorly relative to its height than in most crocodyliforms, in which the centrum is anteroposteriorly elongated (figure 3). The right parapophysis is prominent, and the lateral surface of the centrum has deep depressions above and below it. The neurocentral suture is still open and located in the dorsal depression, between the parapophysis and diapophysis. The articular faces of the centrum are amphicoelous. Its ventral surface is not well enough preserved to determine the presence of the hypapophysis.

In the specimen MACN-RN 1044 two left ribs, associated with cervical vertebrae three and four, have been preserved. They have the anterior process overlapped by the posterior process of the preceding rib, a plesiomorphic character present in all crocodyliforms and related forms (Mook, 1921; Colbert and Mook, 1951; Whetstone and Whybrow, 1983).

Vertebra X. Only a fragment of the neural arch is preserved, in which there is a continuation of the morphological trends present in the preceding vertebrae. The base of the neural spine increases in its anteroposterior length and the prezygapophyses are smaller than in preceding vertebrae.

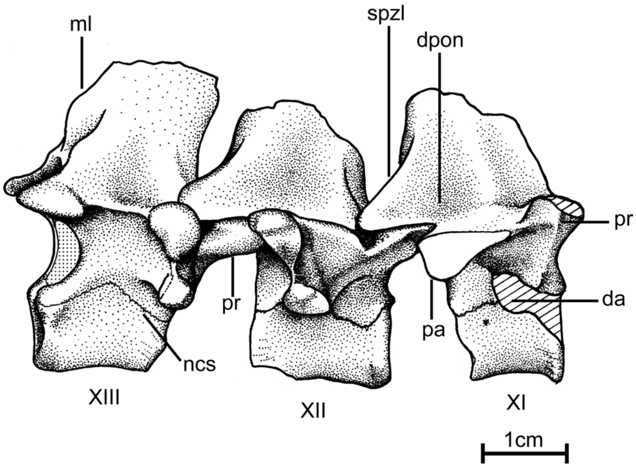

Figure 4. Anterior dorsal vertebrae (XI to XIII) of ***Notosuchus terrestris*** (MACN-RN 1037) in lateral view. Abbreviations (see also previous figures): **da,** diapophysis; **ncs,** neurocentral suture./ *Vértebras dorsales anteriores (XI a XIII) de* Notosuchus terrestris *(MACN-RN 1037) en vista lateral. Abreviaturas (véanse también las figuras anteriores):* **da:** *diapófisis;* **ncs,** *sutura neurocentral.*

Anterior dorsal vertebrae. Three vertebrae have been preserved which possibly are vertebrae eleven, twelve and thirteen due the relative positions of the parapophyses and the neurocentral suture (figure 4).

In contrast to *Malawisuchus* (Gomani, 1997; p. 285), the neural spines of these vertebrae are anteroposteriorly large, with a rectangular shape in lateral view, as in dorsal vertebrae of Crocodylia (Hoffstetter and Gasc, 1973). The rectangular shape of the spines is partially due to the development of anterior and posterior medial thin laminae, which are continuous with the lateral surface of the neural spine, like the cervical medial thin laminae of Crocodylia (Frey, 1988). These laminae are also present in dorsal vertebrae of *Chimaerasuchus* (IVPP V8274), *Uruguaysuchus* (Rusconi, 1933; fig. 39), *Mariliasuchus* (UFRJ 50-R), and *Araripesuchus* (AMNH 24450), while in Crocodylia these laminae are reduced or absent in dorsal vertebrae. The lateral depression between the base of the neural spine and the postzygapophysis, present in some anterior cervicals, is also present in these vertebrae (figure 4). This feature was observed in dorsal vertebrae of *Malawisuchus* (Gomani, 1997; p. 285) and is also present in *Uruguaysuchus aznarezi* (Rusconi, 1933; fig. 38).

The zygapophyses of these vertebrae are similar in size to those of the tenth vertebra. In contrast to the condition of the cervicals, the articular surface of the postzygapophyses faces ventrally on a horizontal plane, similar to the condition present in Crocodylia. The suprapostzygapophyseal laminae are still present but greatly reduced. *Malawisuchus* (Gomani, 1997; p. 285), *Uruguaysuchus* (Rusconi, 1933; fig. 38, 39), and

Araripesuchus (AMNH 24450) have suprapostzygapophyseal laminae in anterior dorsal vertebrae. The prezygapophyses are projected anteriorly beyond the neural arch edge, as in *Malawisuchus* (Gomani, 1997; p. 285). In Crocodylia these processes are short and do not exceed the anterior neural arch margin.

As mentioned, the identification of these vertebrae is based upon the fact that, as in Crocodylia, the parapophysis in the eleventh vertebra is located at the neurocentral suture and more anteriorly than the diapophysis. The twelfth and thirteenth vertebrae have their parapophyses above the neurocentral suture and anteroposteriorly aligned with the diapophyses (figure 4). The diapophyses of these three vertebrae gradually increase in size, however in Crocodylia these processes are proportionally longer than in *Notosuchus*. The transverse process is located at the same dorsoventral height than the postzygapophyses and its base is anteroposteriorly expanded. Therefore, its posterior edge is close to the anterior margin of the postzygapophyses, forming a shallow laterally opened notch between them. A similar condition is present in posterior dorsal vertebrae of *Chimaerasuchus* (IVPP V8274) and *Mariliasuchus* (UFRJ 50-R). Unlike Crocodylia, on the anterior surface of the transverse process of the two last vertebrae there are a series of small crests and depressions surrounded by a scarring surface, which would serve for tendinous or aponeurotic muscle attachment areas.

In contrast to the condition present in the cervical vertebrae of *Notosuchus*, the anteroposterior length of the pedicels of the neural arches and centra increases posteriorly in these dorsal vertebrae. The centra are amphicoelous and there is no sign of a hypapophysis on the ventral surface, showing the plesiomorphic condition for these characters among Crocodyliformes. The anterior dorsal centra of *Notosuchus* are narrower than in Crocodylia and are strongly compressed at the midpoint of its anteroposterior length, bearing thus the spool shaped condition, previously noted for other mesoeucrocodylians (Buscalioni and Sanz, 1988).

Posterior dorsal vertebrae. The specimens MPCA PV 249 and MUC-PV 287 have fragmentary remains of the posteriormost presacral vertebrae. These remains have strong similarities to those of the specimen MLP 204 described as possibly belonging to *Notosuchus* (Woodward, 1896; fig. 6).

The neural spines are incompletely preserved, however, a large anteroposterior length at their base and the presence of a medial lamina along the posterior edge of the spine between the postzygapophyses can be observed in several vertebrae. The suprapostzygapophyseal laminae are well developed in these vertebrae as well as the depression located on the lateral surface of these laminae (figure 5).

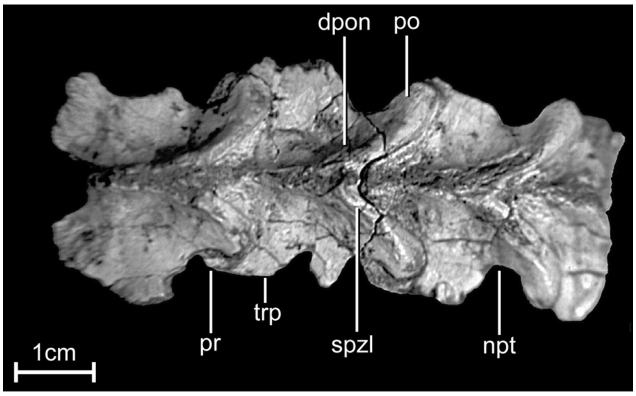

Figure 5. Posterior dorsal vertebrae of ***Notosuchus terrestris*** (MUC-PV 287) in dorsal view. Abbreviations (see also previous figures): **npt,** laterally opened notch between postzygapophysis and transverse process; **po,** postzygapophysis; **trp,** transverse process / *Vértebras dorsales posteriores de* Notosuchus terrestris *(MUC-PV 287) en vista dorsal. Abreviaturas (véanse también las figuras anteriores):* ***npt,*** *abertura lateral entre la postzigapófisis y el proceso transverso;* ***po,*** *postzigapófisis;* ***trp,*** *proceso transverso.*

The transverse processes of the posteriormost dorsals are oriented perpendicular to the anteroposterior axis of each vertebra and are slightly expanded distally. This contrasts with the condition present in extant taxa in which there is no distal expansion and the processes are slightly oblique to the anteroposterior axis of the vertebrae.

The postzygapophyses increase in size posteriorly and are positioned at the same height as the transverse processes as in *Chimaerasuchus* (IVPP V8274), and not dorsal to them as in most crocodylians (see Buscalioni *et al.*, 1986). The articular surface of the zygapophyses is nearly horizontal in all the preserved posterior dorsal vertebrae, a condition also found in *Chimaerasuchus* (IVPP V8274) and *Uruguaysuchus* (Rusconi, 1933; fig. 39). In contrast, neosuchian taxa (*e.g.*, Crocodylia) have their zygapophyses facing slightly oblique to the horizontal plane. The prezygapophyses, also located at the same height as the transverse processes, arise from them and their articular surface is continuous with the dorsal surface of the transverse process (figure 5).

Sacral vertebrae. The sacral vertebrae are only known in two specimens (MUC-PV 287 and MPCA-PV 249). Although both specimens have poorly preserved sacral elements, some interesting features can be noted.

The first sacral is only present in MUC-PV 287 and lacks the neural spine and zygapophyses. The transverse process is wide and has on its ventral surface a deep depressed area, in which the *pars medialis* of the *m. pubo-ischio-femoralis internus* is attached in extant crocodiles. The centrum of this vertebra is anteroposteriorly shorter and less spool-shaped than centra of posterior dorsal vertebrae.

Although it is badly preserved, the sacral element posterior to the first sacral vertebrae of MUC-PV 287 seems to be composed of two fused vertebrae. Four characters present in the neural arch of this sacral element support this interpretation. First, the length of this element is almost twice the length of the first sacral vertebra, while in most crocodyliforms the first and second sacrals are similar in length. Second, the neural spine has well differentiated anterior and posterior zones, each of them lateromedially widened and connected to each other by a continuous thin lamina. Third, the transverse process has a wide and laterally opened notch at the same point at which the neural spine is lateromedially constricted. Fourth, the depression present near the posterior end of the neural arch in all other vertebrae of *Notosuchus* (between the base of the neural spine and postzygapophyses), is located here on the anterior half of the neural arch, just anterior to the point in which the transverse process is notched and the neural spine is thin. The fusion of the last two sacral vertebrae of *Notosuchus* is a remarkable autopomorphic feature , currently unknown in any other crocodyliform. This morphology contrasts with the widespread and plesiomorphic condition of two differentiated sacral vertebrae of most crocodyliforms. However, the presence of three unfused sacral vertebrae was reported in some atoposaurids (*e.g.*, *Alligatorellus*, *Montsecosuchus*; Buscalioni and Sanz, 1988, 1990a).

The postzygapophyses of this element are notably reduced, positioned much higher than the transverse process, and closer to each other in comparison to other vertebrae of *Notosuchus*. The articular surfaces of these processes are broken but those of the first caudal prezygapophyses are oblique to the horizontal plane, in contrast to the condition present in presacral vertebrae.

Caudal vertebrae. The specimen MPCA-PV 249 has preserved the first seven caudal vertebrae and a fragmentary eighth element. The specimen MUC-PV 287 includes four caudal vertebrae in articulation with the sacrum, of which only the first two have preserved the neural arches. The caudal vertebrae of *Notosuchus* are smaller than those of specimens of extant taxa of equivalent sizes.

Caudal I-III. In the first two caudals, the neural spines are anteroposteriorly large, although they are not as expanded as in those of dorsal vertebrae. These spines are dorsoventrally tall and transversely narrow and their posterior edges bear a medial lamina between the postzygapophyses.

The prezygapophyses of the first caudal vertebra are notably reduced in comparison with those of the second and third caudals, which are well developed and projected anteriorly. The articular surfaces of the prezygapophyses of the first vertebrae are exposed more vertically than those of the second and third caudals, which form an angle of approximately 45 degrees with the sagittal plane. The postzygapophyses of these vertebrae are located dorsally respect to the transverse processes and lack suprapostzygapophyseal laminae, in contrast to the condition of presacral vertebrae of *Notosuchus*.

The transverse processes are anteroposteriorly short and directed posterolaterally. The anterior margins reach the anterior edge of the neural arch below the prezygapophyses. In the first caudal there is a marked triangular depression located ventral to the anterior ridge of the transverse process. On the dorsal surface of the transverse processes of these caudals there is another depressed area. In the first caudal this dorsal depression is distinct from the triangular depression found on the lateral surface of the neural arch (between the neural spine and the postzygapophysis). In contrast, in the second and third caudals this dorsal depression is confluent with the triangular posterior depression, forming an elongated and obliquely extended depression.

The pedicels of the neural arch of the three first caudals are anteroposteriorly shorter than those of preceding and subsequent vertebrae. The height of the neural arches, instead, decreases posteriorly along the caudal series.

It is not possible to determine if the centra are amphyplatan or amphycelous, however, they are not procoelic or biconvex as in derived neosuchians. The lateromedial compression found at the midpoint in dorsal vertebrae of *Notosuchus*is is less profound in caudal elements. On the ventral surface of the centrum two longitudinal ridges are present situated anterior to a widening of the centrum in which the articular facets for the hemal arches are located. In MUC-PV 287 the first vertebrae with such facets is the third caudal, while in MPCA-PV 249 they are already present in the second caudal vertebra. In extant crocodilians, this variation is usually considered as a form of sexual dimorphism, since female crocodylians lack a hemal arch in the second caudal vertebrae (Romer, 1956).

Caudal IV-VII. The neural spines of these caudals are anteroposteriorly shorter than in anterior caudals and the medial laminae located on the posterior edge are reduced or absent (figure 6). The *incisura vertebralis caudalis* is also extremely reduced in these caudal vertebrae.

As in preceding caudals, the transverse processes of these vertebrae contact the anterior edge of the neural arches below the prezygapophyses. The elongated and oblique depression located on the dorsal surface of the transverse process is also present in these caudal vertebrae. The zygapophyses are progressively reduced in size posteriorly and their articular surfaces are also reduced and horizontally exposed.

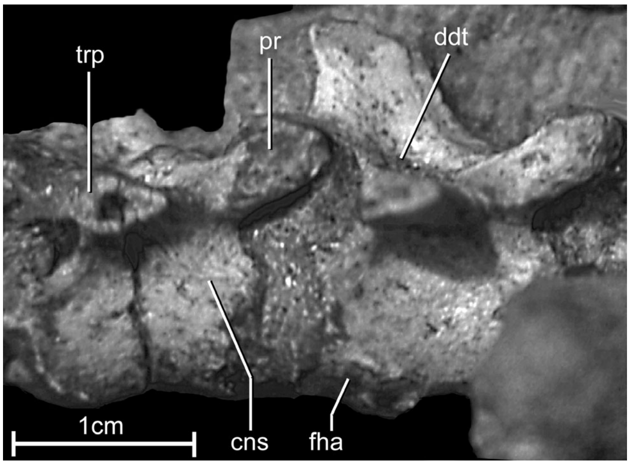

Figure 6. Distal caudal vertebrae of ***Notosuchus terrestris*** (MPCA-PV 249) in lateral view. Abbreviations (see also previous figures): **cns,** closed neurocentral suture; **ddt,** oblique depression on the dorsal surface of the transverse process; **fha,** articular facet for hemal arches / *Vértebra caudal distal de* Notosuchus terrestris *(MPCA-PV 249) en vista lateral. Abreviaturas (vénse también figuras anteriores):* **cns,** *sutura neuroctral cerrada;* **ddt,** *depresión oblicua en la cara dorsal del proceso transverso;* **fha,** *faceta articular para los arcos hemales.*

The centrum is anteroposteriorly longer and lateromedially compressed in comparison to anterior caudals. The neurocentral sutures of the posterior caudals are completely closed in both specimens, in contrast to the condition of anterior caudal and presacral vertebrae of all known specimens of *Notosuchus* in which it remains opened (figure 6). On the ventral surface the wide facets for the hemal arches occupy the posterior half of the vertebral centrum.

Shoulder girdle

Scapula. Scapular remains are preserved in two specimens (MACN-RN 1037 and MACN-RN 1044). As in most crocodylomorphs, a constricted area (figure 7) separates the dorsal and ventral expansions of the scapula. This element is dorsoventrally shorter and anteroposteriorly wider than in most crocodyliforms (*e.g.*, *Protosuchus* AMNH 3024; *Orthosuchus* SAM K-409; *Chimaerasuchus* IVPP V8274; *Uruguaysuchus* (Rusconi, 1933), Crocodylia). The dorsal expansion is well developed relative to the scapular height (anteroposterior length of dorsal expansion/scapular height ratio = 0.72). The anterodorsal region of the scapula is notably expanded, thus, the anterior border is highly concave compared to the posterior border, a character shared by all crocodylomorphs (except for thalattosuchians and crocodylians). The anteroventral end is missing, however, the ventral expansion appears to be smaller than in most crocodyliforms.

In anterior view, the scapula presents a continuous curvature, similar to the condition observed in Crocodylia but less marked than in some protosuchians (Nash, 1975; p. 255). In this view, the scapula is thin except for the ventral region, close to the glenoid cavity. The thickening of the deltoid region is a widespread character among Crocodyliformes, however, in *Notosuchus* it is less developed than in Crocodylia.

In lateral view, a hardly noticeable crest is present on the posterior edge above the glenoid cavity, resembling that of *Sunosuchus* (Wu *et al.*, 1996). Such crest is more developed in Crocodylia, showing a rugose surface for the attachment of the *m. triceps* (Nash, 1975). On the anterior margin there is a small acromial crest (figure 7), located more ventrally than in other crocodyliforms (*e.g.*, Crocodylia, *Orthosuchus* SAM K-409, *Chimaerasuchus* IVPP V8274). Since the anteroventral end is missing, further details of this crest cannot be observed. The scapula forms the dorsal half of the glenoid cavity, being this facet hemisellar as in crocodilians (figure 7).

Coracoid. The left coracoid is preserved in the specimens MUC-PV 287 and MACN-RN 1037, although the latter has its ventral end missing (figure 8). In both specimens the dorsal and ventral expansions are less developed than in other crocodylomorphs, except for *Hyposaurus* (Buscalioni and Sanz, 1990b).

In anterior view the coracoid has a convex lateral surface and a concave medial surface. The curvature in the shaft is continuous between the ventral and dorsal expansion, in contrast to the condition present in other crocodyliforms (*e.g.*, *Orthosuchus* SAM K-409, *Uruguaysuchus* (Rusconi, 1933; fig. 32), *Caiman*),

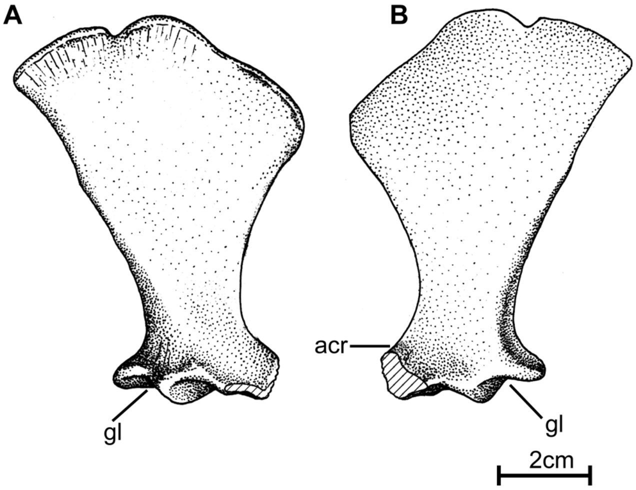

Figure 7. Left scapula of ***Notosuchus terrestris*** (MACN-RN 1037) in (**A**) medial and (**B**) lateral views. Abbreviations: **acr,** acromion crest; **gl,** glenoid cavity./ *Escápula izquierda de* Notosuchus terrestris *(MACN-RN 1037) en vistas medial* **(A)** *y lateral* **(B)**. *Abreviaturas:* **acr,** *cresta acromial;* **gl,** *cavidad glenoidea.*

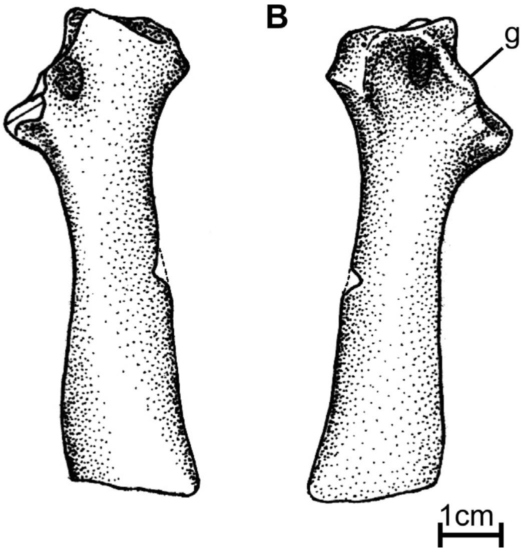

Figure 8. Left coracoid of ***Notosuchus terrestris*** (MACN-RN 1037) in **(A)** medial and **(B)** lateral views. See abbreviations from previous figures / *Coracoide izquierdo de* Notosuchus terrestris *(MACN-RN 1037) en vistas medial* **(A)** *y lateral* **(B)**. *Abreviaturas en figuras anteriores.*

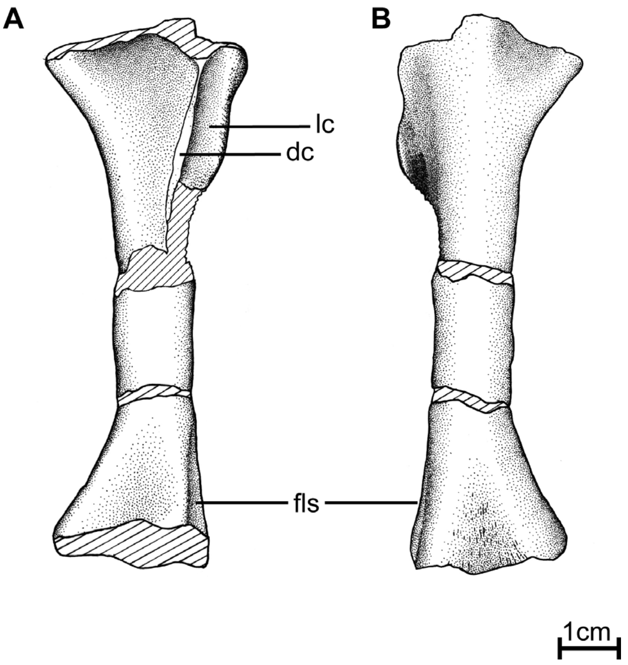

Figure 9. Left humerus of ***Notosuchus terrestris*** (MACN-RN 1037) in **(A)** anterior and **(B)** posterior views. Abbreviations: **dc,** deltoid crest; **fls,** flat lateral surface of distal humerus; **lc,** narrow and elongate concavity lateral to the deltoid crest./ *Húmero izquierdo de* Notosuchus terrestris *(MACN-RN 1037) en vistas anterior* **(A)** *y posterior* **(B)**. *Abreviaturas:* **dc,** *cresta deltoide;* **fls,** *superficie lateral plana del húmero;* **lc,** *concavidad alargada y estrecha lateral a la cresta deltoide.*

in which there is a marked angle at the compressed area between the dorsal and ventral expansions.

A robust process supports the ventral half of the glenoid cavity, which is oriented posterodorsally. The dorsal surface of the coracoid is partially preserved in the specimen MACN-RN 1037 but is complete in a proximal end of a coracoid found in the same levels (MACN-RN 1024). On this coracoid, the articular surface for the scapula has a triangular contour and is perpendicular to the glenoid cavity surface. This fragmentary specimen is tentatively referred to *Notosuchus terrestris* based on the presence of a poorly expanded proximal end of the coracoid.

Fore limb

Humerus. The specimens MACN-RN 1037 and MUC-PV 287 have preserved the left humerus (figure 9), while the specimen MPCA-PV 250 has a complete right humerus. Additionally, a humeral proximal end (MACN-RN 1042) was found in the same locality as MACN-RN 1037 (Paso Córdova). This humerus is approximately 30% larger than that of MACN-RN 1037 but bears some features found to be autapomorphic for *Notosuchus* and hence is provisionally referred to this taxon. The distal end of the humerus of the specimen MLP 215 referred to *Notosuchus* by Woodward (1896) lacks diagnostic characters to undoubtedly refer it to *Notosuchus terrestris*.

The ratios between the proximal and distal expansions with respect to humerus length are 0.296 and 0.231, respectively. These ratios denote a more gracile humerus in *Notosuchus* than in *Crocodylus* (Mook, 1921), but stouter than in *Malawisuchus* (Gomani, 1997; p. 288) and some basal crocodylomorphs (*e.g., Terrestrisuchus* (Crush, 1984), *Protosuchus* AMNH 3024). *Uruguaysuchus* (Rusconi, 1933; fig. 8) and *Chimaerasuchus* (IVPP V8274) have similar proportions to those of *Notosuchus*.

In lateral view the humerus of *Notosuchus* presents a sigmoid shape, since its proximal end is slightly curved backwards and its distal portion directed anteriorly. In anterior view, the lateral edge of the humerus is not convex as in Crocodylia, due to the lateral expansion of the process that supports the deltoid crest (figure 9.A).

The deltoid crest is lower and thinner than in other crocodyliforms (*e.g.,* Crocodylia, *Chimaerasuchus* IVPP V8274, *Gobiosuchus* ZPAL MgR-II/67, and *Orthosuchus* SAM K-409) and is not medially curved. This crest has its origin at the dorsolateral corner of the humerus (figure 10.A) and runs parallel to the lateral margin down to the origin of the shaft, where it disappears. Between the crest and the lateral edge there is a narrow and elongate concavity (figure 9.A, 10.A). As in *Chimaerasuchus* (Wu and Sues, 1996; IVPP V8274) and *Uruguaysuchus* (Rusconi, 1933; plate 2) a circular depression is present on the posterior face, below the proximal end (figure 10.B). Just

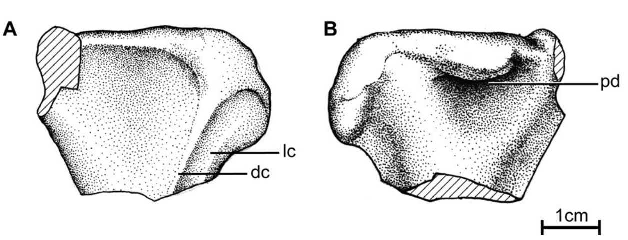

Figure 10. Proximal end of left humerus of ***Notosuchus terrestris*** (MACN-RN 1042) in **(A)** anterior and **(B)** posterior views. Abbreviations (see also previous figures): **pd,** posterior circular depression below articular head / *Extremo proximal del húmero izquierdo de* Notosuchus terrestris *(MACN-RN 1042) en vistas anterior* **(A)** *y postrior* **(B)**. *Abreviaturas (véanse también las figuras anteriores):* **pd,** *depresión circular posterior debajo de la cabeza articular.*

below the proximal end the bone surface presents the same scarring as Crocodylia, which serves in extant crocodiles as attachment areas for strong ligaments. It is not possible to observe in any specimen the elongated rugose area found in Crocodylia for the *m. triceps* attachment on the posterior face at the limit between the shaft and the proximal expansion.

The distal end is not completely preserved but some interesting features can be noted. In anterior and posterior view there are two supracondylar ridges that enclose a small concavity between them. The medial ridge is more developed in the anterior face, whilst in the posterior face, the lateral is more pronounced. The lateral surfaces of the distal part of the humerus are broad and flat as in *Uruguaysuchus* (Rusconi, 1933; fig. 11) and *Araripesuchus* (AMNH 24450), in contrast to the convex surface found in some basal crocodylomorphs (*e.g., Hesperosuchus*, Colbert, 1952, AMNH 6758) and derived neosuchians.

Ulna. The ulna of the specimen MPCA-PV 250 is completely preserved, while in the specimens MACN-RN 1037 and MUC-PV 287 the distal and proximal articular surfaces are missing. In its proximal region, the ulna is anteroposteriorly expanded and lateromedially compressed, with flat lateral and medial surfaces. *Notosuchus* has a stouter ulna than most crocodyliforms; *e.g., Chimaerasuchus* IVPP V8274, *Malawisuchus* (Gomani, 1997; p. 288), *Crocodylus* (Mook, 1921), and *Protosuchus richardsoni* AMNH 3024), since relative to its length both the shaft and the proximal end are more developed. The proximal end of the ulna has a forward curvature seen in lateral view, and thus, the proximal articular surface is exposed anterodorsally (figure 11), condition present in most crocodylomorphs. This region has a wide concave surface that articulates with the medial condyle of the humerus, and lateral to this facet a convex surface contacts the humeral intercondylar surface. The region lateral to this convex surface and the olecranon process have not been preserved in any specimen.

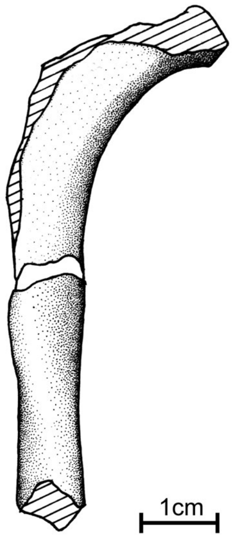

Figure 11. Left ulna of ***Notosuchus terrestris*** (MACN-RN 1037) in medial view / *Ulna izquierda de* Notosuchus terrestris *(MACN-RN 1037) en vista medial.*

Along the shaft there is a transition from the flat morphology of the lateral and medial surfaces at the proximal region mentioned above, towards a cylindrical cross section at the distal end. Such transition takes place differentially in the lateral and medial faces; in the latter the transition occurs at the proximal end (figure 11) of the shaft while in the lateral face, a flat surface is present almost down to the distal end of the shaft.

The distal articular end of the ulna has a complex articular surface limited medially by the two oblique processes. These are much more developed than in Crocodylia, especially the posterior one (figure 12). In the anterolateral surface of the distal region of the ulna, there is a well developed and rugose bulge. The distal articular surgace of the ulna would have a continuous articulation with both the radiale and ulnare, as in crocodylians. This contrasts with the condition of basal crocodylomorphs, in which the medial articulation with the radiale is separated and perpendicular to the ulnare articulation (Clark, pers. com.).

Radius. The right radius of specimen MPCA-PV 250 (figure 13) was completely preserved, in contrast to those of specimens MACN-RN 1037 and MUC-PV 287, in which the radius distal end is missing. As in most crocodyliforms, the proximal end is lateromedially expanded with respect to its anteroposterior development. The proximal articular surface has a concave surface bounded by a lateral and medial convex and swollen articular surfaces. The medial region is more developed and is located more distally than the lateral region. Below the lateral expansion of the proximal end of the radius, there is a thin longitudinal crest running along the posterior surface of the bone. This crest disappears before the beginning of the shaft.

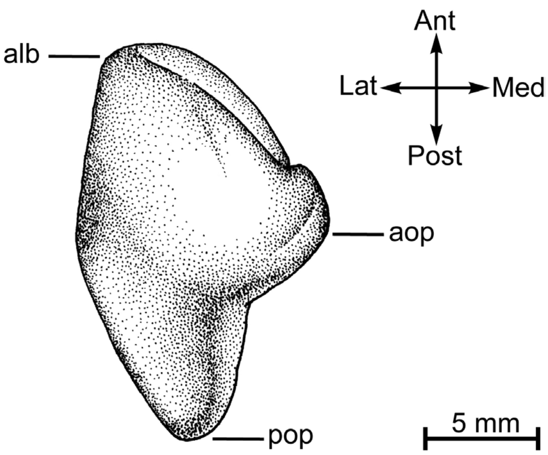

Figure 12. Right ulna of ***Notosuchus terrestris*** (MPCA-PV 250) in distal view. Abbreviations: **alb,** anterolateral bulge; **aop,** anterior oblique process; **pop,** posterior oblique process./ *Ulna derecha de* Notosuchus terrestris *(MPCA-PV 250) en vista distal. Abreviaturas:* **alb,** *promontorio anterolateral;* **aop,** *proceso oblicuo anterior;* **pop,** *proceso obicuo posterior.*

The shaft of the radius has an oval cross section and its major axis is oriented lateromedially. The posterior surface of the distal region of the radius has an elongate longitudinal concavity for the distal contact with the ulna (figure 13). The distal end has an anterolateral-posteromedial expansion that approximately forms a 30 degrees angle with the proximal lateromedial expansion. The anterolateral edge of the distal region of the radius is more slender than the posteromedial edge. Thus, in distal view, the articular surface of the radius is tear drop-shaped. The distal edge of the radius is inclined obliquely, being the posteromedial edge located more distally than the anterolateral edge, in contrast with the condition present in basal crocodylomorphs, such as *Hesperosuchus* (Colbert, 1952; AMNH 6758) and *Dibothrosuchus* (Wu and Chatterjee, 1993; IVPP V7907) in which the distal edge of the radius is perpendicular to its proximodistal axis.

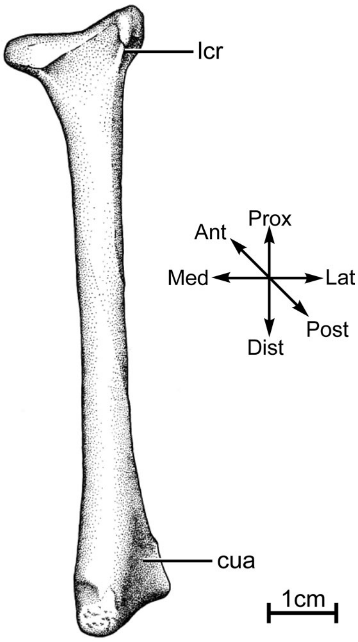

Figure 13. Right radius of ***Notosuchus terrestris*** (MPCA-PV 250) in posterior view. Abbreviations: **lcr,** thin longitudinal crest; **cua,** concavity for ulnar articulation / *Radio derecho de* Notosuchus terrestris *(MPCA-PV 250) en vista posterior. Abreviaturas:* **lcr,** *crasta longitudinal delgada;* **cua,** *concavidad para articulación de la ulna.*

Proximal carpals. The specimens MACN-RN 1037 and MPCA-PV 250 have an elongated radiale and ulnare that form an additional segment of the forelimb, a condition postulated to be synapomorphic of Crocodylomorpha (Clark, 1986).

The radiale is constricted between the enlarged proximal and distal ends. A slightly marked ridge, more developed in MACN-RN 1037, runs proximodistally along this carpal, dividing its anterior face (figure 14.A). The proximal end is hatchet-shaped due to the presence of an expansion on the lateral edge that forms a wide surface of articulation with the ulnare (figure 14). This condition is also present in several crocodyliform taxa (*e.g., Montsecosuchus*

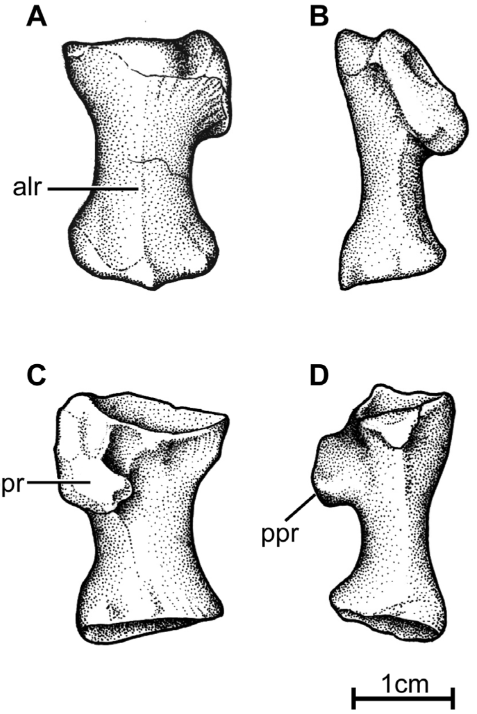

Figure 14. Left radiale of ***Notosuchus terrestris*** (MACN-RN 1037) in **(A)** anterior, **(B)** lateral, **(C)** posterior and **(D)** medial views. Abbreviations: **alr,** anterior longitudinal ridge; **ppr,** articular process directed posteriorly./ *Radial izquierdo de* Notosuchus terrestris *(MACN-RN 1037) en vistas anterior* **(A)**, *lateral* **(B)**, *posterior* **(C)** *y medial* **(D)**. *Abreviaturas:* **aln,** *cresta longitudinal anterior;* **ppr,** *proceso articular dirigido posteriormente.*

(Buscalioni and Sanz, 1990a; p. 250), *Orthosuchus* SAM K-409, *Chimaerasuchus* IVPP V8274, and *Sunosuchus* (Wu *et al.*, 1996)). However, it is absent in Crocodylia (Mook, 1921) and some basal crocodylomorphs (*e.g., Protosuchus* AMNH 3024, *Terrestrisuchus* (Crush, 1984; p. 144), and *Dibothrosuchus* IVPP V7907). This expansion is flat and exposed anterolaterally, as in other crocodyliforms (Buscalioni and Sanz, 1988). On the posterolateral surface of this region there is a posteriorly directed process that bears an articular surface that probably contacted the ulna (figure 14.C-D). The proximal articular surface of the radiale has an oblique edge, congruent with the morphology of the radius distal end. The distal articular surface is concave, kidney-shaped, and faces posteroventrally.

The ulnare is much more marked constricted between the proximal and distal expansions in comparison with the radiale. The distal end is more expanded than the proximal end (figure 15), as in most non-crocodylian crocodylomorphs. On the posterior edge of the proximal end, a process projects posteriorly determining the triangular shape of the proximal articular surface. The ulnare bears two distinct distal articular surfaces, the medial more extensive than the lateral.

Distal carpals. Two distal carpals of the left forelimb were preserved in MACN-RN 1037. These elements were in close association with the left manus although they were not found in natural position (figure 15). One of these distal carpals is slightly bigger than the other and has a convex proximal articular surface composed by two surfaces joined proximally at a wide angle. The other element is oval shaped and its articular surfaces are flat and rounded.

Extant crocodylians also have two distal carpals, but in contrast to the condition of *Notosuchus*, living forms have only one ossified distal carpal and the other remains as a cartilaginous lamella. In fossil taxa a wide variation in the number of distal carpals was previously reported (see Buscalioni *et al.*, 1997), ranging from one to three ossified elements. The condition noted for *Notosuchus* is also present in some basal crocodyliforms [*e.g., Orthosuchus* (Nash, 1975; p. 258)].

Digits. Four metacarpals with some articulated phalanges have been preserved from the left manus of MACN-RN 1037 and MUC-PV 287. In MPCA-PV 250 only the first metacarpal was preserved in articulation with the first phalanx. Metacarpal I is the shortest and stoutest of the four metacarpals (figure 16), and is more robust than in most crocodyliforms except for *Chimaerasuchus* (IVPP V8274) and some thalattosuchians. Its proximal end has a lateromedial expansion and a small crest on its dorsal face. The first phalanx of this digit is short, wide, and quadrangular, and is articulated to an incomplete second phalanx in the specimen MACN-RN 1037. This phalanx possibly is the ungual due to its strong lateromedial compression and the curvature along its proximodistal axis. Proximally, metacarpal I overlapps the proximomedial end of metacarpal II, as in most crocodyliforms. Metacarpals II and III are the longest elements of the metacarpus. The first phalanx of the second digit is shorter than the same element of the first digit. Fragmentary remains of metacarpal IV are preserved but it is impossible to accurately measure its total length. In the MUC-PV 287 specimen there is a disarticulated ungual phalanx that is almost as long as the third metacarpal, slightly recurved, lateromedially broad, and lacking proximodistal grooves on the lateral surface.

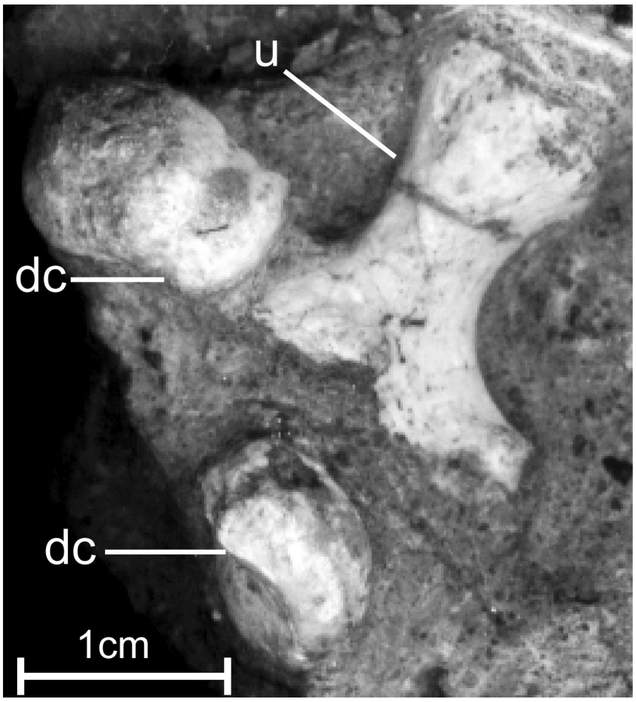

Figure 15. Left ulnare and distal carpals of ***Notosuchus terrestris*** (MACN-RN 1037) in posterior view. Abbreviations: **dc,** distal carpals ; **u,** ulnare / *Ulnario izquierdo y carpales distales de* Notosuchus terrestris *(MACN-RN 1037) en vista posterior. Abreviaturas:* **dc,** *carpales distales;* **u,** *ulnario.*

Pelvic girdle

Ilium. The specimens MACN-RN 1044, MPCAPV 249, and MUC-PV 287 preserve the ilium. The ilium of specimen MLP 215 referred to *Notosuchus* by Woodward (1896) has marked differences with the ilium of the new specimens described here. This specimen lacks some autapomorphic characters of *Notosuchus terrestris* (*e.g.,* a well developed dorsal roof of the acetabulum), and thus, it cannot be referred to this taxon.

The anterodorsal corner of MUC-PV 287 has a poorly developed anterior process that resembles the condition of *Chimaerasuchus* (IVPP V8274), *Araripesuchus* (AMNH 24450), and *Theriosuchus* (Wu *et al.*, 1996). The dorsal surface of the ilium of the three specimens of *Notosuchus* is flat, rugose, lateromedially wide, and does not have the characteristic iliac blade present in most crocodyliforms (figure 17). This latter characteristic was also noted for *Chimaerasuchus* (Wu and Sues, 1996; p. 694). The lateral expansion of the dorsal surface of the ilium of *Notosuchus* forms an extensive acetabular roof (figures 17, 18). Thus, the acetabulum is even deeper than in non-neosuchian crocodylomorphs (*e.g.*, *Orthosuchus* SAM K-409; *Protosuchus* AMNH 3024; *Araripesuchus* AMNH 24450; *Chimaerasuchus* IVPP V8274).

The postacetabular process is directed posteroventrally (figure 17.A), as in *Uruguaysuchus* (Rusconi, 1933; fig. 18), *Chimaerasuchus* (IVPP V8274), *Orthosuchus* (SAM K-409), and *Protosuchus* (AMNH 3024). In contrast, other forms have the postacetabular process directed posteriorly (*e.g.*, *Dibothrosuchus* IVPP V7907) or posterodorsally (*e.g.*, Crocodylia). The dorsal surface of the ilium narrows posteriorly, being blade-like at the posterior end of the postacetabular process (figure 17.B). The anterior end of this process faces laterally, but the posterior end faces laterodorsally. Thus, the postacetabular process is twisted along its anteroposterior axis (figure 17). The medial surface of the ilium is smooth in its dorsal half, and rugose in the ventral area, corresponding to the attachment marks of sacral ribs.

Hind limb

Femur. The specimen MPCA-PV 249 has the proximal half of the femur preserved in articulation with the ilium. Details of the proximal end cannot be observed since this zone, inside the acetabulum, is covered with sediment. However, there is a well developed fourth trochanter. Medial to this trochanter there is a prominent process for the insertion of the *m. coccygeofemoralis*, similar to the condition of *Mahajangasuchus* (Buckley and Brochu, 1999; p. 162), *Araripesuchus* (AMNH 24450), and *Uruguaysuchus* (Rusconi, 1933; fig. 9). The surfaces of these areas of muscular insertion are rugose and separated by a depressed area that bears slightly marked rugosities.

Woodward (1896) referred several femora to *Notosuchus terrestris*. One of these elements (MLP 215) lacks the well developed process for the insertion of the *m. coccygeofemoralis*. Therefore, it cannot be referred to *Notosuchus terrestris*.

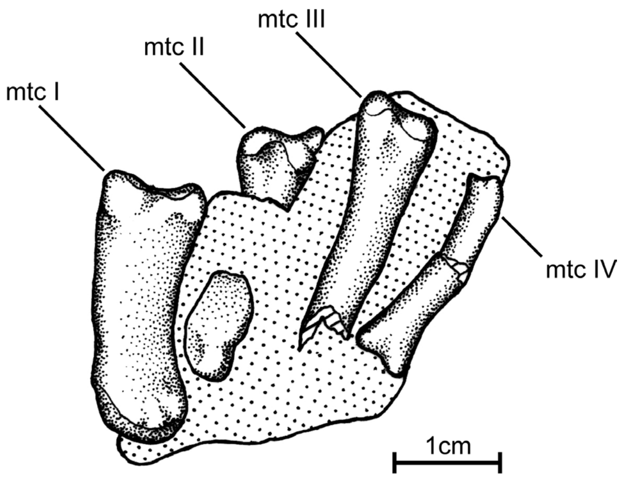

Figure 16. Left metacarpals of ***Notosuchus terrestris*** (MACN-RN 1037) in ventral view. Abbreviations: **mtc I-IV,** metacarpals I to IV./ *Metacarpales izquierdos de* Notosuchus terrestris *(MACN-RN 1037) en vista ventral. Abreviaturas:* **mtc I-IV,** *metacarpales I a IV.*

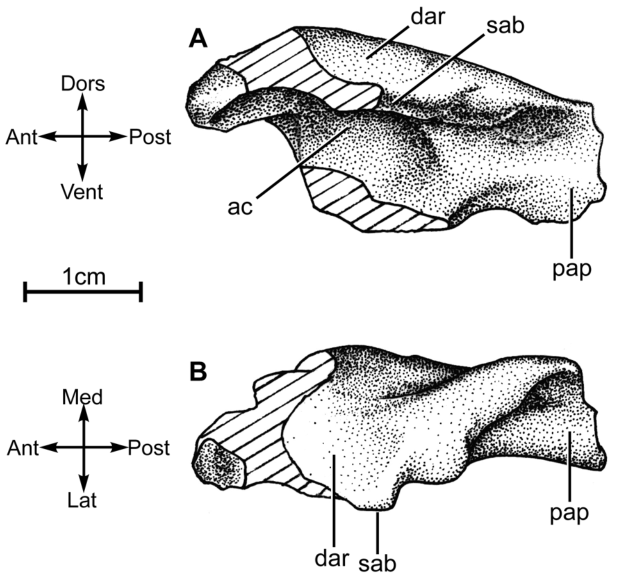

Figure 17. Left ilium of ***Notosuchus terrestris*** (MACN-RN 1044) in **(A)** lateral and **(B)** dorsal views. Abbreviations: **ac,** acetabulum; **dar,** flat dorsal surface of acetabular roof; **pap,** postacetabular process; **sab,** supraacetabular buttress / *Ilion izquierdo de* Notosuchus terrestris *(MACN-RN 1044) en vistas lateral* **(A)** *y dorsal* **(B)**. *Abreviaturas:* **ac:** *acetábulo;* **dar,** *superficie dorsal plana del techo del acetábulo;* **pap,** *proceso postacetabular;* **sab,** *soporte supraacetabular.*

Dorsal armor

Osteoderms. Three pairs of osteoderms aligned in two parallel rows have been preserved associated with a fragmentary skull of *Notosuchus* (MACN-RN 1027). Osteoderms were also preserved in the specimen MPCA-PV 249. Additionally, similar isolated osteoderms were found in the same beds of the Paso Córdova locality (MACN-RN 1043).

The parasagittal rows of osteoderms contact each other medially without overlapping. Along the rows, each osteoderm is overlapped by the preceding osteoderm. The osteoderms are pentagonal, and lack the anterolateral process present in protosuchids and some basal mesoeucrocodylians (*e.g.*, *Hsisosuchus* Young, 1953, the Fruita crocodyliform Clark, 1985). There is a lateromedially centered longitudinal ridge on the dorsal surface of each osteoderm (figure 19). Laterally and medially to this ridge the dorsal surface of the osteoderm are exposed dorsolaterally and dorsomedially, forming a 150 degrees angle between them.

The ornamentation of the osteoderms consists of slightly marked ridges and grooves, similarly to those of the skull of *Notosuchus*. The ornamentation covers all the dorsal surface of the osteoderms except for the region that is overlapped by the preceding plate. This overlapped region is smooth, flat and faces anterodorsally (figure 19). The ventral surface is concave, smooth, and has two longitudinal grooves. In extant forms, similar grooves serve for the attachment of ligaments that join each osteoderm to the neural spines of anteriorly positioned vertebrae (Frey, 1988).

Discussion

The postcranial remains of *Notosuchus terrestris* offer novel information about morphological diversity among Mesozoic crocodyliforms. This information appears to be relevant to both the mode of life and the phylogenetic relationships of this crocodyliform. In this section, several characters are discussed in the context of their relevance for understanding the mode of life of *Notosuchus terrestris*.

An interesting feature of the remains described here is the presence of a deep acetabulum covered dorsally by a thick bony buttress in the ilium of *Notosuchus*. This character was also noted in several taxa such as sphenosuchians, protosuchians, and also some mesoeucrocodylians (Parrish, 1987; Nash, 1975; Hecht, 1991). However, the supraacetabular buttress and the correlated depth of the acetabulum are much more developed in *Notosuchus* than in other crocodylomorph taxa (*e.g.*, *Dibothrosuchus elaphros* Simmons IVPP V 7907; *Protosuchus richardsoni* Brown AMNH 3024; *Orthosuchus stormbergi* SAM K-409 *Araripesuchus gomesi* Price AMNH 24450). This character was suggested to be indicative of an upright stance in the crocodylomorph hindlimb for several basal taxa (Parrish, 1987; Nash, 1975; Whetstone and Whybrow, 1983). This type of locomotion was hypothesized to be the plesiomorphic condition of crocodylomorphs, so that the 'semi-erect' type of locomotion observed in Crocodylia was secondarily acquired in this group (Parrish, 1987). The presence of this condition in *Notosuchus* and other mesoeucrocodylians (*e.g.*, *Araripesuchus*, *Malawisuchus*, Hecht, 1991; Gomani, 1997), suggests that the sprawling type of locomotion was certainly secondarily acquired in the evolutionary history of crocodylomorphs, but only by the neosuchian clade related to amphibious or aquatic habitats (figure 20). The supposedly upright stance is congruent with the terrestrial habits inferred for *Notosuchus terrestris* based on cranial characters by previous authors (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991).

The entire cervical series of *Notosuchus* presents similarities with the posterior cervical region of Crocodylia. Along the cervical series of *Notosuchus* the presence of several characters (*e.g.*, elongated spines, enlarged zygapophyses, and depression between prezygapophyses) may indicate the existence of marked movements in the dorsal arching

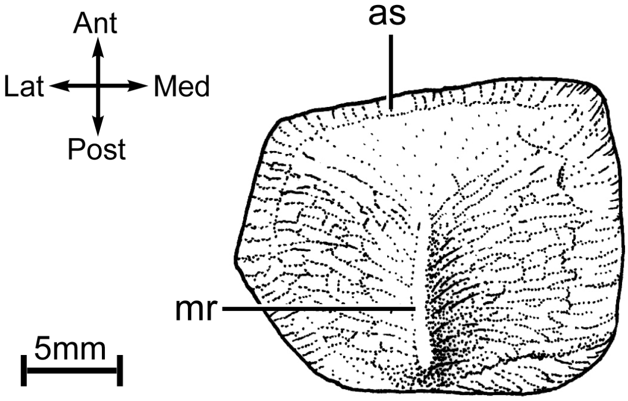

Figure 19. Parasagittal osteoderm of ***Notosuchus terrestris*** (MACN-RN 1043) in dorsal view. Abbreviations: **as,** articular surface overlapped by preceeding osteoderm; **mr,** longitudinal medial ridge./ *Osteodermo parasagital de* Notosuchus terrestris *(MACN-RN 1043) en vista dorsal. Abreviaturas:* **as,** *superficie articular solapada por el osteodermo precedente;* **mr,** *cresta media longitudinal.*

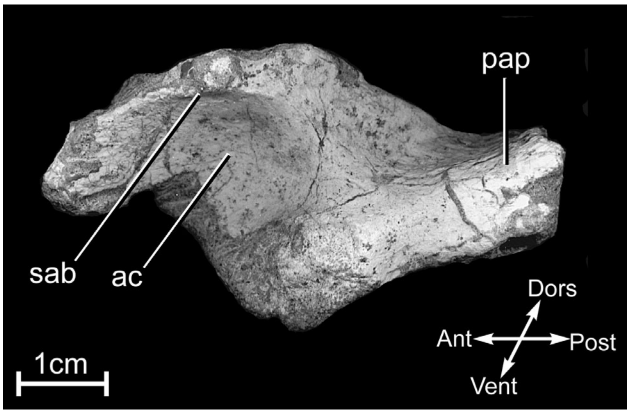

Figure 18. Left ilium of ***Notosuchus terrestris*** (MACN-RN 1044) in lateroventral view. See abbreviations from previous figures./ *Ilion izquierdo de* Notosuchus terrestris *(MACN-RN 1044) en vista lateroventral. Véanse abreviaturas en figuras anteriores.*

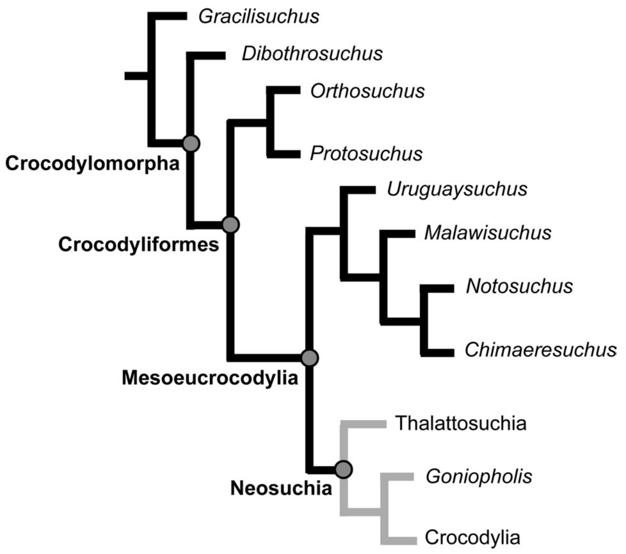

Figure 20. Phylogenetic relationships of Crocodyliformes based on Pol (2003). Crocodyliforms of which there is no current information were pruned from the tree. The presence the supraacetabular buttress of the ilium is optimized on the cladogram. Black lines represent the plesiomorphic condition (supraacetabular buttress present) and gray lines represent the derived condition (supraacetabular buttress absent)./ *Relaciones filogenéticas de los Crocodyliformes basadas sobre Pol (2003). Los crocodiliformes de los cuales no se dispone de información fueron eliminados del árbol. La presencia del soporte supraacetabular del ilion se optimiza en el cladograma. Las líneas negras representan la condición plesiomórfica (soporte supraacetabular presente) y las líneas grises representan la condición derivada (soporte supraacetabular ausente).*

of these vertebrae region, far anteriorly than in extant forms.

Another interesting character of the vertebrae described here is the presence of an open neurocentral suture in presacral vertebrae of all the *Notosuchus* specimens studied. Brochu (1996) proposed the closure of this suture as a size-independent criterion for measuring maturity in Crocodylia. Although this criterion might be extremely useful within the Crocodylia clade, its applicability for non-crocodylian crocodyliforms remains unexplored. The presence of opened neurocentral sutures in all the studied specimens of *Notosuchus* suggests that either these specimens are immature or that this criterion is not valid for this taxon. An argument against the former interpretation is that some vertebral elements (*e.g.* MACN-RN 1037) are associated with one of the largest skulls (anteroposterior length: 280 mm) among the known sample of *Notosuchus* that include more than 50 skulls collected in different localities of Bajo de la Carpa Formation during the last century. However, another size-independent measure of maturity would be preferred to determine if these specimens are not fully mature or if the criteria proposed by Brochu (1996) for Crocodylia is not valid for *Notosuchus terrestris* and, possibly, for related taxa. Further studies in other basal mesoeucrocodylians are needed in order to test validity of this criterion for basal members of the crocodyliform clade.

Conclusions

The postcranial skeleton of crocodyliforms was traditionally considered as conservative and lacking phylogenetic information (Langston, 1973), or bearing characters varying at high hierarchical levels (e.g., procoelic vertebrae, pubis distal expansion). The study and comparison of the remains described here revealed that diversity in postcranial morphology of Crocodyliformes is not as conservative as previously thought (Pol, 1999; Nobre, 2000). This variation in postcranial morphology offers new information both on the mode of life of fossil crocodyliforms and on the phylogenetic relationships of these taxa and underscore the importance of considering postcranial information in phylogenetic studies.

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References

Benton, M.J. and Clark, J.M. 1988. Archosaur phylogeny and the relationships of Crocodyliformes. In: M.J. Benton (ed.), *The Phylogeny and Classification of Tetrapods 1*, Clarendon Press, Oxford, pp. 295-338.

Bonaparte, J.F. 1991. Los vertebrados fósiles de la formación Río Colorado, de la ciudad de Neuquén y sus cercanías, Cretácico superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología* 4: 17-123.

Brochu, C.A. 1996. Closure of neurocentral sutures during crocodilian ontogeny; implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* 16: 49-62.

Buckley, G.A. and Brochu, C.A. 1999. Am enigmatic new crocodile from the Upper Cretaceous of Madagascar. In: D.M. Umwin (ed.), *Special Papers in Palaeontology 60: Cretaceous Fossil Vertebrates, Palaeontological Association*, London, pp. 149-175.

Buscalioni, A.D. and Sanz, J.L. 1988. Phylogenetic relationships of the Atoposauridae (Archosauria, Crocodylomorpha). *Historical Biology* 1: 233-250.

Buscalioni, A.D. and Sanz, J.L. 1990a. *Montsecosuchus depereti* (Crocodylomorpha, Atoposauridae), new denomination for *Alligatorium depereti* Vidal, 1915 (Early Cretaceous, Spain): Redescription and phylogenetic relationships. *Journal of Vertebrate Paleontology* 10: 244-254.

Buscalioni, A.D. and Sanz, J.L. 1990b. The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 60: 129-150.

Buscalioni, A.D, Sanz, J. L., Casanovas, M. L. and Santafe, J. V. 1986. An Eususchian crocodile from the Upper Cretaceous of Spain (Vilamitjana, Province of Lerida). *Journal of Vertebrate Paleontology* 6: 209-214

Buscalioni, A.D., Ortega, F., Rasskin-Gutman, D. and Pérez-Moreno, B.P. 1997. Loss of carpal elements in crocodilian limb evolution: morphogenetic model corroborated by paleobiological data. *Biological Journal of the Linnean Society* 62: 133-144.

Carrier, D.A. 1987. The Evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* 13: 326-341.

Carvalho, I.S. and Bertini, R.J. 1999. *Mariliasuchus*: um Crocodylomorpha (Notosuchia) de Cretáceo da Bacia Bauru, Brasil. *Geología Colombiana* 24: 83-105.

Clark, J.M. 1985. [*A new crocodylomorph from the Late Jurassic Morrison Formation of western Colorado, with a discussion of relationships within the 'Mesosuchia'*. M.S. thesis, University of California, Berkeley, 86 pp. Unpublished].

Clark, J.M. 1986. [*Phylognetic relationships of the Crocodylomorph Archosaurs*. Ph.D. Thesis, University of Chicago, 556 pp. Unpublished].

Clark, J.M. 1994. Patterns of evolution in Mesozoic Crocodyliformes. In: N.C. Fraser and H-D. Sues (eds.), *In the Shadow of Dinosaurs*. Cambridge University Press, Cambridge, pp. 84-97.

Colbert, E.H. 1952. A pseudosuchian reptile from Arizona. *Bulletin, American Museum of Natural History* 99: 561-592.

Colbert, E.H. and Mook, C.C. 1951. The ancestral crocodilian *Protosuchus*. *Bulletin, American Museum of Natural History* 97: 143-182.

Crush, P.J. 1984. A late Upper Triassic sphenosuchid crocodilian from Wales. *Palaeoncology* 27: 131-157.

Frey, E. 1988. Anatomie des körperstammes von *Alligator mississippiensis* Daudin. *Stuttgarter Beiträge zur Naturkunde* A, 424: 1-106.

Gasparini, Z.B. de 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo Infraorden de los Mesosuchia (Crocodilia). *Ameghiniana* 8: 83-103.

Gomani, E.M. 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds, Northern Malawi. *Journal of Vertebrate Paleontology* 17: 280-294.

Hecht, M.K. 1991. *Araripesuchus* Price, 1959. In: J.G. Maisey (ed.), *Santana fossils: an illustrated atlas*, T.F.H Publications, New York, pp. 340-347.

Hoffstetter, R. and Gasc, J.P. 1973. Vertebrae and ribs of modern repitles. In: C. Gans and T. Parsons, (eds.), *Biology of Reptilia* Vol. 1: 201-233.

Hugo, C.A. and Leanza, H.A. 2001. Hoja Geológica 3969-IV, General Roca. Provincias de Río Negro y Neuquén. *Boletín Servicio Geológico Minero Argentino, Instituto de Geología y Recursos Minerales* 308: 1-65.

Langston, W. Jr. 1973. The crocodilian skull in historical perspective. In: C. Gans and T. Parsons (eds.), *Biology of Reptilia*. Vol. 9: 263-284.

Mook, C.C. 1921. Notes on the postcranial skeleton in the Crocodilia. *Bulletin, American Museum of Natural History* 44: 67-100.

Nash, D.S. 1975. The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. *Annals of the South African Museum* 67: 227-329.

Nobre, P.H. 2000. [*Morfologia pós-craniana de Notosuchia (Crocodylomorpha, Mesosuchia), do Ctretáceo do Brasil*. Rio de Janeiro. Master Thesis, Instituto de Geociências, Universidade Federal do Rio de Janeiro. 83p. Unpublished]

Parrish, J.M. 1987. The origin of crocodilian locomotion. *Paleobiology* 13: 396-414.

Pol, D. 1999. [*El esqueleto postcraneano de* Notosuchus terrestris *(Archosauria: Crocodyliformes) del Cretácico Superior de la Cuenca Neuquina y su información filogenética*. Tesis de Licenciatura, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. 158 pp. Unpublished.]

Pol, D. 2003. New materials of *Sphagesaurus huenei* (Crocodylomorpha: Meseoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 23: 817-831.

Price, L.I. 1950. On a new crocodilian, *Sphagesaurus*, from the Cretaceous of the State of São Paulo, Brazil. *Anais Academia Brasileira de Ciencas* 22: 77-83.

Price, L.I. 1959. Sobre um Crocodilideo Notossúquido do Cretácico Brasileiro. *Departamento Nacional da Produçao Mineral Río de Janeiro, Boletim* 188: 1-55.

Romer, A.S. 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bulletin, American Museum of Natural History* 48: 533-552.

Romer, A.S. 1956. *Osteology of Reptiles*. Chicago University Press, Chicago, 772 pp.

Rowe, T. 1986. Homology and the Evolution of the deep dorsal Thigh Musculature in birds and the other Reptilia. *Journal of Morphology* 189: 327-346.

Rusconi, C. 1933. Sobre reptiles cretáceos del Uruguay (*Uruguaysuchus aznarezi*, n. g. n. sp.) y sus relaciones con los notosúquidos de Patagonia. *Instituto de Geología y Perforaciones Boeltín* 19: 1-64.

Whetstone, K.N. and Whybrow, P.J. 1983. A "cursonial" crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. *Occassional Papers, Museum Natural History University of Kansas* 106: 1-37.

Woodward, A.S. 1896. On two mesozoic crocodilians, *Notosuchus* (genus novum) and *Cynodontosuchus* (gen. nov.) from the red sandstones of Territory of Neuquén (Argentina). *Anales del Museo de La Plata* 4: 1-20.

Wu, X.-C. and Chatterjee, S. 1993. *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. *Journal of Vertebrate Paleontology* 13: 58-89.

Wu, X.-C. and Sues, H.-D. 1996. Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. *Journal of Vertebrate Paleontology* 16: 688-702.

Wu, X.-C., Sues, H.-D. and Sun, A. 1995. A plant-eating crocodyliform reptile from the Cretaceous of China. *Nature* 376: 678-680.

Wu, X.-C., Sues, H.-D. and Brinkman, D.B. 1996. An Atoposaurid neosuchian (Archosauria: Crocodyliformes) from the Lower Cretaceous of Inner Mongolia (People's Republic of China). *Canadian Journal of Earth Sciences* 33: 599-605.

Young, C.C. 1953. New fossil reptiles from Szechuan China. *Acta Paleontologica Sinica* 1: 1-87.

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