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A BASAL ABELISAURIA NOVAS, 1992 (THEROPODA-CERATOSAURIA) FROM THE CRETACEOUS OF PATAGONIA, ARGENTINA

Rodolfo A. CORIA

Dirección General de Cultura de Neuquén, Museo "Carmen Funes". 8318 Plaza Huincul, NEUQUÉN. ARGENTINA
E-mail: coriarod@neunet.com.ar

Leonardo SALGADO

Museo de Paleontología y Geología, Universidad Nacional del Comahue. Buenos Aires 1400, 8300 NEUQUÉN. ARGENTINA

ABSTRACT: A new abelisaur theropod, *Ilokelesia aguadagrandensis* gen.nov., sp.nov., is described, characterized by having: a) quadrate with lateral condyle very reduced and posterior border of the articular surface formed completely from medial condyle, b) cervical vertebrae with very reduced diapo-postzygapophysial laminae, c) posterior dorsal vertebrae with infraparapophysial laminae ventrally concave, with parapophyses ventrally oriented, d) dorsal vertebrae lacking pleurocoels, e) caudal vertebrae in central third of the tail with distally expanded transverse processes bearing cranially and caudally projected processes and f) distal edge of caudal transverse processes slightly concave in the mid part. This new theropod represents the most plesiomorphic abelisaur taxon, sharing with Abelisauridae (*Abelisaurus* BONAPARTE & NOVAS, 1985 and *Carnotaurus* BONAPARTE, 1985) and Noasauridae (*Noasaurus* BONAPARTE & POWELL, 1980 and *Ligabueino* BONAPARTE, 1996) supraorbital ossification of postorbital, postorbital with intraorbital projection in the jugal process, quadrate with lateral condyle reduced, cervical vertebrae with reduced neural spine, well developed prezygo-epipophyseal laminae and distally expanded caudal transverse processes. *Ilokelesia* gen. nov. retains postorbital with jugal process perpendicular to horizontal branch, quadrate foramen and cervical epipophyses lacking cranial projection.

RESUMEN: Se describe un nuevo terópodo abelisaurio, *Ilokelesia aguadagrandensis* gen. nov., sp.nov. caracterizado por poseer: a) cuadrado con cóndilo externo muy reducido y borde posterior de la superficie articular completamente formado por el cóndilo interno, b) vértebras cervicales con lámina diapo-postzigapofisial muy reducida, c) vértebra dorsal con lámina infraparapofisial ventralmente cóncava, con parapófisis orientadas ventralmente, d) vértebra dorsal posterior sin pleurocelos, e) vértebras caudales del tercio central de la cola con procesos transversos expandidos distalmente con procesos orientados cranial y caudalmente y f) procesos transversos caudales ligeramente cóncavos en la parte media. Este nuevo terópodo representa el taxón abelisaurio más plesiomórfico, compartiendo con Abelisauridae (*Abelisaurus* BONAPARTE & NOVAS, 1985 y *Carnotaurus* BONAPARTE, 1985) y Noasauridae (*Noasaurus* BONAPARTE & POWELL, 1980 y *Ligabueino*, BONAPARTE, 1996) osificación supraorbital del postorbital, postorbital con proyección intraorbital en el proceso jugal, cuadrado con el cóndilo externo reducido, vértebras cervicales con espinas neurales reducidas, lámina prezigo-epipofisial bien desarrollada y procesos transversos caudales expandidos distalmente. *Ilokelesia* gen. nov. retiene postorbital con proceso jugal perpendicular a la rama horizontal, foramen cuadrado y epipófisis cervicales carentes de proyección cranial.

INTRODUCTION

The record of Cretaceous theropod dinosaurs from South America is composed by a complex and rather diversified group of genera whose phylogenetic relationships still remain poorly understood (see BONAPARTE, 1996). In the last few years, many and interesting new taxa have been reported from Patagonia (CORIA & SALGADO, 1995; BONAPARTE, 1996; NOVAS, 1997; NOVAS & PUERTA, 1997). At present, the main Cretaceous theropod clade in South America, with the greatest amount of genera involved seems to be the Abelisauria (NOVAS, 1992), including *Abelisaurus comahuensis* BONAPARTE & NOVAS, 1985, *Carnotaurus sastrei* BONAPARTE, 1985, *Xenotarsosaurus bonapartei* MARTINEZ *et al.*, 1986, *Noasaurus leali* BONAPARTE & POWELL, 1980, and the recently published *Ligabueino andesi* BONAPARTE, 1996. Although the South American record is the best known, the Abelisauria seems to be a group of theropods widely distributed in the Cretaceous, since its presence has been reported from Africa, Madagascar, India and Europe (BONAPARTE, 1991b; BUFFETAUT *et al.*, 1988; SAMPSON *et al.*, 1996).

In 1991, the first theropod remains from the Huincul Member, Río Limay Formation were reported (CORIA *et al.*, 1991), being represented by a fragmentary but diagnostic specimen and proposed to be the sister group of Abelisauridae and Noasauridae. In the present paper, this new theropod is described in detail and their phylogenetic relationships are discussed. Finally, the global relationships of the Neoceratosauria (*Ceratosaurus* + Abelisauria) (NOVAS, 1989, 1992) are revised.

SYSTEMATIC PALEONTOLOGY

Dinosauria, OWEN 1842

Theropoda, MARSH 1881

Ceratosauria, MARSH 1884

Neoceratosauria, NOVAS 1989

Abelisauria, NOVAS 1992

Ilokelesia gen. nov.

Type species: *Ilokelesia aguadagrandensis* sp. nov.

Diagnosis: Medium-sized theropod, distinguished by the following autapomorphies: quadrate with lateral condyle very reduced and posterior border of the articular surface formed completely from medial condyle; cervical vertebrae with poorly defined diapo-postzygapophysial laminae; posterior dorsal vertebrae with infraparapophysial laminae

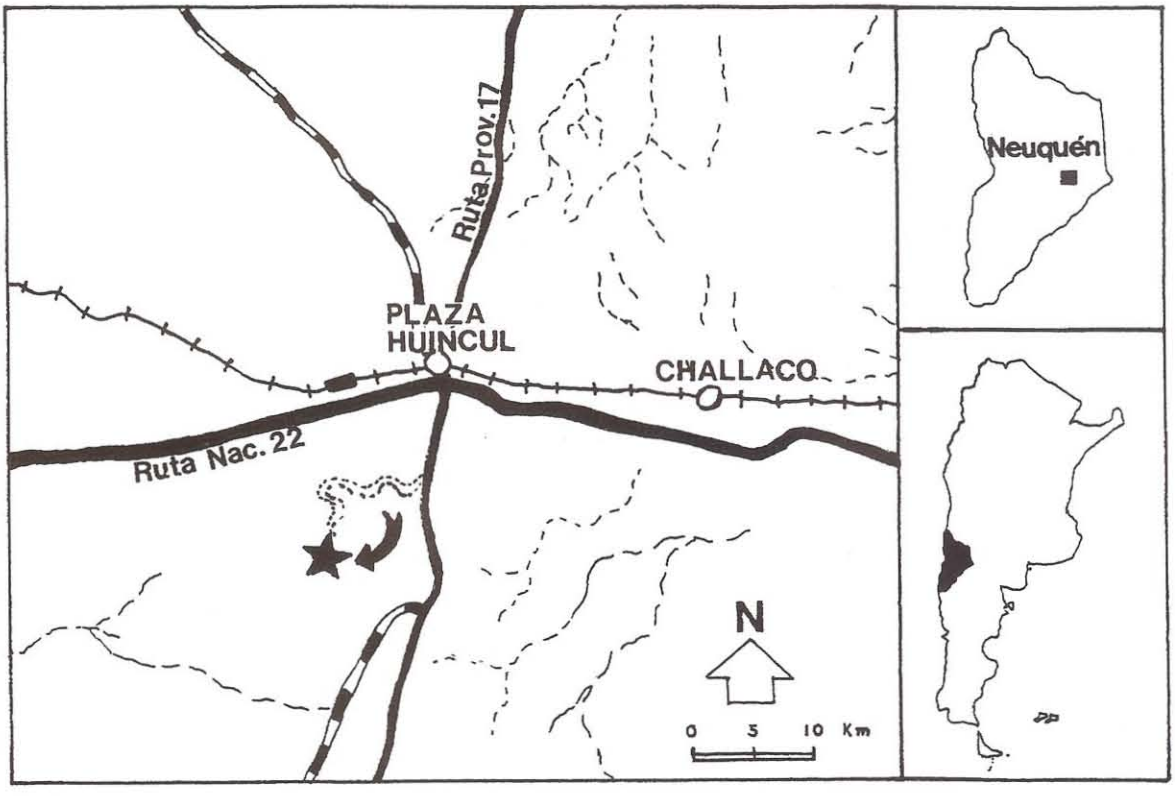

Fig. 1 - Map showing the location of the site where the holotype of *Ilokelesia aguadagrandensis* gen.nov., sp.nov. was found.

ventrally concave, and parapophysis ventrally oriented; posterior dorsal vertebrae lacking pleurocoels; caudal vertebrae in central third of the tail with distally expanded transverse processes bearing cranially and caudally projecting processes; distal edge of caudal transverse processes slightly concave in the mid part.

Etymology: From the indigenous Mapuche language, *ilo*, flesh; and *kelesio*, lizard, a flesh-eating reptile.

Ilokelesia aguadagrandensis sp.nov.

(Fig. 2-10)

Diagnosis: As for genus.

Holotype: PVPH-35. Right postorbital, right quadrate, occipital condyle, 3rd? cervical vertebra partially preserved, 4th? cervical vertebra, posterior dorsal vertebra, five articulated mid caudal vertebrae, three fragmentary cervical ribs, eight proximal haemal arches, eight preungual phalanges, two ungual phalanges.

Horizon and locality: Río Limay Formation, Huincul Member, Neuquén Group (Albian - Cenomanian). From Aguada Grande, 15 km southern Plaza Huincul City, Neuquén Province, Argentina (Fig. 1).

Etymology: From Aguada Grande, where the specimen was found.

DESCRIPTION

POSTORBITAL

A nearly complete postorbital is preserved (Fig. 2). It is "T"- shaped, with a long, strong jugal process, which is vertically oriented with a flattened latero-dorsal end and is triangular in cross- section. It meets the horizontal branch at a right angle. Distally, the jugal process exhibits a relatively weak suture for the jugal. In dorsal view, moderate rugosities are apparent. In lateral view, the dorsal portion presents a brow-like supraorbital process like in *Abelisaurus* (MPCA-11098) (Fig. 3D) and *Giganotosaurus* (CORIA & SALGADO, 1995) (MUCPv-CH-1). The process for the lacrimal is thick. In medial view, a facet for articulation with the laterosphenoid is visible. In lateral view the horizontal branch of the postorbital exhibits a dorsal boss, with its apex located above the caudal edge of the jugal process (Fig. 2A). The dorsal edge of the lacrimal process becomes nearly horizontal distally. There is an intraorbital projection as in *Abelisaurus, Carnotaurus* (Fig. 3D-E), *Giganotosaurus* and *Tyrannosaurus* (OSBORN, 1905). It is placed below the mid point of the cranial side of the jugal process, and is slightly upwardly inclined. It does not reach the distal end of the jugal process. The lateral surface of the jugal process is proximally flat and wide; the distal end is rod-shaped. The caudal edge bears a wide longitudinal groove.

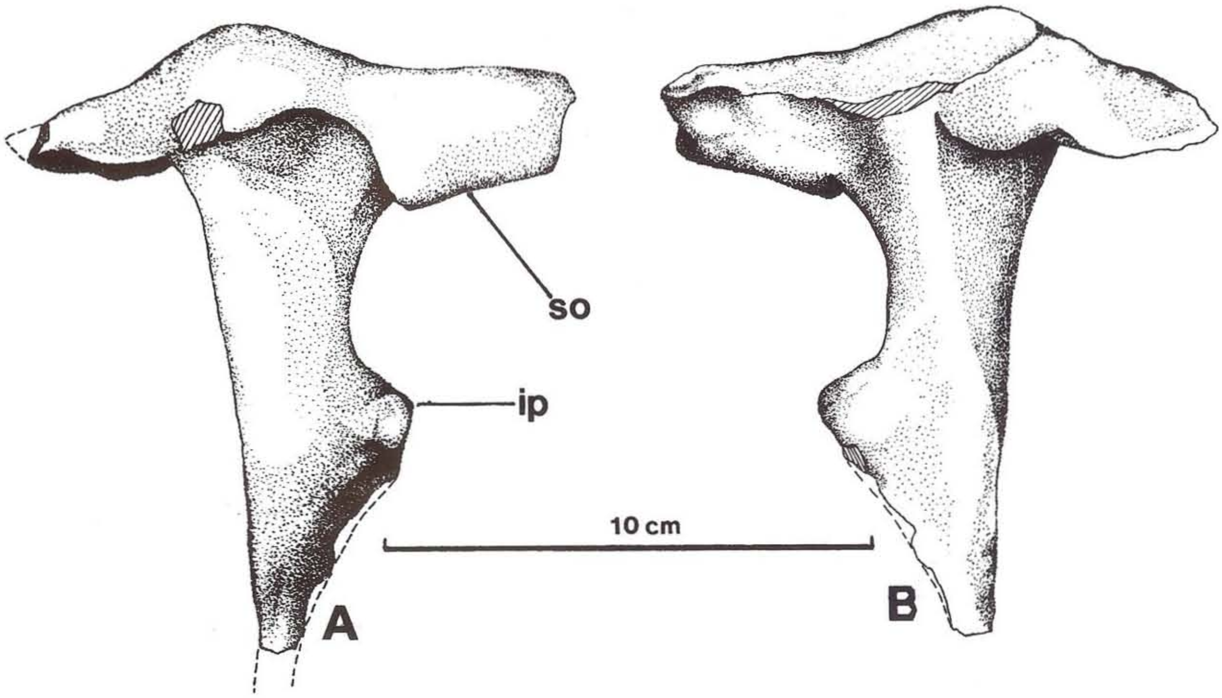

Fig. 2 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. Right postorbital. **A** - Lateral view. **B** - Medial view. Abbreviations: ip - Intraorbital process; so - Supraorbital ossification.

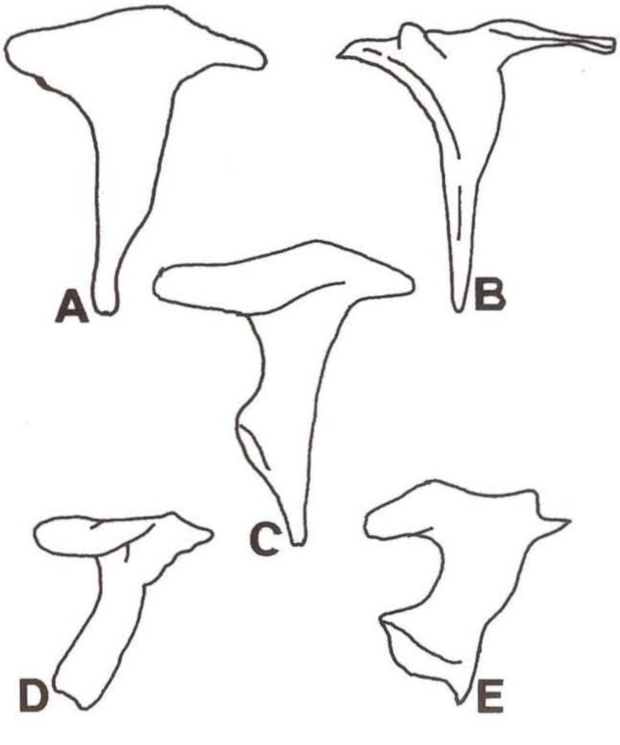

Fig. 3 - Comparison of left postorbital in lateral view. **A** - *Allosaurus* (MADSEN, 1976). **B** - *Ceratosaurus* (USNM-4735). **C** - *Ilokelesia* gen.nov. **D** - *Abelisaurus* (MPCA-11098). **E** - *Carnotaurus* (MACN-CH-894).

QUADRATE

A right quadrate is represented by two portions which are unconnected (Fig. 4). The dorsal portion exhibits the condyle for articulation with the squamosal. The cranial surface is transversally concave. The medial process which articulates with the pterygoid is not preserved. The lateral lamina is preserved only dorsally. In caudal view, the squamosal condyle slopes dorso-laterally. The ventral portion of the quadrate includes the cranio-mandibular articulation. The medial border is very concave, and the lateral is broken. There is a conspicuous process situated 2.5 cm above the lateral condyle.

The articular surface is formed by two condyles. In posterior view, the articulation looks transversely convex. The lateral condyle is quite small and slightly transversally oriented. A relatively deep fossa occurs above the lateral condyle. The medial condyle is larger than the lateral one, and is antero-laterally oriented. The dorsal and ventral edges of the medial condyle exceed those of the lateral in size. The cranial end of the medial condyle protrudes beyond that of the lateral condyle.

CERVICAL VERTEBRAE

3rd? Cervical. This vertebra has preserved only its right half. The neural arch is relatively long and low. In lateral view, large pneumatic foramina are visible below the transverse process. There is an extensive lamina connecting the prezygapophysis with the epipophysis, which sharply separates the lateral and dorsal areas of the neural arch. The epipophysis is well developed, backwardly oriented, and lacks an cranial projection. The lateral surface of the centrum bears two pleurocoels.

4th?Cervical (Fig. 5). This vertebra is complete. The neural arch is relatively high, with a laterally compressed, relatively reduced neural spine which however reaches the level of the epipophysis. As in the vertebra described above, the epipophyses are well developed, postero-laterally oriented, with no cranial projections. In lateral view the post-diapophysial lamina is reduced, being represented by a shallow ridge (Fig. 5B). The lateral edge of the prezygapophyses is also connected to the epipophyses by a thin lamina that clearly separates the dorsal from lateral surfaces of the neural arch like in *Carnotaurus* (MACN-CH-894) and *Noasaurus* (PVL-4061) (Fig. 6C-D).

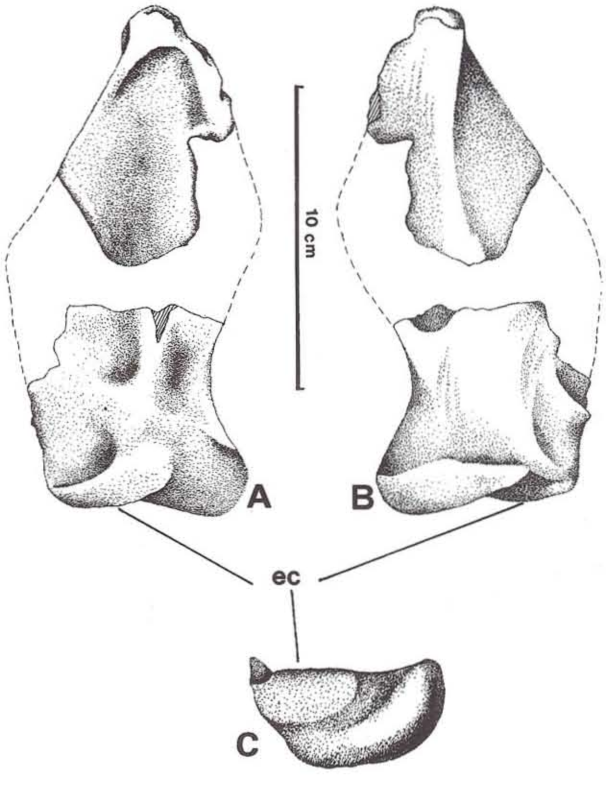

Fig. 4 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. Right quadrate. **A** - Cranial view. **B** - Caudal view. **C** - Ventral view. Abbreviations: ec - Lateral condyle.

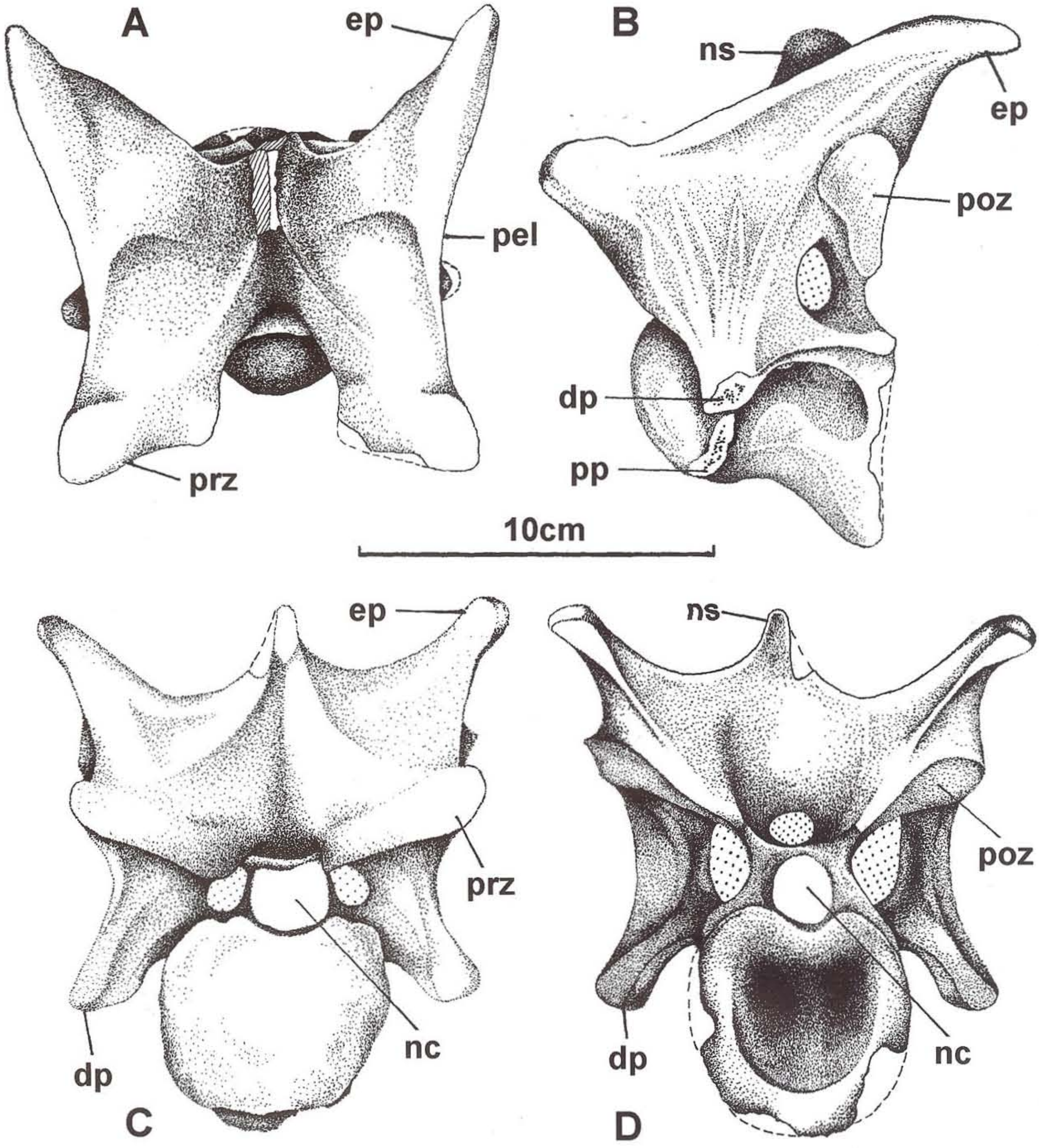

Fig. 5 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. 4^{th}? cervical vertebra. **A** - Dorsal view. **B** - Lateral view. **C** - Cranial view. **D** - Caudal view. Abbreviations: dp - Diapophysis; ep - Epipophysis; nc - Neural canal; ns - Neural spine; pel - Prezygo-epipophyseal laminae; poz - Postzygapophysis; pp - Parapophysis; prz - Prezygapophysis.

In anterior view a deep depression is present below the neural spine (Fig. 5C). In posterior view another depression is situated above the neural canal, although it is not so deep as the anterior one (Fig. 5D). There are two foramina on each side of the neural canal. The centrum is opisthocoelus, low and slightly compressed laterally. Pleurocoelic foramina are situated below the infradiapophysial laminae. In ventral view, a small keel is cranially placed. In cervical neural arches of *Carnotaurus* (MACN-CH-894) (Fig. 6D), *Noasaurus* (PVL-4061)(Fig. 6C), *Ligabueino* (MACN-N-42) and *Ceratosaurus* (GILMORE, 1920) (Fig. 6A), the dorsal surface of the diapophysis is clearly differentiated from the posterior side by a well-marked lamina which connects the diapophysis with the cranial edge of the postzygapophysis. In *Ilokelesia* gen.nov., although this lamina is present, it is not well-marked and forms a shallow edge. In *Carnotaurus* and *Noasaurus* (Fig. 6C-D), the diapo-postzygapophysial lamina contributes to the formation of the cranial border of a deep cavity. In *Ilokelesia*, the diapo-postzygapophysial lamina does not participate of the margin of such a cavity which is situated well behind the lamina.

Dorsal vertebrae

The only preserved dorsal vertebra is from the posterior part of the presacral column (Fig. 7). The neural spine and right transverse process are missing. In dorsal view (Fig. 7A), the distal end of the left transverse process is cranio-caudally expanded like in *Ceratosaurus* (USNM-4735) and *Carnotaurus* (MACN-CH-894) (Fig. 8C-D). The diapophysis and parapophysis are connected by a well-developed parapo-diapophysial lamina. The infraparapophysial lamina is well-developed, separating the parapophysis from the sagital plane. Thus, both parapophysis and diapophysis are at the same level. The parapophysis is, however, located below the diapophysis and faces ventrally. In lateral view the infradiapophysial lamina is caudally concave, while the infraparapophysial lamina is cranially concave as in *Carnotaurus* (Fig. 8B). A thick lamina connects the parapophysis with the center of the shaft of the infradiapophysial lamina separating two wide cavities. The prezygapophysis bears a ventral process which is ventro-cranially oriented as in *Carnotaurus*. There is a supraprezygapophysial lamina connecting the prezygapophysis with the dorsal surface of the transverse process. Both this lamina and the base of the infra-parapophysial lamina limit a large cavity that penetrates into the neural arch. The hypantrum is wide. In caudal view, the articular surfaces of the postzygapophyses are medio-ventrally oriented. The hyposphene is deep and well-developed. The centrum is low and its articular surfaces are concave, seeming to be wider than high. The lateral surfaces bear marked depressions just below the juncture of the centrum and the neural arch, but no pleurocoelic foramina are present. In ventral view, a very poorly defined median keel can be observed, which is cranially situated. In the dorsal vertebrae of *Carnotaurus* (Fig. 8C-D) and other ceratosaurs, parapophyses are upward or laterally facing. *Ilokelesia* gen.nov. is unique in having: 1) an infradiapophysial lamina which is ventrally concave, and 2) parapophyses oriented downwards to nearly reach the level of the neural canal (Fig. 8A-B). There are shallow depressions on each side of the dorsal centrum of *Ilokelesia* gen.nov., but no pleurocelic foramen, in contrast with most theropods where dorsal vertebrae are known, in which a pleurocoelic foramen is present in the lateral side of the centrum throughout the dorsal series.

Caudal vertebrae

Five articulated caudal vertebrae are preserved. All exhibit reduced neural spines which are laterally compressed and caudally positioned (Fig. 9). The prezygapophyses are elongated, with their articular surfaces sloping inward. The postzygapophyses are small. The transverse processes project laterally, perpendicular to the dorsoventral axis of the vertebrae and slightly behind the midpoint of the centrum. The distal ends are very expanded like in *Carnotaurus* (Fig. 10E-H), but with cranial and caudal projections (Fig. 10I-J). This condition is not present in more primitive neoceratosaurs like *Ceratosaurus* (Fig. 10A-D). The distal edge are slightly concave in the mid part. The dorsal surface of the neural arch is broad (Fig. 9A). It is divided by a shallow crest, which connects the anterior border of the neural arch to the cranial ridge of the neural spine. This is interpreted as the prespinal lamina. The first centrum of the series is the longest. The centra are amphicoelous. No pleurocoels are visible on the lateral surface of the centra. A shallow longitudinal groove is present along the ventral face of all centra (Fig. 10J).

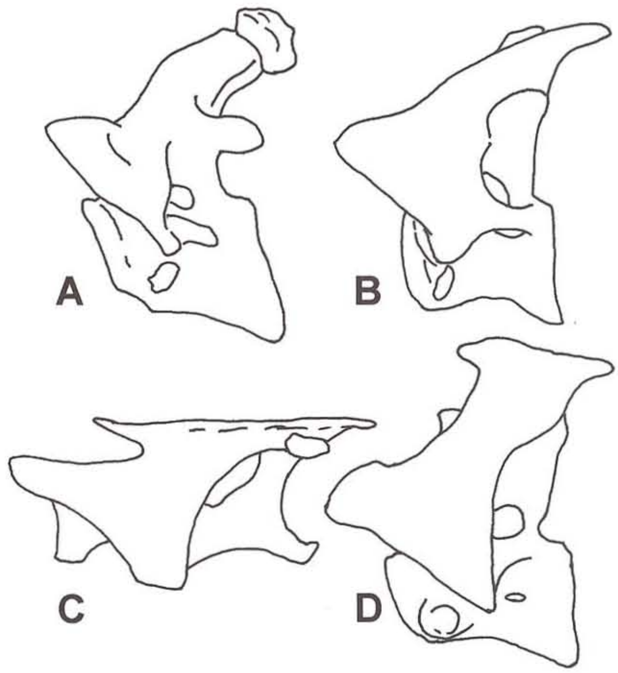

Fig. 6 - Comparison of cervical vertebra in lateral view. **A** - *Ceratosaurus* (Gilmore, 1920). **B** - *Ilokelesia* gen.nov. **C** - *Noasaurus* (PVL-4061). **D** - *Carnotaurus* (MACN-CH-894).

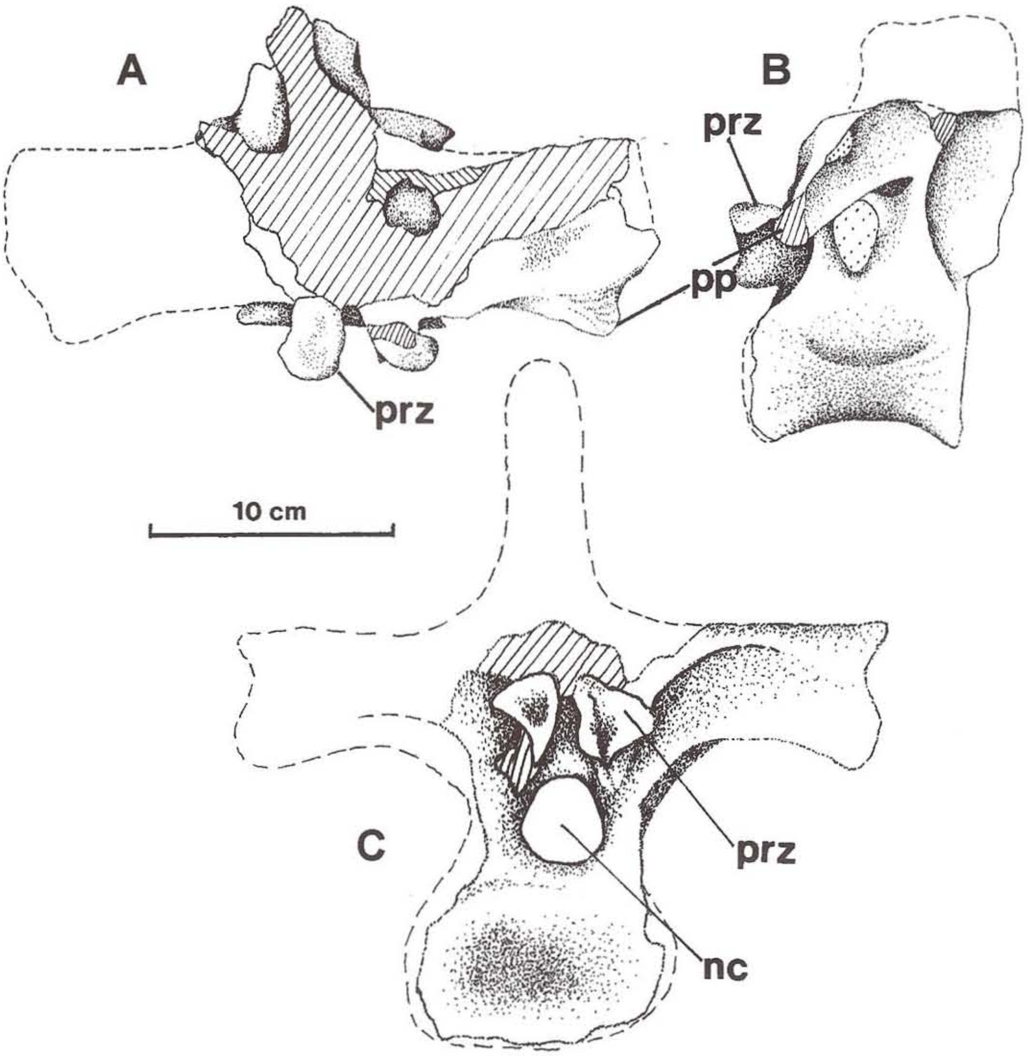

Fig. 7 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. Posterior dorsal vertebra. **A** - Dorsal view. **B** - Lateral view. **C** - Anterior view. Abbreviations: nc - Neural canal; pp - Parapophysis; prz - Prezygapophysis.

CERVICAL RIBS

Three fragmentary cervical ribs are preserved. The proximal end presents a well defined capitulum and tuberculum (Fig. 11). A conspicuous process projects cranially below the capitulum and is connected to it by a thin lamina. The ventral surface of the shaft is broad and flat proximally. Dorsal and ventral ridges link the shaft to the capitulum. The fragmentary shaft is a rod-like bone, with a slightly sigmoid curvature, probably resulting from a post-mortem deformation.

HAEMAL ARCHES

Three almost complete cranial haemal arches are preserved as well as major portions of five additional more caudal arches (Fig. 12). They are proportionally long and slender. The articular ends are relatively wide, finishing in a single articular facet which encloses the haemal canal dorsally.

The haemal arches are slightly caudally recurved. The anterior ones are slender, although relatively stouter than the more caudal ones. The transverse diameter of the haemal spine is slightly smaller than the antero-caudal diameter but the caudal spines are strikingly laterally compressed. The proximal ends bear two cranial projections; the distal ends are unexpanded. Below the haemal canal, on the caudal face, there is a shallow groove along the proximal half of the haemal spine.

PHALANGES

Ten pedal phalanges have been preserved, including two unguals. The specimen provides much information pertaining to phalangeal morphology.

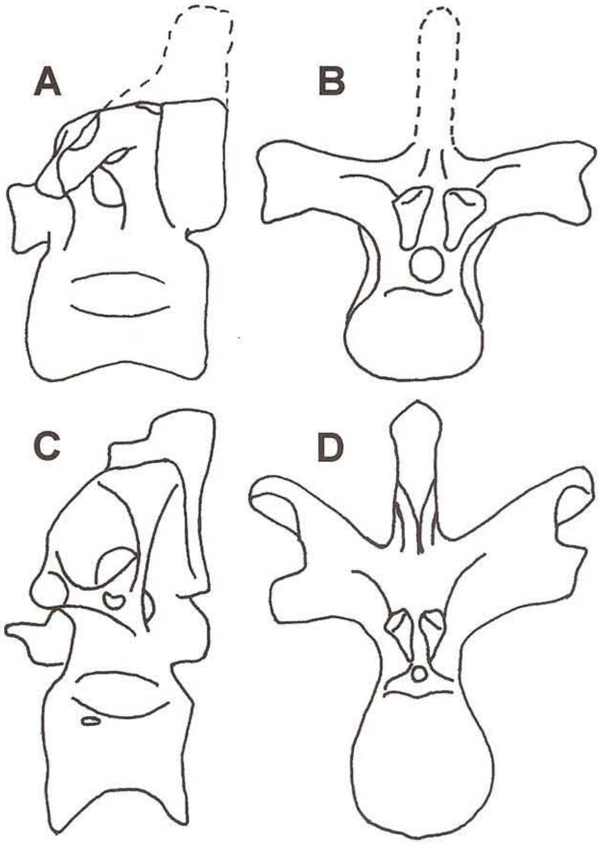

Fig. 8 - Comparison of posterior dorsal vertebra. **A-B** - *Ilokelesia* gen.nov. **C-D** - *Carnotaurus* (MACN-CH-894). A, C - Lateral views. B, D - Anterior views.

The preungual phalanges show the typical morphology present in most mid and large-sized theropods with wide, concave proximal articular surfaces and well developed distal articulations. Phalanx II-1 is a long, slightly laterally compressed and asymmetrical element and the phalanx II-2 is shorter and stouter than II-1. The phalanx III-1 is the stoutest among those preserved (Fig. 13A-F) with its distal articular end lacking central groove. This feature helps to identify phalanx III-2 which has no a central keel in its proximal articular end (Fig. 13G-L). The phalanx IV-3 is short and stout and its anterocaudal axis is slightly longer than the transverse axis. The phalanx IV-4 is small and similar to the preceding one although it is much shorter. Thus, the proximal and distal ends are very close to each other.

Ungual Phalanges

The element is concave below, convex above, rather stout and rather asymmetrical (Fig. 14). The proximal end is heavily built and bears a caudally oriented dorsal projection. A median keel divides the articular surface. The medial edge is concave dorsally. The medial surface bears a caudally bifurcating groove. The lateral side is flatter. The ventral surface is shallowly excavated; there is no flexor tubercle. The distal end of the phalanx, though acuminate, is relatively blunt.

PHYLOGENETIC DISCUSSION

Ceratosaurian monophyly has already been proposed by several authors (Gauthier, 1986; Gauthier & Padian, 1985; Rowe, 1989; Rowe & Gauthier, 1990, Holtz, 1994), as the plesiomorphic sister taxon of all remaining theropods. This taxon, postulated to have originated during Late Triassic time, has been extended with the inclusion of South American Cretaceous theropods (Bonaparte, Novas & Coria, 1990; Bonaparte, 1991b; Novas, 1989, 1992). Bonaparte, Novas & Coria (1990) recognized a systematic entity on the superfamily level, the Ceratosauroidea, which would contain the families Ceratosauridae, Abelisauridae and Noasauridae. We shall follow Novas (1992) in the recognition of the Abelisauria as the sister group of *Ceratosaurus*. *Ceratosaurus* and Abelisauria, in turn, were proposed by the same author as forming the Neoceratosauria (Novas, 1989, 1992), the sister

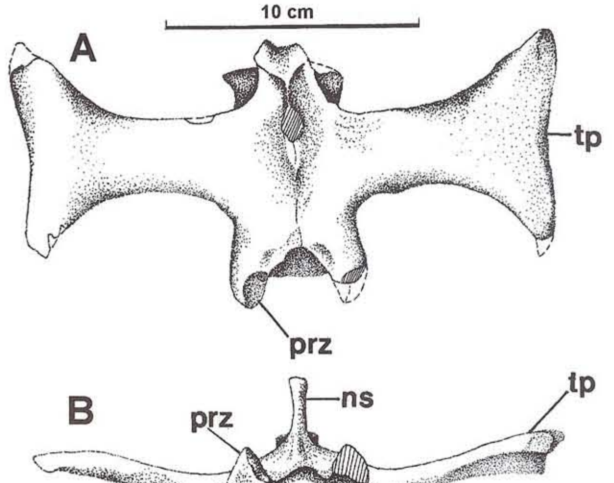

Fig. 9 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. Caudal vertebra. **A** - Dorsal view. **B** - Cranial view. **C** - Lateral view. Abbreviations: ns - Neural spine; prz - Prezygapophysis; tp - Transverse process.

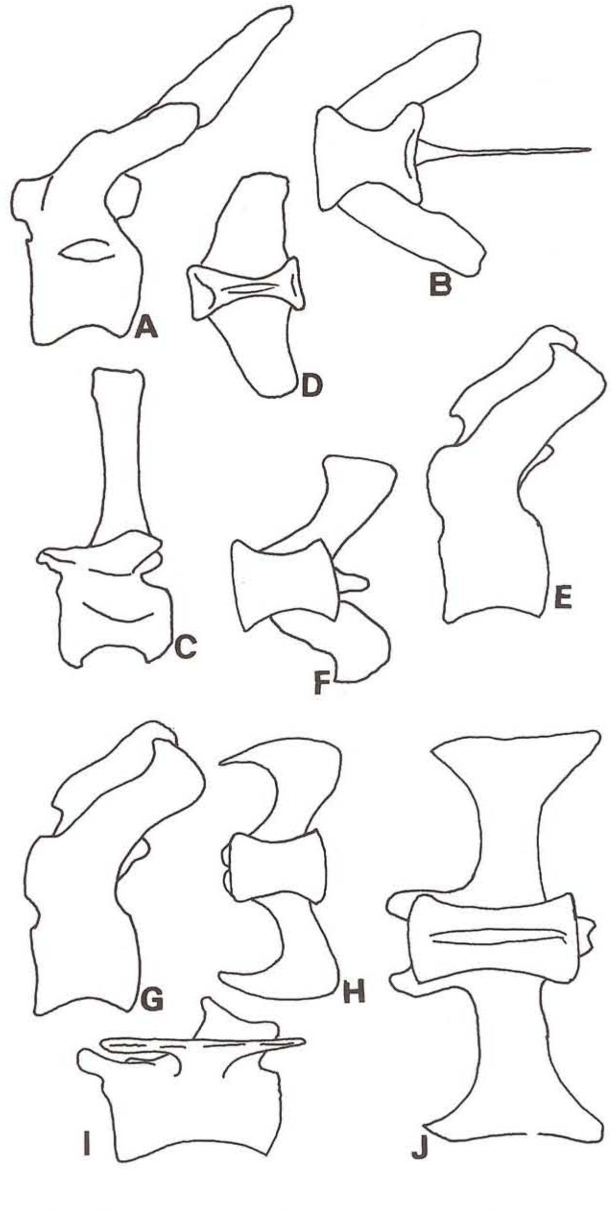

Fig. 10 - Comparison of caudal vertebra. **A-D** - *Ceratosaurus* (GILMORE, 1920). **E-H** - *Carnotaurus* (MACN-CH-894). **I-J** - *Ilokelesia* gen.nov. A, B, E, F - Proximal caudal vertebrae; C, D, G, H, I, J - Mid-caudal vertebrae; A, C, E, G, I - Lateral views; B, D, F, H, J - Ventral views.

group of Coelophysoidea (*Dilophosaurus* WELLES, 1984; *Coelophysis* COPE, 1887) and related forms (HOLTZ, 1994).

In the present paper, *Ilokelesia* gen.nov. was compared with all abelisaur theropods from South America, and also with *Ceratosaurus* (GILMORE, 1920), *Dilophosaurus* (WELLES, 1984) and the higher Coelophysidae because their close relationships with the Abelisauria. Abelisaurids have been also reported outside South America (BONAPARTE, 1996; SAMPSON *et al.*, 1996) bearing significant paleobiogeographic information. However, those specimens are rather fragmentary, and they do not contribute any significant anatomical information for phylogenetic analysis. Recently, a well preserved theropod specimen was discovered in Madagascar, with unquestionable abelisaur affinities (SAMPSON *et al.*, 1997). The anatomical information of such a remarkable specimen was not available at the moment the present paper was currently done.

None of the characters used in the analyses are autapomorphic for the taxa under consideration. Seven ceratosaur taxa were chosen in order to make an approach to the phylogenetic position of *Ilokelesia* gen.nov. Forty six cranial and postcranial characters were polarized using Tetanurae and Herrerasauridae as successively more distant outgroups. The data matrix was analyzed using Farris's program Hennig 86, version 1.5.

A single most parsimonious tree of 48 steps with a consistency index of 0.93 and retention index of 0.93 was obtained. In the tree, *Ilokelesia* gen.nov. is shown to be the sister group of Abelisauroidea (NOVAS, 1989) which includes Noasauridae and

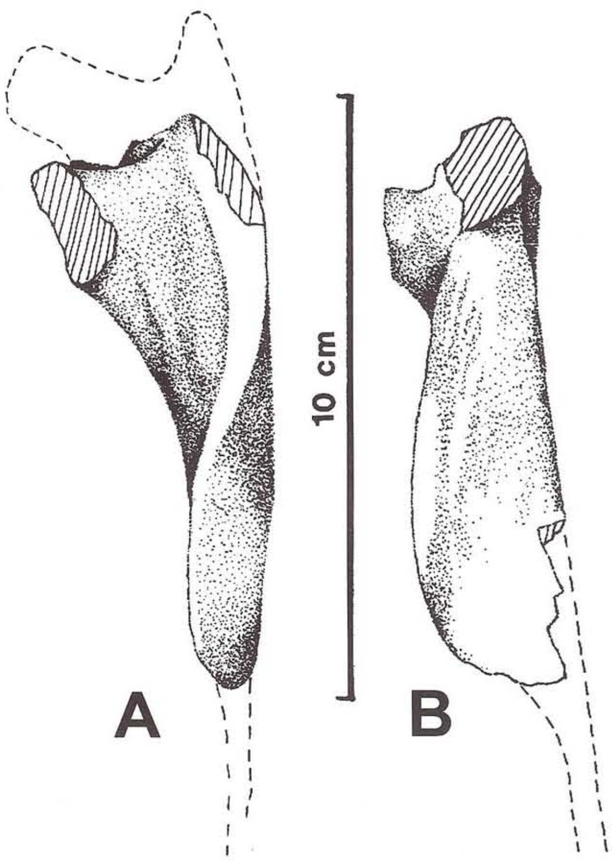

Fig.11 - *Ilokelesia aguadagrandensis* gen.nov.,sp.nov. Holotype. Left cervical rib. **A** - Lateral view. **B** - Ventral view.

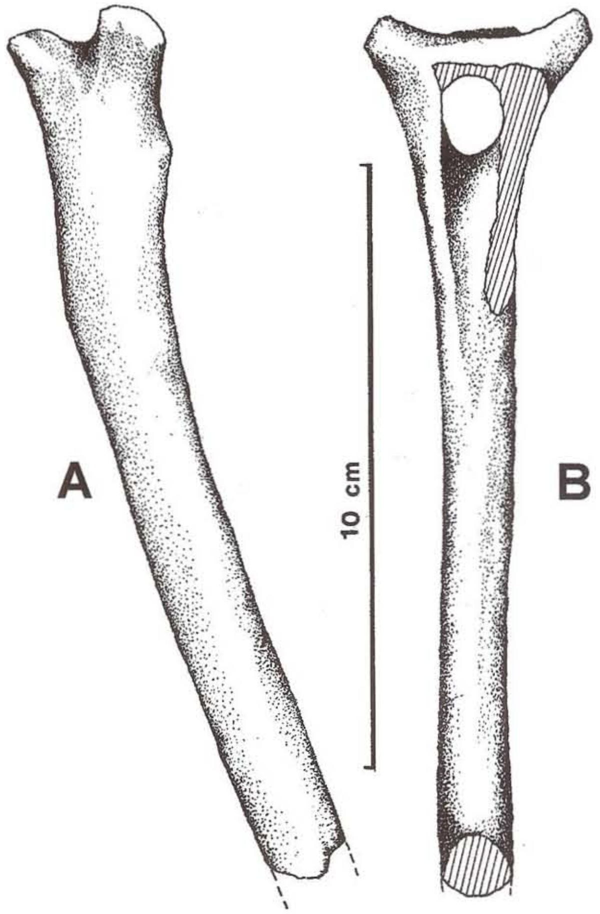

Fig.12 - *Ilokelesia aguadagrandensis* gen.nov.,sp.nov. Holotype. Anterior haemal arch. **A** - Lateral view. **B** - Caudal view.

Abelisauridae (Fig.15), sharing the following apomorphies:

- Postorbital with intraorbital projection

The postorbital of *Ilokelesia* shares with those of *Carnotaurus* BONAPARTE, 1985; *Abelisaurus* BONAPARTE & NOVAS, 1985; and *Giganotosaurus* CORIA & SALGADO, 1995; the presence of an intraorbital projection, although it retains the perpendicular orientation between the horizontal and jugal ramii as in *Ceratosaurus* (GILMORE, 1920) and *Allosaurus* (MADSEN, 1976) (Fig. 9). A supraorbital ossification is reminiscent of the condition present in *Abelisaurus* (BONAPARTE & NOVAS, 1985), but also is present in the carcharodontosaurids *Carcharodontosaurus* STROMER, 1931 (SERENO *et al.*, 1996) and *Giganotosaurus* (CORIA & SALGADO, 1995).

- Quadrate with lateral condyle reduced

The ventral articular end of the quadrate of *Ilokelesia* is typically formed from two condyles, separated by a groove, and the lateral condyle is reduced. The lateral condyle is reduced in *Carnotaurus* (MACN-CH- 894), *Abelisaurus* (MPCA-11098), *Torvosaurus* GALTON & JENSEN, 1979 (BRITT, 1991) and apparently in *Dilophosaurus* (WELLES, 1984). According our analysis, this character is considered to be a synapomorphy of the Abelisauria, being independently developed in *Dilophosaurus*. In *Ceratosaurus* and primitive Tetanurae (i.e. *Allosaurus, Giganotosaurus*) the condyles are equal in size. BRITT (1991) described a marked cranial protrusion of the medial condyle in *Torvosau-*

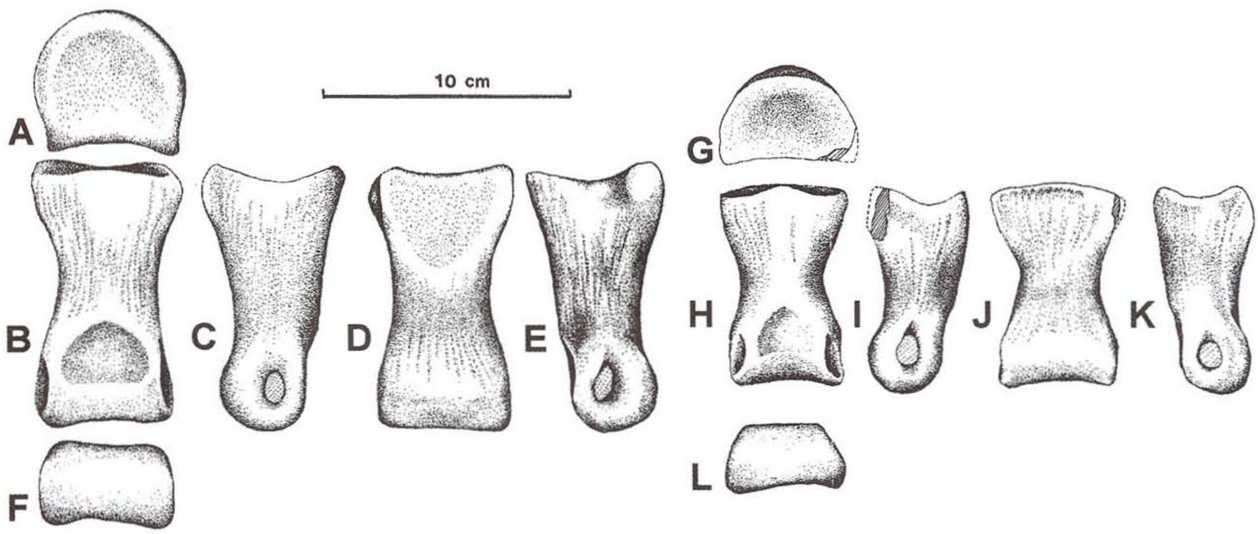

Fig. 13 - *Ilokelesia aguadagrandensis* gen.nov., sp.nov. Holotype. **A-F** - Proximal phalanx of digit III? **G-L** - Midphalanx of digit III? **A,G** - Proximal views. **B,H** - Dorsal views. **C,I** - Right lateral views. **D,J** - Ventral views. **E,K** - Left lateral views. **F,L** - Distal views.

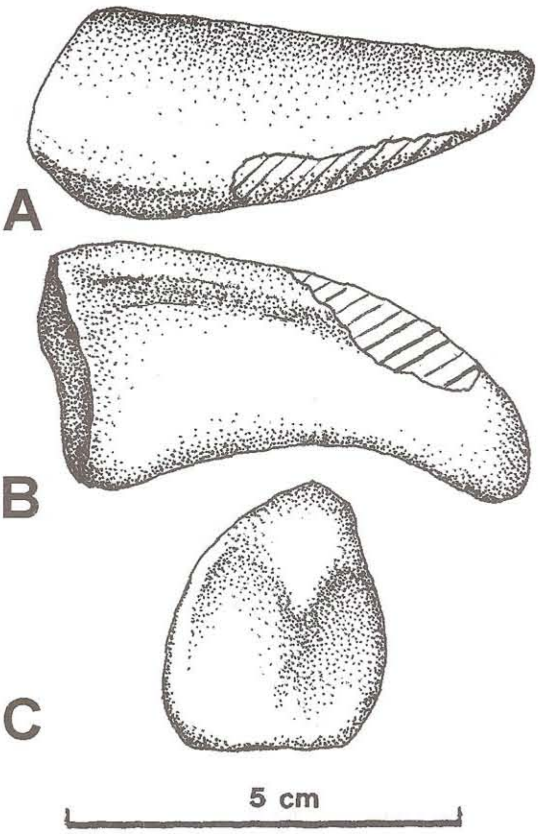

Fig. 14 - *Ilokelesia aguadagrandensis* gen.nov., sp. nov. Holotype. Ungual phalanx. **A** - Dorsal view. **B** - Medial view. **C** - Caudal view. Scale: 5 cm.

rus, which is also present in *Ilokelesia* gen.nov. However, we can recognize here the autapomorphic condition: almost all of the caudal border of the distal articular end of the quadrate is formed from the medial condyle.

• Dorsal surface of cervical neural arches clearly delimited from lateral side of diapophyses by a highly developed prezygapo-epipophysial lamina

Ilokelesia gen.nov. shares with *Carnotaurus* and *Noasaurus* in having the dorsal surface of the cervical neural arches well separated from the lateral surface by a prezygapo-epipophysial lamina (BONAPARTE, 1996). In contrast, *Ilokelesia* retains epipophysis with no cranial projection, as occurs in *Noasaurus* and *Carnotaurus*.

• Cervical ribs with caudal branches wide and strongly flattened

Ilokelesia gen.nov. possesses cervical ribs quite similar to those of *Carnotaurus* and in lesser degree to *Noasaurus* in being proximally wide and flat, with a distal, rod-like shaft.

• Caudal vertebra with transverse process bearing antero- caudally expanded distal ends

Caudal vertebrae of *Carnotaurus* bear transverse processes with expanded distal ends having a conspicuous cranial projection. In *Ilokelesia* gen.nov., the transverse process bear also strong caudal projections (Fig. 14). In *Carnotaurus* also, the distal ends of caudal transverse processes are

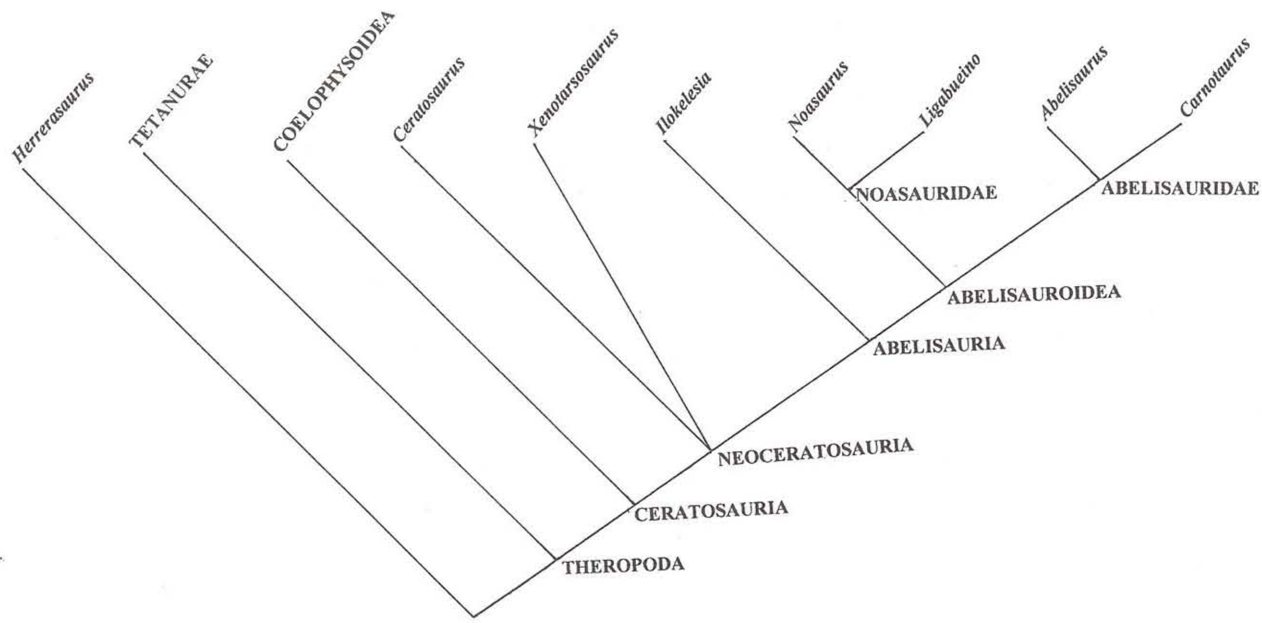

Fig. 15 - Cladogram showing the phylogenetic position of *Ilokelesia* gen.nov. among Abelisauria.

convex; while in *Ilokelesia* gen.nov. the distal edge of transverse processes are slightly concave.

Ceratosaurus and *Dilophosaurus* + higher Coelophysidae are successively more remote sister groups of Abelisauria. Although *Ilokelesia* gen.nov. shares with *Dilophosaurus* + higher Coelophysidae the lack of pleurocoelic foramina in dorsal vertebrae, this character is interpreted as an homoplasy.

On the other hand, *Ilokelesia* gen.nov. is plesiomorphic with respect to Abelisauroidea (NOVAS, 1989) in having: a) jugal process of postorbital perpendicular to horizontal branch, b) well-developed neural spines on cervical vertebrae, and c) cervical epipophyses lacking cranial projection.

In this way, the Ceratosauria is seen to be composed of two clearly distant clades (NOVAS, 1989, 1992; HOLTZ, 1994): the Coelophysoidea (HOLTZ, 1994) for *Dilophosaurus, Liliensternus* WELLES, 1984, and more derived forms (*sensu* ROWE & GAUTHIER, 1990) representing the oldest ceratosaurian theropods, and the Neoceratosauria, including *Ilokelesia* gen.nov. and *Ceratosaurus* as the successive sister groups of the Abelisauria, including the youngest record for the Ceratosauria, surviving into the Late Cretaceous.

MARTINEZ *et al.* (1986) described *Xenotarsosaurus bonapartei* MARTINEZ *et al.*, 1986 (UNPSJB-Pv-184 y 612), a medium-sized theropod from Bajo Barreal Formation (Lower Santonian), and assigned it to the family Abelisauridae. NOVAS (1989) proposed the presence of concave articular surface in the dorsal centra as an autapomorphy of *Xenotarsosaurus* MARTINEZ *et al.*, 1986, based upon a single cranial dorsal vertebrae. The caudal dorsal of *Ilokelesia* gen.nov. bears a similar condition, which could be interpreted as a synapomorphy of both genera. Also the presence of deep pre- and postspinal depressions in the only neural arches known of *Xenotarsosaurus*, is herein proposed as a synapomorphy of all the Neoceratosauria. At present, there is no available material for making comparisons between *Xenotarsosaurus* and *Ilokelesia* gen.nov., so the mutual affinities of both taxa remain unclear. Although we do not reject the validity of *Xenotarsosaurus* as a monophyletic taxon, its phylogenetic position not only among the Abelisauria but also among the Neoceratosauria is considered to be problematic (CORIA & RODRIGUEZ, 1993).

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ABBREVIATIONS

PVPH - Paleontología de Vertebrados, Museo "Carmen Funes" de Plaza Huincul, Neuquén, Argentina; MACN - Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MPCA - Museo Provincial "Carlos Ameghino" Cipolletti, Río Negro, Argentina; MUCPv-CH - Museo de la Universidad Nacional del Comahue, Paleontología de Vertebrados, colección Chocón, Argentina; PVL - Paleontología de Vertebrados, Instituto Lillo, Tucumán, Argentina. UNPSJB-Pv - Universidad Nacional de la Patagonia "San Juan Bosco", Paleontología de Vertebrados, Comodoro Rivadavia, Chubut, Argentina; USNM - United State National Museum, Smithsonian Institute, Washington DC, USA.

APPENDIX I

Diagnosis of taxa present in the cladogram of Figure13. Autapomorphies are not considered.

Ceratosauria GAUTHIER, 1986

1. Ventral groove in cranial caudal centra (ROWE & GAUTHIER, 1990)
2. Two pairs of pleurocoels in cervical vertebra (ROWE & GAUTHIER, 1990).
3. Dorsal vertebra with transverse processes strongly oriented backward and triangular in dorsal view (ROWE & GAUTHIER, 1990).
4. Pubis with fenestra below obturator foramen (ROWE & GAUTHIER, 1990).
5. Sacrum with transverse processes, ribs anc neural arche: fused to each another, and sacral ribs fused to ilia (ROWE & GAUTHIER, 1990).
6. Pubis, ischium and ileum fused to each another (ROWE & GAUTHIER, 1990).
7. Trochanteric shelf (ROWE & GAUTHIER, 1990).
8. Sulcus in base of crista tibio-fibularis (ROWE & GAUTHIER, 1990).
9. Astragalus and calcaneum fused to each other and to the tibia (ROWE & GAUTHIER, 1990).
10. Ascending process of astragalus vertically oriented (ROWE & GAUTHIER, 1990).
11. Distal tarsals II and III fused to metatarsals (ROWE & GAUTHIER, 1990).

Coelophysoidea HOLTZ, 1994

12. Presence of subnarial gap (ROWE & GAUTHIER, 1990).
13. Reduction of axial parapophyses (ROWE & GAUTHIER, 1990).
14. Absence of axial pleurocoels (ROWE & GAU- THIER, 1990).
15. Presence of alveolar ridge in maxilla (Higher Coelophysisdae, ROWE & GAUTHIER, 1990).

16. Absence of dorsal pleurocoels.

Neoceratosauria NOVAS, 1989

17. Axis with pleurocoels behind prezigapophyses; many foramina surrounding diapophyses (NOVAS, 1992).

18. Sacrum composed of seven vertebrae, with sacral 3, 4 and 5 strongly fused and transversally compressed (NOVAS, 1992).

19. Horizontal axis of ileum as long as femur (NOVAS, 1992).

20. Ulna less than 28 percent of femur length (NOVAS, 1992).

21. Manual phalanges strongly reduced (NOVAS, 1992).

22. Neural spines of cervical vertebrae antero- caudally reduced (NOVAS, 1992).

Abelisauria NOVAS, 1992

23. Dorsal surface of cervical neural arches clearly delimited from lateral surface of diapophyses. (BONAPARTE, 1996).

24. Cervical ribs with caudal process wide and flat.

25. Caudal vertebrae with transverse processes distally expanded.

26. Presence of deep pre-and postspinal depressions (Basins?).

Abelisauroidea NOVAS, 1989

27. Maxilla with ascending ramus subvertical, no contact with lacrymal (NOVAS, 1992).

28. Neural spines of cervical vertebrae strongly reduced (NOVAS, 1992).

29. Epipophyses axially extensive with cranial and caudal processes (NOVAS, 1992).

Abelisauridae BONAPARTE & NOVAS, 1985

30. Premaxilla antero-caudally short and dorso-ventrally high, with no caudal narial ramus (NOVAS, 1989).

31. Basioccipital deep below occipital condyle (NOVAS, 1989).

32. Atlas with enlarged epipophyses (NOVAS, 1989).

33. Maxillary fenestra partially visible in lateral view (NOVAS, 1989).

34. Subnarial fenestra between premaxilla and maxilla absent (NOVAS, 1989).

35. Antorbital fenestra with lateral and medial borders on the same level (NOVAS, 1989).

36. Dorsal surface of frontal separated from postorbital (NOVAS, 1989).

37. Cranial ramus of lacrymal virtually absent (NOVAS, 1989).

38. Lacrymal with no horn nor pneumatic foramina (NOVAS, 1989).

39. Lacrymal with ventral process dorso- ventrally shortened, convex cranial margin and sinuous caudal margin (NOVAS, 1989).

40. Postorbital slopes anteroventrally, with dorsal margin postero-ventrally inclined and caudal edge of ascending ramus cranially inclined (NOVAS,1989).

41. Postorbital with cranial edge deeply concave and ventral process antero- ventrally inclined, dividing orbital fenestra into two sectors (NOVAS,1989).

42. Quadrate lacking quadratic foramen and strongly fused to quadrate- jugal (NOVAS,1989).

43. Parietal with saggital crest transversally thickened caudally (NOVAS,1989).

44. Occipital crest transversally expanded (NOVAS,1989).

Noasauridae BONAPARTE & POWELL, 1980

45. Cervical neural arches low and craniocaudally elongated.

46. Square dorsal process in proximal articular surfaces of distal pedal phalanges.

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