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A new Abelisauridae (Dinosauria: Theropoda) from northwest Patagonia

Jorge O. CALVO[1], David RUBILAR-ROGERS[2,3] and Karen MORENO[4]

Abstract. A new theropod Abelisauridae is described, *Ekrixinatosaurus novasi* gen. et sp. nov., of northwestern Patagonia (Neuquén Province, Argentina). A preliminar cladistic analysis placed *Ekrixinatosaurus* together with *Majungatholus* and Carnotaurini; and the sister group is *Ilokelesia*. The presence of this specimen in Albian-Cenomanian beds allows us to support the early divergence (pre-Senonian) of this clade, and the hypothesis of the presence of Abelisauridae in continental Africa. The present distribution of Abelisauridae indicates: 1) a vicariance of this clade based on a pre-Cenomanian pan-Gondwanic distribution; 2) dispersion throughout terrestrial bridges. In both cases, the absence of Abelisauridae in continental Africa can be considered a bias of the fossil record.

Resumen. UN NUEVO ABELISAURIDAE (DINOSAURIA: THEROPODA) DEL NOROESTE DE LA PATAGONIA. Se describe un nuevo terópodo Abelisauridae, *Ekrixinatosaurus novasi* gen. et sp. nov., del noroeste de la Patagonia (provincia del Neuquén, Argentina). Un análisis cladístico preliminar ubica a *Ekrixinatosaurus* en un nodo junto a *Majungatholus* y Carnotaurini; y a *Ilokelesia* como grupo hermano. La presencia de este espécimen en capas del Albiano-Cenomaniano permite sustentar la divergencia temprana (pre-Senoniana) de este clado y la hipótesis de la presencia en Africa continental de Abelisauridae. La presente distribución de Abelisauridae puede reflejar: 1) una vicarianza de este clado a partir de una distribución pan-Gondwánica pre-Cenomaniana; 2) dispersión a través de puentes terrestres. En ambos casos, la ausencia de Abelisauridae en África continental puede considerarse un sesgo del registro fósil.

Key words. Dinosauria. Abelisauridae. Systematic. Phylogeny. Patagonia.

Palabras clave. Dinosauria. Abelisauridae, Sistemática. Filogenia. Patagonia.

Introduction

Abelisauridae a family of big Gondwanic predators very abundant during the Late Cretaceous. Both in diversity and in numbers of specimens, abelisaurids are the best documented theropod dinosaurs in South America (Novas, 1997). However, most of these fossils are known only from isolated fragmentary bones or partial skeletons. Until now, *Carnotaurus sastrei* (Bonaparte, 1985; Bonaparte *et al.*, 1990) and *Aucasaurus garridoi* (Coria *et al.*, 2002) are the most complete specimens of the family Abelisauridae. We describe a new Abelisauridae theropod, *Ekrixinatosaurus novasi* gen. et sp. nov. based on a partial skeleton found disarticulated and dispersed over 15 m^2. The present anatomical description focuses on the most novel information preserved in *Ekrixinatosaurus novasi*, including portions of the skeleton that are unknown, unpublished, or poorly preserved in other abelisaurs. The discovery occurred due to excavations for building a gas pipeline (Gasoducto del Pacífico Company) in Bajo del Añelo (figure 1), Neuquén Province, Argentina.

The known distribution of Abelisauridae members in South America, Madagascar and India have allowed to evaluate the hypothesis of a dispersion route between South America and the Indo - Madagascar plate through Antarctica by a terrestrial bridge (Kerguelen Plateau) during the late Cretaceous (Sampson *et al.*, 1998). This hypothesis is based on a divergence of the clade, posterior to the separation of Africa and South America. However, the recent report of an Abelisauridae maxilar in Cenonian-Turonian beds has changed the divergence of this clade toward the same continental break (Lamanna *et al.* 2002). According to these authors, this finding may show a pan-Gondwanic distribution of this family.

Abbreviation. MUCPv, Museo Universidad Nacional del Comahue, Paleovertebrados, Neuquén.

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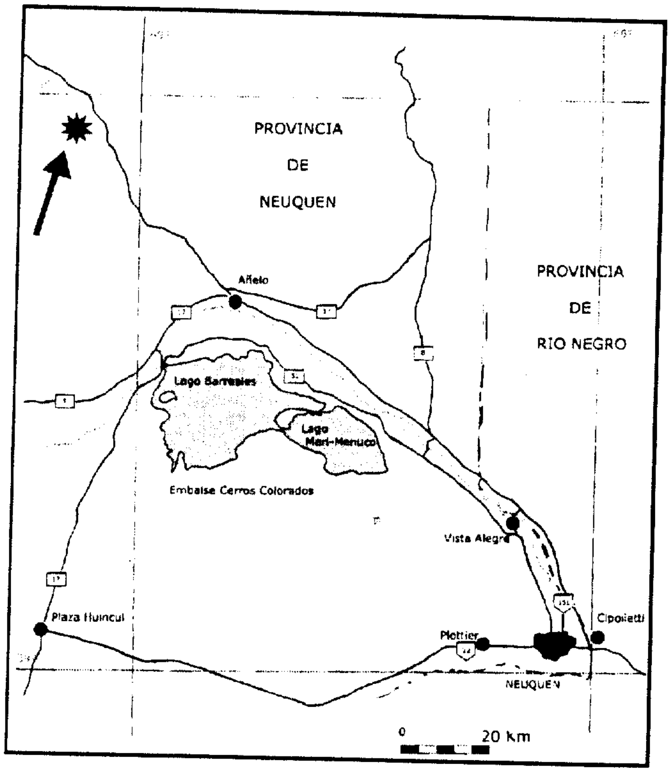

Figure 1. Map of Neuquén Province (northwest Patagonia) showing where *Ekrixinatosaurus novasi* was found / *Mapa de la provincia del Neuquén (noroeste de la Patagonia) mostrando la localidad de hallazgo de* Ekrixinatosaurus novasi.

Systematic paleontology

THEROPODA Marsh, 1881
NEOCERATOSAURIA Novas, 1992
ABELISAURIA Novas, 1992
ABELISAURIDAE Bonaparte and Novas 1985

Ekrixinatosaurus gen. nov.

Type species. *Ekrixinatosaurus novasi* sp. nov.

Etymology. From the Greek *Ekrixi*, meaning "explosion"; the Latin *nato*, meaning "born", referred to the fact that the fossil was discovered after its rocky tomb was dynamited; and the Greek *saurus*, meaning "reptile" or "lizard".
Diagnosis. As for the species.

Ekrixinatosaurus novasi sp. nov.
Figures 2, 3, 4, 5, 6, 7, 8

Holotype. MUCPv-294, a well preserved disarticulated skeleton with elements including: left and partial right maxillae; basicranium; both dentaries; teeth; cervical, a dorsal, sacral and caudal vertebrae; haemal arches; ribs; ilia, pubis and proximal ischia; left and distal end of right femur; left tibia; left astragalus and calcaneum; proximal end of left fibula and right tibia; metatarsals; phalanges; and a pedal ungual.
Etymology. *novasi*, in honor of Dr. Fernando Novas for his important contributions to the study of abelisaurid theropods.
Diagnosis. *Ekrixinatosaurus novasi* is a large abelisaur theropod, between 7 to 8 m of total length, distinguished by the following characters: presence of a fenestra between the postorbital and the anterior border of the frontal; protuberance directed backward on the contact between the parietals with the paraoccipital process. Cervical vertebrae cranio-caudally compressed; cervical neural spines as tall as the epipophyses; mid-posterior cervical centrum with ventral side flattened; two wide foramina in the mid-posterior cervicals; small preespinal depression with a pneumatic excavation connected to the neural canal in the middle-posterior cervicals; small pre-spinal lamina in mid-cervicals; tibia with a swelling at midshaft.
Locality. Approximately 34 km northwest of Añelo, Neuquén Province, northwestern Patagonia, Argentina (figure 1).

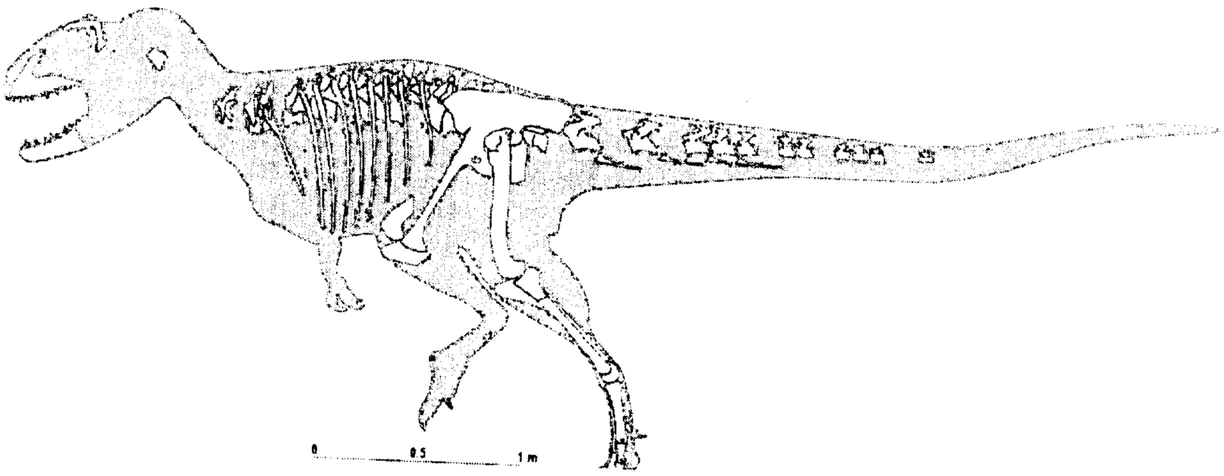

Figure 2. Skeletal reconstruction of *Ekrixinatosaurus novasi* gen. et sp. nov. Scale bar 1 m / *Reconstrucción del esqueleto de* Ekrixinatosaurus novasi *gen. et sp. nov. Escala 1 m.*

Horizon. The material comes from red beds belonging to the Candeleros Formation, Río Limay Group, Albian-Cenomanian ("Middle" Cretaceous) (Calvo, 1999). The Candeleros Formation has surrendered an assemblage of vertebrate remains: the theropod *Giganotosaurus* (Coria and Salgado, 1995), the sauropods *Rebbachisaurus* and *Andesaurus* as well as some titanosaurid remains, the crocodile *Araripesuchus*, a pipid frog, fragments of turtles, pterosaur tracks and a wide variety of dinosaur trackways (Calvo, 1991, 1999).

Description

Skull

The supraoccipital has a prominent posterior projection. The occipital crest is a relatively thin bone composed of the parietals and part of the squamosal. In posterior view the crest is convex and the parietal is horizontal. The paraoccipital process is not complete distally; however, it is subtriangular and directed ventroposteriorly. The occipital condyle and basioccipitals are missing. The parietals are fused to the frontals. There is a protuberance directed backward on the contact between the parietals with the paraoccipital process. The frontal is a wedge-shaped block with a flat dorsal surface. The median suture is fused and is a straight line. The anterior portion of the frontal is missing. The contact between frontal and postorbital is fused. Both participate on the anterior border of the supratemporal fenestra. The postorbital is incomplete, just its dorsal portion is preserved and part of the ventral process. The postorbital has a robust anterior projection that produces a fenestra between the postorbital and the anterior border of the frontal. The squamosal is small and triradiate. The anterior ramus is covered by the posterior projection of the postorbital. It is not possible to see if the squamosal participates in the supratemporal fenestra. The ventral projection has a subtriangular section. The posteroventral projection is small. The parasphenoid is a medial ossification that is widely fused to the ventral faces of the frontals. Ventrally this ossification is laminar.

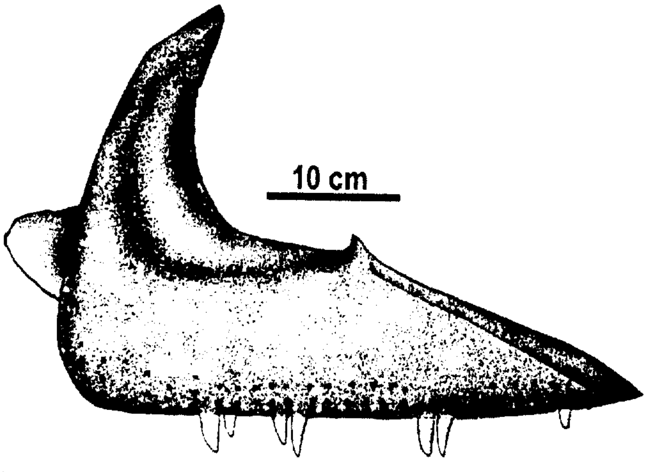

Figure 3. *Ekrixinatosaurus novasi*, left maxilla showing the ascendant subvertical ramus. Scale bar 10 cm / *Maxilar izquierdo mostrando la rama ascendente subvertical. Escala 10 cm.*

The maxilla is short (42 cm long) and high, with one dorsoventrally elongated maxillary fenestra located near the anterior border of the preorbital opening (figure 3). There are 16 alveoli, some with teeth. They are flattened laterally with anterior and posterior serrations.

Mandible. The dentary is short with a convex ventral border (figure 4). It is low and elongated anteroposteriorly. In lateral view it is curved with its distal end rounded. In medial view, the Meckelian groove is shallow anteriorly, becoming deeper and wider posteriorly. It extends near the lower border of the dentary. The posterior third of the dentary is vertically expanded. The interdental plates occupy half of the lingual surface from the first alveoli to the seventh, then becomes smaller posteriorly.

Postcranial skeleton

Vertebral column

Presacral vertebrae. Few presacral vertebrae are preserved in the holotype specimen MUCPv-294. There is a small, poorly preserved anterior cervical. The neural arch is partially preserved, just a small distal portion of the diapophysis and is directed backward. The centrum is opisthocoelous and longer than wide. In lateral view, the anterior face of the centrum makes a sharp angle with the anteroposterior plane, indicating the limits of the dorsoventral flexion of the neck. There are two small pleurocoels on the lateral side of the centrum (figure 5). The parapophysis is well developed. In ventral view there is a prominent hypapophysis that extends from the middle of the centra to the anterior border. In posterior view a large cavity that leads into the neural arch is exposed.

There is a complete mid-posterior cervical vertebrae (figure 5). The neural spine is low and broad, barely surpassing the level of the epipophysis. The neural arch has a small preespinal lamina, and small prespinal depressions. The epipophysis are well developed, posterolaterally oriented and with no cranial projections. In lateral view the diapophyseal lamina is reduced. The parapophysis are well developed. In anterior view the neural arch has two big pneumatic cavities above the neural channel. There is

Figure 4. *Ekrixinatosaurus novasi*, left dentary with the convex ventral border. Scale bar 10 cm / *dentario izquierdo con el borde ventral convexo. Escala 10 cm.*

a centroprezygapophyseal lamina that surrounds anteriorly a lateral depression. The postzygapophyses are large and directed obliquely and ventrally. In posterior view the wide depression behind the neural spine has two rather large fenestrae that lead into the neural arch.

A dorsal centrum is known and it is amphiplatyan. In anterior view, the articular face is circular and it is bigger than the posterior one. In lateral view there is a depression with a small pleurocoel placed anteriorly. The lateral side is convex dorsoventrally and concave anteroposteriorly.

Caudal vertebrae. Anterior caudal vertebra are large and robusts. The centra are amphicoelous. The lateral surface of the centra shows a slight depression. The ventral face of the transverse processes has a strong ridge that extends from the anterior portion of the centra to the distal end of the transverse process. In lateral view, the distal end of the transverse process extends beyond the posterior face of the centra. The thin laminar neural spine is directed backward. Middle and posterior caudals are also amphicoelous and their centra are longer than high. The transverse processes are directed backward and slightly upward. Middle caudals present fore and aft process on the distal end of the transverse processes (figure 6). Posteriorly, the caudals have horizontal transverse processes. The neural spine, placed posteriorly, is high, laterally compressed and directed backward. Both postzygapophyses and prezygapophyses are well developed.

Hindlimb

The left femur is complete (figure 7). The diaphysis is almost straight in posterior view, but in lateral view is slightly sigmoidal. The head is directed anteromedially at 45° with respect to the femur axis. The head is hemispherical, with the articular surface smooth. The anterior trochanter, partially preserved, projects anteriorly. The fourth trochanter is robust and prominent; its crest is directed posteromedially. At the distal end the condyles project posteriorly. The internal tibial condyle is larger and it is compressed laterally as are the external tibial and the fibular. The external tibial condyle is small. In medial view, at the distal end, there is a strong ridge that clearly separates the medial and anterior faces.

Tibia, astragalus and calcaneum. These three bones are fused. The left tibia (69 cm) is shorter and more slender than the femur. In anterior view the diaphysis is straight. The distal end is twisted 90° with respect to the proximal one. The cnemial crest is well developed, its internal border is convex and the external one is concave. The articulation for the femur has a lateral articular condyle bordered in posterior view by a sulcus. Distally the tibia is wider in order to accommodate the fused astragalus and calcaneum (figure 8). A suture is seen between the tibia and astragalus-calcaneum in anterior view, but none between astragalus and calcaneum. The ascending process of the astragalus is small (6 cm).

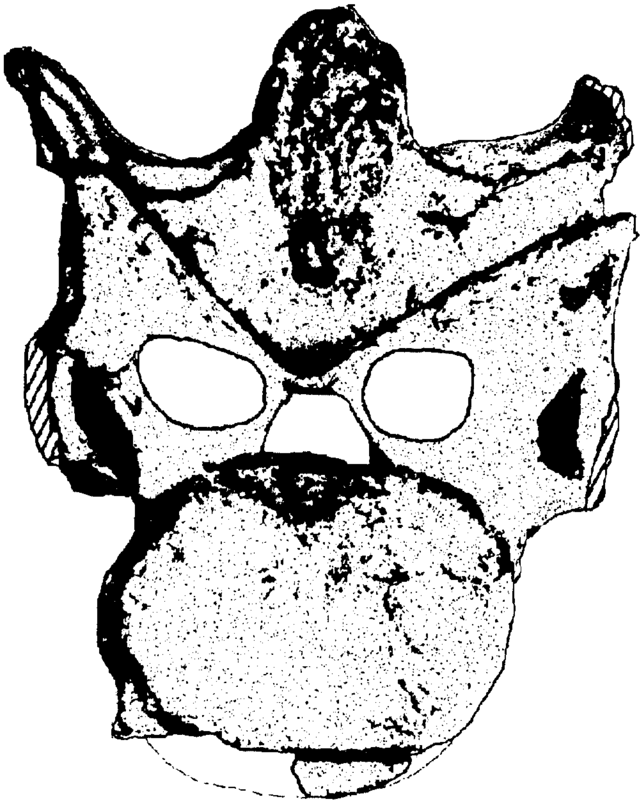

Figure 5. *Ekrixinatosaurus novasi*, mid-posterior cervical vertebra (in anterior view) showing the hypertrophied epipophyses and the height of the neural spine / *cervical media-posterior (en vista anterior) mostrando la epitrofisis hipertrofiada y la altura de la espina neural.*

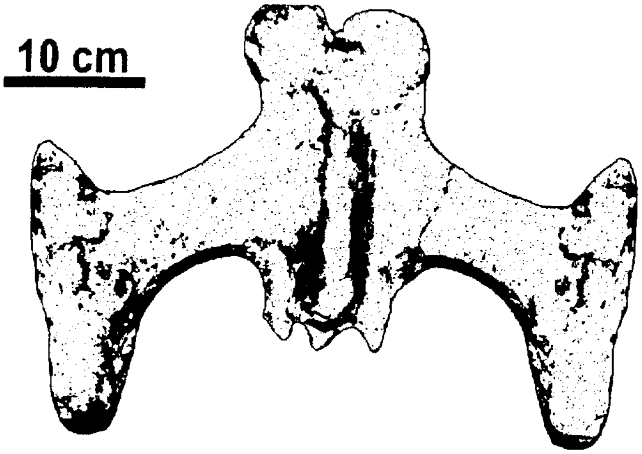

Figure 6. *Ekrixinatosaurus novasi*, mid-caudal in dorsal view showing the antero-posteriorly expanded distal end of the transverse processes. Scale bar 10 cm / *vértebra media-caudal en vista dorsal mostrando la expansión distal del proceso transverso. Escala 10 cm.*

Discussion and comparisons

The skull is estimated to be ~ 83 cm long based on comparison with *Carnotaurus* and *Majungatholus* (Bonaparte *et al.*, 1990; Sampson *et* al., 1998). Unfortunately, *Abelisaurus* does not have a complete maxilla but its preserved size is similar to *Ekrixinatosaurus*. On the other hand, the femoral length of *Ekrixinatosaurus* is 77 cm (figure 7), whereas that of *Carnotaurus* was estimated to be 103 cm. The *Ekrixinatosaurus* skull / femur length ratio is estimated to be 1.08 whereas in *Carnotaurus* it is believed to have been about 0.58 and *Ceratosaurus* = 1.00. *Ekrixinatosaurus* possesses a robust maxilla, with a subvertical ascending process and fused interdental plates, as in other members of Abelisauria. Based on the shape of the ascending process of the maxilla the preorbital opening is higher than long, similar to that present in *Carnotaurus*. The dentary is short with a convex ventral border as in other Abelisauridae and *Ceratosaurus* (figure 4). In the basicranium the supraoocipital has a prominent posterior projection as in *Carnotaurus*. The protuberance directed backward from the contact between the parietals with the paraoccipital process is an autapomorphy of *Ekrixinatosaurus*. The postorbital has an anterior robust projection that produces a fenestra between the postorbital and the anterior border of the frontal, this condition is not present in other members of the Abelisauridae (character present here as autapomorphy). A lateral projection of the postorbital is present as in *Abelisaurus*.

Ekrixinatosaurus has hypertrophied epipophyses and deep postspinal depressions as in Abelisauria (Novas, 1992). Unlike *Carnotaurus*, the posterior face of each anterior cervical centrum is strongly concave while the anterior surface is almost flat. In the mid-posterior cervicals the neural arch is relatively high with anteroposteriorly compressed neural spine, which is different than *Ilokelesia* (Coria and Salgado, 1998). Like in *Carnotaurus*, *Noasaurus*, *Ilokelesia* and *Aucasaurus* there is a lamina that connects the epipophysis with the prezygapophysis that separates the dorsal surface of the neural arch from the lateral surface. *Ilokelesia* has an autapomorphy, cervical vertebrae with poorly defined diapopostzygapofiseal laminae. This character is also present in *Ekrixinatosaurus*. It is probably a synapomorphy for Abelisauridae.

The anterior dorsal vertebrae are amphiplatyan. It shares with *Carnotaurus* the presence of pleurocoels in dorsals; this character is not present in *Ilokelesia*.

All preserved sacrals are fused to the sacral ribs and to the ilium as in adult Ceratosauria.

On caudal vertebrae the posterolaterally projecting transverse processes are inclined slightly dorsally, which is different than *Ilokelesia* where they are perpendicular to the dorsoventral axis of the vertebra, and to *Carnotaurus* where they are strongly inclined upward. Anterior caudals show wide transverse processes that are cranially expanded at the

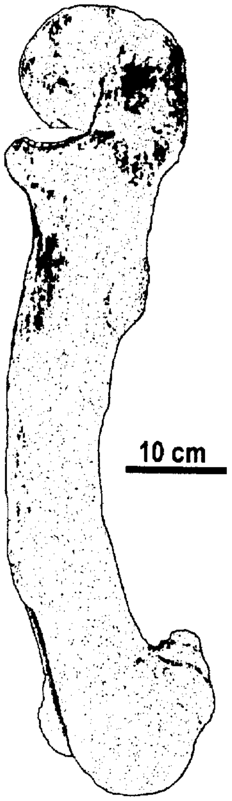

Figure 7. *Ekrixinatosaurus novasi*, left femur in lateral view. Scale bar 10 cm / *fémur izquierdo en vista lateral. Escala 10 cm.*

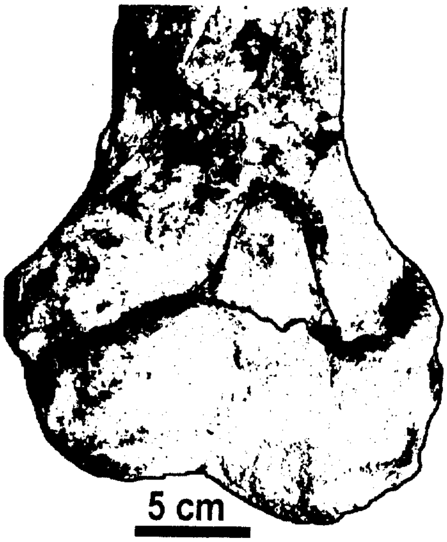

Figure 8. *Ekrixinatosaurus novasi*, co-ossified astragalus and calcaneum; note the short ascending process on the astragalus / *astrágalo coosificado y calcáneo; nótese el proceso ascendente corto en el astrágalo.*

distal end as in *Carnotaurus* (figure 6). In *Ekrixinatosaurus* the transverse processes are directed slightly upward and backward. The ventral side of each transverse process has a strong ridge along all its length. *Ekrixinatosaurus* is the first abelisaurid with posterior caudals that are known. These are amphicoelous and have laterally flattened subtriangular neural spines. As in *Carnotaurus* the distal end of the transverse process is expanded having a process directed anteriorly. *Ekrixinatosaurus* shares with *Ilokelesia* the fore and aft process on the distal end of the transverse processes in middle caudals: this character was defined as autapomorphic for *Ilokelesia*. However, we consider this character as a synapomorphy of the Abelisauridae. The distal edge of the caudal transverse processes is slightly concave in the middle in *Ilokelesia* and *Ekrixinatosaurus*. It has been considered an autapomorphy of *Ilokelesia*, but we interpret it as a synapomorphy of Abelisauridae.

The length of the ilium is close to that of the femur as in other members of the Neoceratosauria.As in all Ceratosauria the tibia, astragalous and calcaneous are fused.

Phylogenetic relationships

The phylogenetic relationships between *Ekrixinatosaurus* and the most complete members of Abelisauridae were evaluated in a preliminary cladistic analysis using some diagnostic characters (see appendix). *Ekrixinatosaurus* is more closely related to Carnotaurini (Coria *et al.*, 2002) than to Neoceratosauria. Thirteen binary characters were used. The matrix was analyzed using PAUP 4.0*b10 (Swofford, 2000) under heuristic search, and character-state transformations were evaluated under ACCTRAN optimization. This analysis produced two most parsimonious trees with a Tree Length of 14, Consistency Index of 0.9286 and Retention Index of 0.9375 (figure 9.A). Strict consensus tree generates a politomy among *Majungatholus*, *Ekrixinatosaurus* and *Carnotaurini*; however, *Ilokelesia* is placed as the sister group (figure 9.B).

Phylogenetic studies place abelisaurids within a big subdivision of Theropoda, the Ceratosauria (Gauthier, 1986; Rowe and Gauthier, 1990; Novas, 1991; Holtz, 1994). At least two principal groups are recognized within Ceratosauria: Coelophysoidea, (Upper Triassic and Lower Jurassic) which includes *Coelophysis* (Cope, 1889), *Syntarsus* (Raath, 1969) and *Dilophosaurus* (Welles, 1984) from North America, Europe and Africa; and Neoceratosauria (Upper Jurassic) which includes *Ceratosaurus* (Gilmore, 1920) from North America and *Elaphrosaurus* (Janensch, 1920, 1929) from Africa. In the Cretaceous the last Neoceratosauria is represented by abelisaurids living in Gondwanan sub-continents (South America, Madagascar and India).

Originally, Ceratosauria included Coelophysidae (*Dilophosaurus*, *Coelophysis* and *Syntarsus*) and *Ceratosaurus* (Rowe and Gauthier, 1990). Later, several authors recognized valid synapomorphies between Abelisauridae and *Ceratosaurus*, and the clade Neoceratosauria (Novas, 1992) was erected to include *Ceratosaurus*, Abelisauridae and *Noasaurus*. Subsequently *Elaphrosaurus* and *Ligabueino* have been included in a clade named Abelisauroidea (Bonaparte, 1991a, 1996; Holtz, 1994). However, the inclusion of *Elaphrosaurus* has been questioned (Holtz, 1994; Padian *et al.*, 1999), as well as the monophyly of this group (Rowe *et al.*, 1997; Padian *et al.*, 1999). Finally, some differences between *Noasaurus* and Abelisauridae (Bonaparte and Powell, 1980; Bonaparte and Novas, 1985) were recognized, and the name Abelisauria was erected by Novas (1992).

The family Abelisauridae (Bonaparte and Novas, 1985; Novas, 1997; Sampson *et al.*, 1998) is characterized by: middle and anterior cervicals with anterior process on each epipophysis; anteroposteriorly short and deep premaxilla; dorsoventrally deep snout at the level of the narial openings; frontals dorsoventrally thickened; posterior surface of the basioccipital wide and smooth below the occipital condyle; loose contacts among dentary, splenial and all theropod postdentary bones; premaxilla with reduced to absent palatal process; rostral process of the lacrimal strongly reduced or absent; lacrimal with pronunced suborbital process; broad lacrimal-postorbital con-

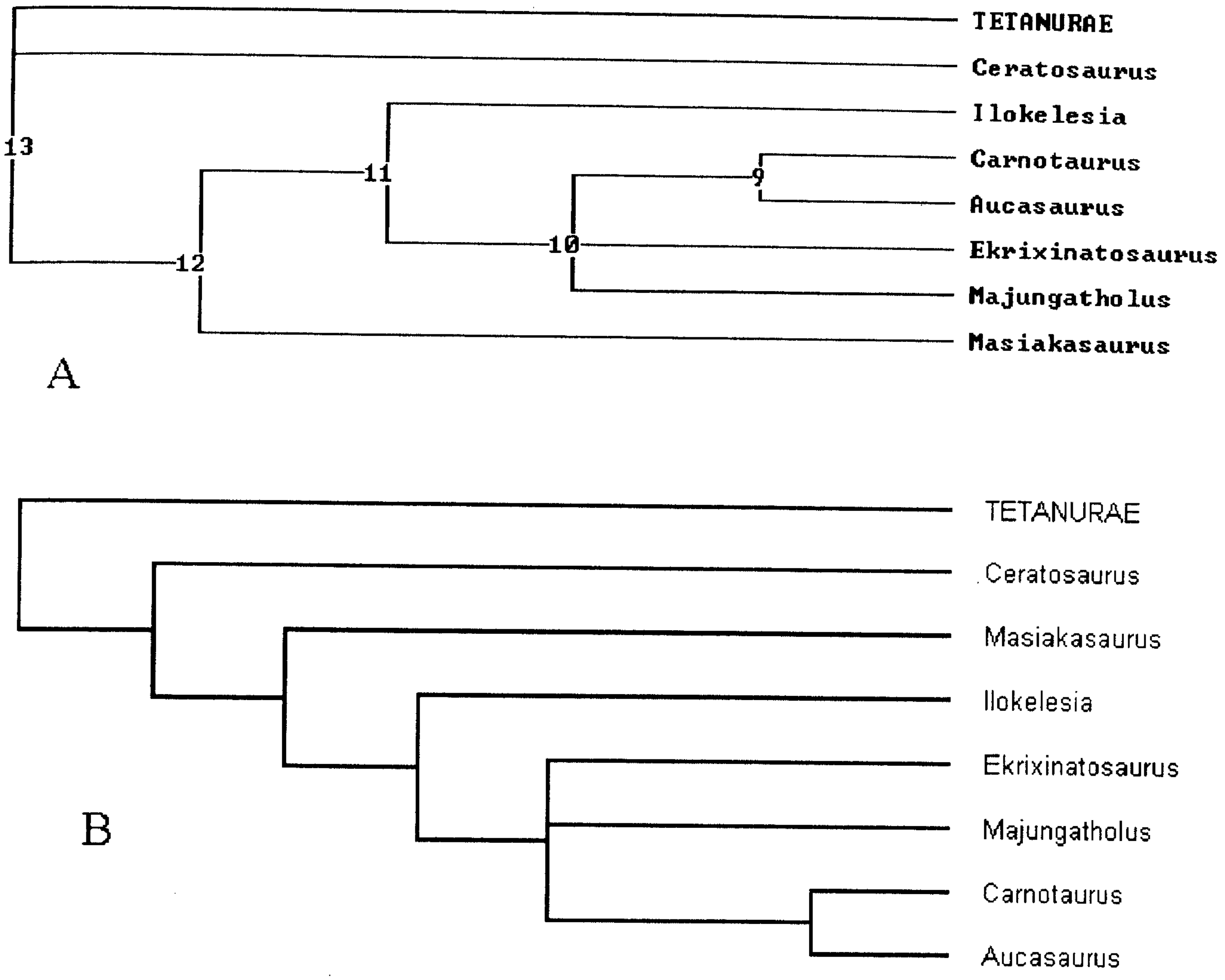

Figure 9. A, one of the two most parsimonious trees obtained in this study showing the phylogenetic relationships of *Ekrixinatosaurus novasi* gen. et sp. nov. The tree is based on 13 characters. TL = 14; CI = 0.9286; RI = 0.9375; RC = 0.8705. **B,** Strict consensus tree / *A, uno de los dos árboles más parsimoniosos que se obtuvieron en este estudio mostrando las relaciones filogenéticas de* Ekrixinatosaurus novasi *gen. et sp. nov. El árbol está basado en 13 caracteres. TL = 14; CI = 0.9286; RI = 0.9375; RC = 0.8705.* ***B,*** *Árbol de consenso estricto.*

tact; long axis of postorbital oriented rostroventral-caudodorsal; postorbital with a pronounced suborbital process. We add: neural spine in posterior cervicals lower than epipophyses, and large transverse processes with fore and aft extensions on the distal end of the middle and posterior caudals, recognized by Coria *et al.* (2002) as an autopomorphy of *Aucasaurus garridoi*.

Fossil record and distribution of abelisaurids

The fossil record of abelisaurids includes *Ligabueino andesi* (Bonaparte, 1996) from the Lower Cretaceous of South America, *Xenotarsosaurus bonapartei* (Martínez *et al.*, 1986), *Ilokelesia aguadagrandensis* (Coria and Salgado, 1998) and *Ekrixinatosaurus novasi* from the "Middle" Cretaceous of South America; *Noasaurus leali* (Bonaparte and Powell, 1980), *Abelisaurus comahuensis* (Bonaparte and Novas, 1985), *Carnotaurus sastrei* (Bonaparte, 1985; Bonaparte *et al.*, 1990), *Velocisaurus unicus* (Bonaparte, 1991b), *Aucasaurus garridoi* (Coria *et al.*, 2002), *Indosuchus raptorius* (Huene and Matley, 1933), *Indosaurus matleyi* (Huene and Matley, 1933), *Majungatholus atopus* and *Masiakasaurus knopfleri* (Sampson *et al.*, 1998; 2001) from the Upper Cretaceous of South America, India and Madagascar.

The fossil record of abelisaurids in continental Africa (Russell, 1996) has been controversial (Sampson *et al.*, 1998). Sampson *et al.* (1998) proposed that the origins of Abelisauridae occurred after the isolation of Africa; therefore, the present distribution of this clade is the result of dispersion between the

Indo-Madagascan province and South America through continental links that persisted until the Late Cretaceous. According to this hypothesis, abelisaurids never existed in continental Africa. On the other hand, Lamanna *et al.* (2002) report an Abelisauridae maxilla from the early Late Cretaceous (middle Cenomanian-Turonian) deposits, extended the origin of this family to pre-Senonian (Coniacian-Maastrichtian) times. These authors suggest that the known occurrence of Abelisauridae may reflect a former pan-Gondwanan distribution. The discovery of *Ekrixinatosaurus* in the Candeleros Formation (Albian-Cenomanian) is consistent with this hypothesis. Nevertheless, an additional scenario is that Abelisauridae entered continental Africa via a landbridge, between NE Brazil and Nigeria-Cameroon, before the major continental fragmentation of the Cenomanian-Turonian. This hypothesis is based on the strong faunal similarity of the Albian-Cenomanian fossil assemblage found in Patagonia represented by carcharodontosaurid theropods (Coria and Salgado, 1995; Sereno *et al.*, 1996), Diplodocimorpha, Titanosauria, and Titanosauridae sauropods; and those recorded in northwestern continental Africa (Calvo, 1999).

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Appendix

List of 13 character and character status of Neotheropoda used for cladistic analysis (table 1). character codes: 0, primitive; 1, derived; ? missing or uncertain. Some sources for the character analysis are: Coria *et al.* 2002; Coria and Salgado, 1998; Gauthier, 1986; Novas, 1991; 1992; Sampson *et al.*, 1998; Carrano *et al.*, 2002.

Cranium

1) Maxilla-jugal contact posteroventral directed: 0, absent; 1, present.
2) Subvertical ascendent ramus of the maxilla: 0, absent; 1, present.
3) Ventral convex border of dentary: 0, absent; 1, present.
4) Skull, external sculpturing: 0, absent; 1, present.
5) Frontals and parietals: 0, unfused, 1, fused.
6) maxilla-jugal contact: 0, short; 1, long, broad.
7) ventral process of postorbital: 0, ventrally; 1, o cranioventrally projected.
8) Intraorbital projection of ventral process of postorbital: 0, absent; 1, present.

Postcranium

9) Cranial process of cervical epipophyses: 0, absent; 1, present.
10) Hypertrophied epipophysis: 0, absent; 1, present.
11) High of neural spine in cervicals: 0, considerably higher than epipophysis; 1, lower or equal than epipophysis.
12) Dorsal surface of cervical neural arches clearly delimited from lateral surface of diapophyses: 0, absent; 1, present.
13) Transverse processes of caudal vertebrae: 0, unexpanded or 1, expanded anteroposteriorly at ends

Table 1. Data matrix for the distribution of the 13 characters listed above among the 8 taxa considered / *Matriz de platos para la distribución de 13 caracteres para los 8 taxones considerados.*

Taxon					5					10			
TETANURAE	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratosaurus	1	0	1	0	0	0	0	0	0	0	0	0	0
Ilokelesia	?	?	?	?	?	?	0	1	0	1	1	1	1
Carnotaurus	1	1	1	1	1	1	1	1	1	1	1	1	1
Ekrixinatosaurus	1	1	1	1	1	?	1	1	0	1	1	1	1
Majungatholus	1	1	1	1	1	1	1	1	0	1	1	1	?
Masiakasaurus	?	?	0	0	?	?	?	?	0	1	1	0	0
Aucasaurus	1	1	1	1	1	1	?	?	1	1	1	1	1