

## Abelisaurid remains (Theropoda, Ceratosauria) from southern Patagonia

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**Abstract.** Here we report the discovery of abelisaurid remains from the Bajo Barreal Formation (Cenomanian-Coniacian) from the northern region of Santa Cruz Province, Patagonia, Argentina. The specimen represents the southernmost record of Abelisauridae in South America. It consists of six associated vertebrae, including cervical 10, dorsal 1, an isolated dorsal centrum, and three caudals from the middle portion of the tail. The vertebrae closely resemble those of other derived abelisaurids (e.g., *Carnotaurus sastrei* Bonaparte, *Aucasaurus garridoi* Coria *et al.*). For example, the cervicals have deep pre- and postspinal cavities, hypertrophied epipophyses, and a dorsal surface of the neural arch that is clearly delimited from the lateral surface of the diapophysis. Caudal vertebrae exhibit the characteristically fan-shaped transverse processes seen in other abelisaurids. However, some morphological distinctions are recognized when compared with *Ilokelesia*, *Xenotarsosaurus*, *Carnotaurus*, *Aucasaurus* and *Majungatholus*. The list of potential synapomorphies of the vertebral column of Abelisauria and Abelisauridae is briefly reviewed. Recent phylogenetic hypotheses on Abelisauridae are discussed.

**Resumen.** RESTOS DE ABELISÁURIDOS (THEROPODA, CERATOSAURIA) DEL SUR DE PATAGONIA. Se informa del hallazgo de restos de un abelisáurido de la Formación Bajo Barreal (Cenomaniano-Coniaciano), del norte de la provincia de Santa Cruz, Patagonia Argentina. Este ejemplar representa el registro más austral de Abelisauridae en América del Sur y consiste en seis vértebras asociadas, incluyendo la cervical 10, la dorsal 1, un centro dorsal aislado y tres caudales de la porción media de la cola. Las vértebras son muy semejantes a las de otros abelisáuridos derivados (*Carnotaurus sastrei* Bonaparte, *Aucasaurus garridoi* Coria *et al.*). Por ejemplo las cervicales tienen profundas cavidades pre- y postespinales, epipófisis hipertrofiadas y la superficie dorsal del arco neural que está claramente delimitada de la superficie lateral de la diapófisis. Las vértebras caudales tienen los característicos procesos transversos en forma de abanico presentes en otros abelisáuridos. Sin embargo se reconocen algunas diferencias morfológicas con *Ilokelesia*, *Xenotarsosaurus*, *Carnotaurus*, *Aucasaurus* y *Majungatholus*. Se examina brevemente la lista de potenciales sinapomorfías de Abelisauria y Abelisauridae y se discuten recientes hipótesis filogenéticas de Abelisauridae.

**Key words.** Abelisauridae. Bajo Barreal Formation. Late Cretaceous. Patagonia. Phylogeny.

**Palabras clave.** Abelisauridae. Formación Bajo Barreal. Cretácico Tardío. Patagonia. Filogenia.

### Introduction

Abelisauridae is a group of Late Cretaceous Gondwanan theropods, formed by *Abelisaurus comahuensis* Bonaparte and Novas (1985), *Carnotaurus sastrei* Bonaparte (1985) and all of their descendants (Novas, 1997). Remains of these animals were found in South America (Bonaparte, 1996; Bonaparte and Novas, 1985; Bonaparte *et al.*, 1990; Coria and Salgado, 2000; Coria *et al.*, 2002; Lamanna *et al.*, 2002; Martínez *et al.*, 1986; Novas and Bandyopadhyay,

1999; Kellner and Campos, 2002), Madagascar (Sampson *et al.*, 1998; Carrano *et al.*, 2002), India (Chatterjee, 1978; Novas and Bandyopadhyay, 1999, 2001), and possibly Africa (Russell, 1996), and Europe (Carrano *et al.*, 2002).

The abelisaurid findings in Argentina come from different Cretaceous units of the provinces of Neuquén, Río Negro and Chubut. Here, we amplify the geographic distribution of this prolific group of theropods with a new record of an abelisaurid from Santa Cruz, a province from the far south of Patagonia (figure 1). The new specimen comes from levels of the Cenomanian-Coniacian Bajo Barreal Formation, widely exposed in the southeastern corner of Chubut and northeastern region of Santa Cruz (Proserpio *et al.*, 1985; H. Pezzuchi, pers. comm.) This finding enlarges the list of theropod specimens documented in the Bajo Barreal Fm., which includes abelisaurids (e.g., *Xenotarsosaurus bonapartei* Martínez

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**Figure 1.** Map of Argentina and Santa Cruz indicating the fossil locality / Mapa de Argentina y Santa Cruz indicando la localidad del hallazgo.

*et al.*, 1986) and an isolated carnosaurine maxilla (Martínez *et al.*, 1986; Lamanna *et al.*, 2002), and varied tetanurans, including a large theropod with hypertrophied ungual phalanges resembling *Megaraptor namunhuaiquii* Novas (1998), and a small basal coelurosaur currently under study (Martínez and Novas, 1997). Thus, the new discovery contributes to a better knowledge of the taxonomic diversity at the time of deposition of the Bajo Barreal Fm., that is, during Cenomanian through Coniacian times (Bridge *et al.*, 2000).

## Material

The following comparative materials were used in this study: *Aucasaurus garridoi* Coria *et al.* MCF-PVPH 236 (Río Colorado Fm., Campanian, NW Patagonia; Coria *et al.*, 2002); *Carnotaurus sastrei* Bonaparte MACN-CH 894 (La Colonia Fm., Maastrichtian, Central Patagonia; Bonaparte *et al.*, 1990; Ardolino and Delpino, 1987); *Ilokelesia aguadagrandensis* Coria and Salgado MCF-PVPH 35 (Huincul Fm., Albion-Cenomanian; NW Patagonia; Coria and Salgado, 2000); *Majungatholus athopus* Sampson *et al.* FMNH PR 2100 and UA 8678

(Maevarano Fm., Campanian-Maastrichtian, Madagascar; Sampson *et al.*, 1998); *Noasaurus leali* Bonaparte and Powell PVL 4061 (Lecho Fm., Maastrichtian; NW Argentina; Bonaparte and Powell, 1980); *Xenotarsosaurus bonapartei* Martínez *et al.* UNPSJB-PV 184 and 612 (Bajo Barreal Fm., Cenomanian; Martínez *et al.*, 1986). Anatomical details on the Brazilian abelisaurid *Pycnonemosaurus nevesi* Kellner and Campos are based on published data (Kellner and Campos, 2002).

**Abbreviations.** MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; MPM, Museo Padre Manuel Molina, Río Gallegos, Provincia de Santa Cruz, Argentina; FMNH, Field Museum of Natural History, Chicago; PVL, Paleontología Vertebrados, Instituto Miguel Lillo, Tucumán; MCF-PVPH, Museo Carmen Funes, Paleontología Vertebrados, Plaza Huincul; MUCPV-CH, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén; UA, Université d’Antananarivo, Antananarivo; UNPSJB-PV, Vertebrate Paleontology, Universidad Nacional de la Patagonia “San Juan Bosco”, Comodoro Rivadavia, Chubut.

## Systematic paleontology

THEROPODA Marsh, 1881

NEOCERATOSAURIA Novas, 1991

ABELISAURIA Novas, 1992

ABELISAUROIDEA Bonaparte, 1991

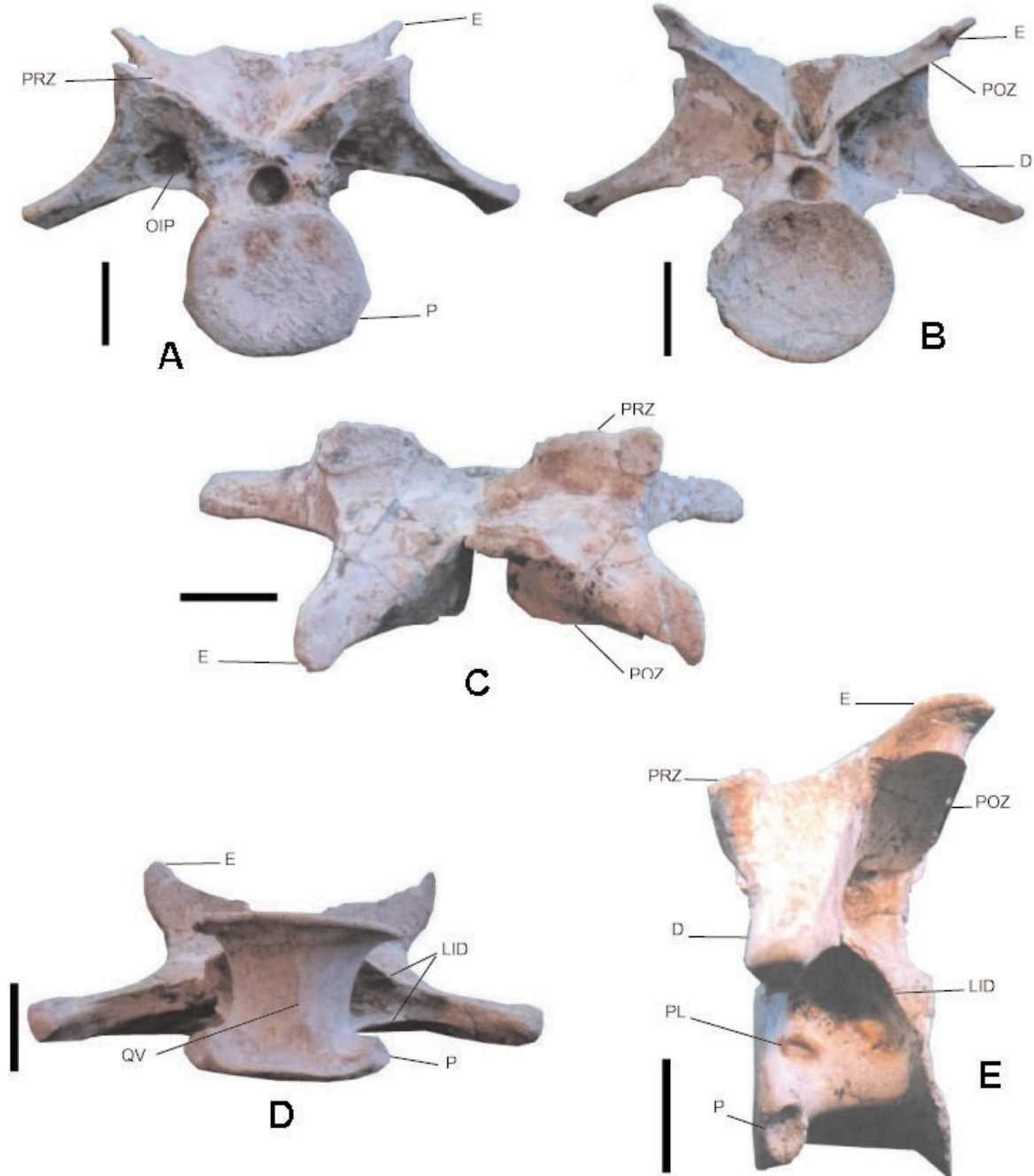
ABELISAURIDAE Bonaparte and Novas, 1985

Abelisauridae indet.

Figures 2-4

**Specimen.** MPM-99, including tenth cervical vertebra, first dorsal vertebra, an isolated dorsal vertebral centrum, and three caudal vertebrae from the mid-section of the tail. The materials were collected in February, 1999 by a joint expedition carried out by the Laboratorio de Paleovertebrados of UNPSJB (Comodoro Rivadavia) and MACN (Buenos Aires).

**Horizon and locality.** Bajo Barreal Fm. (Cenomanian-Coniacian; Bridge *et al.*, 2000), Cañadón de los Corrales, near the “María Fermina” Estancia, 100 km southwest of the town of Las Heras, Santa Cruz Province (figure 1). Radiometric dates support an age range between 95.8 through 91 Ma for the Bajo Barreal Fm. (Bridge *et al.*, 2000), thus corresponding to mid-Cenomanian through early Coniacian (Haq and Van Eysinga, 1994). See Lamanna *et al.* (2002) for an up-to-date review of the faunal content of the Bajo Barreal Fm.

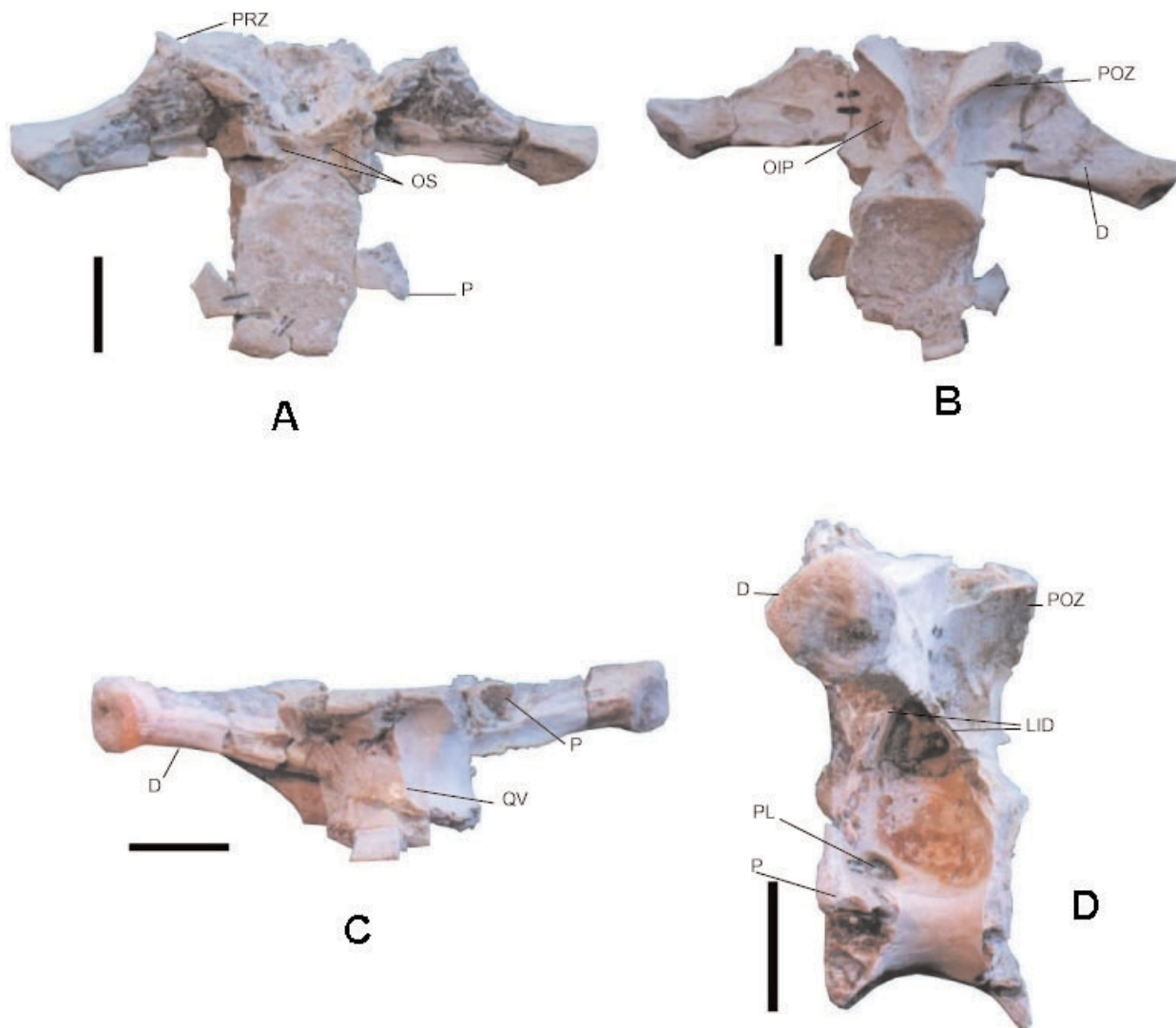


**Figure 2.** MPM 99. Cervical 10. **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral, and **E**, lateral views. Abbreviations: D, diapophyses; E, epipophyses; LID, infradiapophyseal lamina; OIP, infraprezygapophyseal foramen; P, parapophysis; PL, pleurocoel; POZ, postzygapophysis; PRZ, prezygapophysis; QV, ventral keel. Scale 5 cm / MPM 99. Cervical 10. Vistas **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral y **E**, lateral. Abreviaturas: D, diapófisis; E, epipófisis; LID, lámina infradiapofiseal; OIP, foramen infraprezigapofiseal; P, parapófisis; PL, pleurocelo; POZ, postzigapófisis; PRZ, prezigapófisis; QV, quilla ventral. Escala 5 cm.

## Description

**Tenth cervical.** This vertebra (figure 2) is well preserved, lacking only the neural spine. The centrum is slightly keeled ventrally. The articular surfaces are subcircular in shape, being transversely wider than dorsoventrally deep. The cranial articular surface is almost flat whereas the caudal one is slightly concave. The parapophyses are ventrolaterally located

and bear wide articular facets for the cervical ribs. The centrum is deeply excavated laterally, especially on its dorsal half. On the ventral portion of this excavation exist two small pleurocoels, the anterior one larger. The neural arch bears deep pre- and post-spinal cavities. The prezygapophyses are well separated from the axial plane, and their articular surfaces are subrectangular in shape and medially inclined at an angle of 40° with respect to the vertical



**Figure 3.** MPM 99. Dorsal 1. **A**, anterior; **B**, posterior; **C**, ventral and **D**, lateral views. Abbreviations: LID, infradiapophyseal lamina; OS, supraneural foramina. Scale 5 cm / MPM 99. Dorsal 1. Vistas **A**, anterior; **B**, posterior; **C**, ventral y **D**, lateral. Abreviaturas: LID, lámina infradiapofiseal; OS, foramen supraneural. Escala 5 cm.

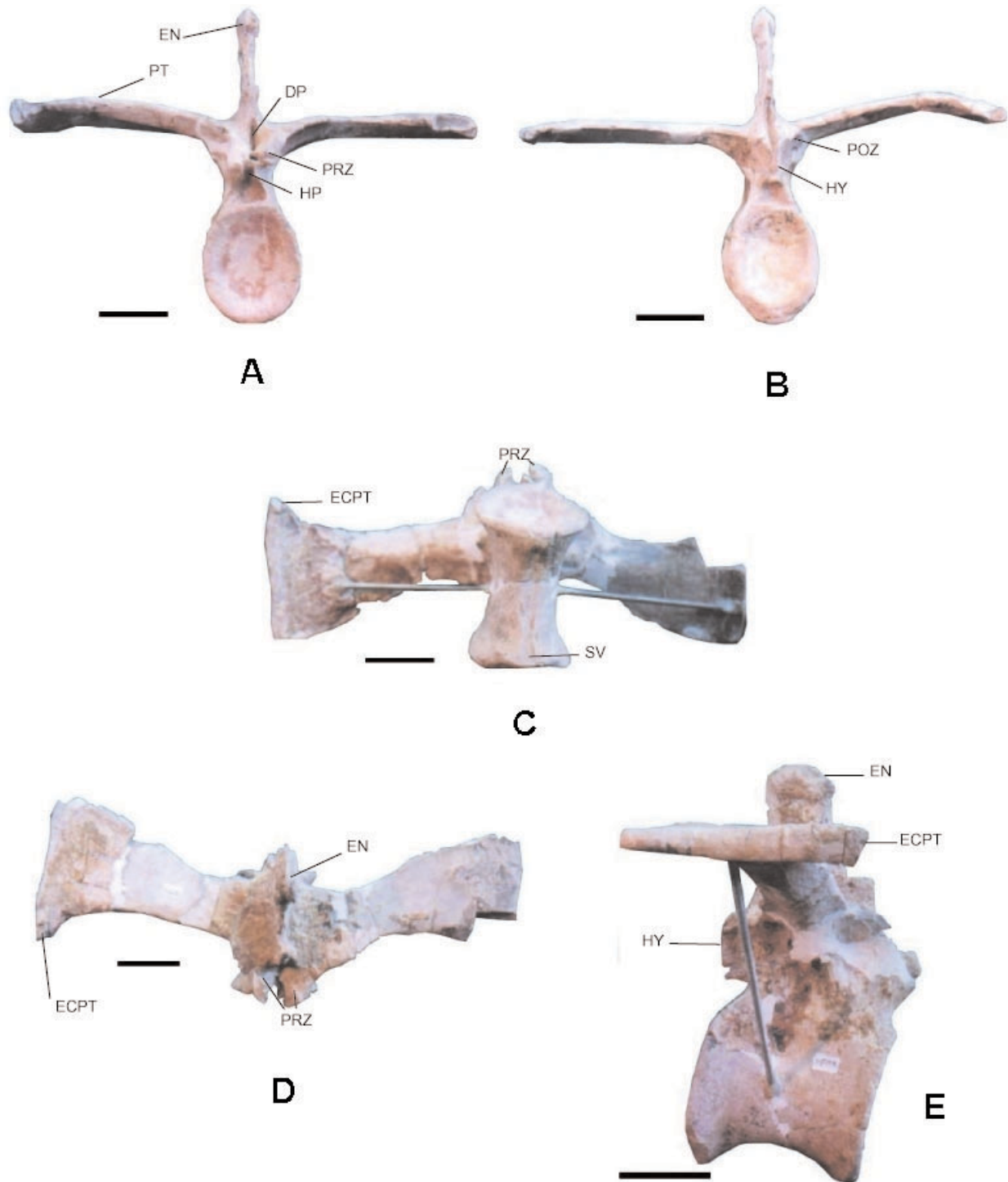
plane. The diapophyses are ventrally inclined and subtriangular in cross-section.

In cranial view a small cavity opens anterolaterally between the prezygapophysis and the base of the diapophyses. The diapophyses possess a pair of ventral buttresses, one projected toward the cranial articular surface of centrum, and another, larger one, projected toward the caudal articular surface. This pair of infradiapophyseal buttresses bounds a deep and subtriangular depression, in the ceiling of which opens a rounded pneumatic foramen. Caudal to the diapophyses and ventral to the postzygapophysis, there exists a rounded cavity above which opens a small pneumatic foramen. The postzygapophyses have subrectangular, ventrolaterally oriented articular facets. Above them emerge the hypertrophied, transversally thick, and rounded epipophyses, which

are laterally and caudally projected. In MPM 99, however, the epipophyses are more laterally inclined than in *Carnotaurus*, and they are not so deep as in the latter taxon. Between the postzygapophyses and the base of the neural spine there exists a narrow but deep excavation. The neural canal is bounded by a pair of small, vertical struts that connect the base of the postzygapophyses with the vertebral centrum.

**First dorsal.** This vertebra (figure 3) affords additional information on an element that is incomplete in *Carnotaurus sastrei* (in which dorsal 1 lacks most of the original surfaces of the base of the neural arch, transverse processes, and neural spine). In MPM 99, this vertebra has the centrum with both articular surfaces damaged and the neural spine is lost. The centrum is craniocaudally short. The cranial articular surface is almost flat whereas the caudal one is slight-





**Figure 4.** MPM 99. Caudal vertebra. **A**, anterior; **B**, posterior; **C**, ventral; **D**, dorsal and **E**, lateral views. Abbreviations: ECPT, cranial projection of the transverse process; EN, neural spine; HP, hypantrum; HY, hyposphene; PT, transverse process; DP, prespinal depression. Scale 5 cm / MPM 99. Caudal vertebra. Vistas **A**, anterior; **B**, posterior; **C**, ventral; **D**, dorsal y **E**, lateral. Abreviaturas: ECPT, proyección craneal del proceso transverso; EN, espina neural; HP, hypantrum; HY, hyposphene; PT, proceso transverso; DP, depresión preespinal. Escala 5 cm.

ly concave. The lateral surface is widely excavated, bearing a pair of small pleurocoels. The parapophyses are located in a slightly more dorsal position than in cervical 10. The neural arch bears wide pre- and

post-spinal cavities. Two small, circular depressions exist on the cranial face of the base of the neural arch, immediately dorsal to the neural canal. The diapophyses project subhorizontally outward; they are

robust and subtriangular in cross-section. On the cranial surface of each diapophysis there is a narrow slot, which opens laterally. The cranioventral surface of the diapophysis is deeply grooved. Below the diapophyses develop a pair of infradiapophysial laminae, which delimit a deep triangular cavity. The prezygapophyses are widely separated and inclined toward the axial plane of the vertebra at an angle of approximately 45°. The articular surface of the postzygapophyses is wide and ventrolaterally oriented. Between the postzygapophysis and the caudal infradiapophyseal lamina opens a large elliptical depression, the major axis of which is dorsoventrally oriented. Above the neural canal there is a pair of small and shallow triangular depressions.

Because this vertebra has broken portions, it becomes evident that both the centrum and neural arch have the complex camellate internal structure of pneumatic vertebrae, characterized by the presence of numerous small spaces (Britt, 1993).

**Mid-dorsal vertebra.** This vertebra is represented by a badly preserved centrum, which resembles the dorsal vertebrae of *Carnotaurus*.

**Caudal vertebrae.** Three caudal vertebrae are preserved (figure 4). The morphology of the most proximal caudal suggests that it may correspond to caudal 8 or 9. Its centrum is elongate, slightly amphicoelous, and ventrally grooved. The caudal articular surface is ventrally expanded, thus defining a pair of modest facets for articulation with the haemal arch. The prezygapophyses are proportionally small and steeply medially inclined; well-developed hypantrum facets exist below the prezygapophyses. A deep pre-spinal fossa exists at the base of the neural spine. The transverse processes are elongate and caudodorsally projected, surpassing the caudal extent of the postzygapophyses. The distal extremity of the transverse processes is fan-shaped. There is a shallow depression at the base of the transverse process, close to the prezygapophyses. In ventral view the transverse processes exhibit a wide longitudinal buttress running along most of the length. The preserved portion of the neural spine indicates that the spine was axially elongate and transversely compressed.

Two other caudals may correspond to the mid-section of the tail. The best preserved one exhibits transverse processes that are more perpendicularly projected with respect to the axial plane than in more proximal caudals. Also, a robust buttress runs along the ventral surface of the transverse process. The extremities of the transverse processes are expanded, reaching a craniocaudal diameter that is 2.5 times larger than the diameter taken at its base. However, the smallest craniocaudal diameter of the process is at its mid-length. On the distal end of the right transverse

process is preserved the base of a cranially pointed process, similar to that seen in other abelisaurids (e.g., *Carnotaurus*, *Aucasaurus*, *Ilokelesia*, *Pycnonemosaurus*). The neural spine is low and laminar, with delicate pre-spinal and post-spinal laminae. Between the prezygapophyses and the base of the neural spine exists a dorsoventrally deep depression, and a deep and elongate excavation is present between the postspinal lamina and the postzygapophyses.

## Comparisons

Cervical, dorsal, and caudal vertebrae were described to some extent for the abelisaurids *Carnotaurus*, *Aucasaurus*, *Ilokelesia*, *Majungatholus*, *Pycnonemosaurus*, *Noasaurus*, *Masiakasaurus* (Sampson *et al.* 2001), and *Laevisuchus* (Huene and Matley, 1933). However, as one of the most complete known abelisaurids, only *Carnotaurus sastrei* was illustrated and described at length (Bonaparte *et al.*, 1990). Specimens corresponding to *Ilokelesia*, *Noasaurus*, *Masiakasaurus*, and *Laevisuchus* preserve some elements of the vertebral column, but unfortunately they are not homologous with these of MPM 99. Besides, the available dorsal 2 of *Xenotarsosaurus* (coming from the same sedimentary unit as MPM 99) is so badly damaged that comparisons become difficult.

The resemblances that MPM 99 shows with *Carnotaurus sastrei* are remarkable, and they extend to cervical, dorsal, and caudal vertebrae. Outstanding similarities include, for example: presence of well developed epipophyses on posterior cervicals, posterior cervicals and anterior dorsal vertebrae ("pectorals") with deep and transversely expanded neural arches, and mid-caudal vertebrae with fan-shaped transverse processes. The following differences, however, are observed between MPM 99 and *Carnotaurus sastrei*: in the new specimen the epipophyses of cervical 10 exhibit a caudal prong, absent in *Carnotaurus*; the postzygapophyses occupy a more horizontal position, and their respective epipophyses project more laterally than dorsally, in contrast with *Carnotaurus* in which these elements are more vertically placed. In MPM 99 the triangular cavity that exists below the diapophyses of cervical 10 is not as wide as in *Carnotaurus*.

Some variations in the degree of opisthocoely are seen by comparing homologous posterior cervicals and first dorsals in abelisaurids: in *Carnotaurus* they are slightly opisthocoelous, while in MPM 99 the cranial articular surface is almost flat. In contrast, the centrum of dorsal 2 of *Xenotarsosaurus* is cranially concave.

Cervical 10 of *Majungatholus* differs from that of

MPM-99 in that the centrum has articular surfaces that are deeper than wide, the triangular cavity that exists below the diapophyses is considerably wide but shallow in its dorsal half, and the posterior pleurocoel is poorly developed. Also, in *Majungatholus* the neural arch of cervical 10 is characterized by the presence of a depression on the anterior surface of the diapophyses, as well as by a lesser development of the epipophyses and by the presence of an accessory foramen inside the infrapostzygapophyseal depressions. Notably, epipophyses of cervical 10 of MPM 99 looks more derived than any other known abelisauroid in having a prominent caudal prong, which is absent in the last cervical of *Majungatholus*.

Concerning the caudal vertebrae of MPM 99, they resemble those of *Carnotaurus* (e.g., the six proximal caudals known) in that the transverse processes are distally expanded, in the presence of notable cranial projections on the distal extremity of the transverse processes, and in the presence of hyposphene-hypantrium articulations. In *Majungatholus*, instead, the transverse processes are not distally expanded.

## Discussion

Three topics concerning the vertebral material described above require consideration: 1) How does the new specimen relate to the abelisaurids already recorded in the Bajo Barreal Formation? 2) Which vertebral traits may be interpreted as synapomorphic of Abelisauridae and Abelisauroidea? 3) How might vertebral characters affect the phylogenetic hypotheses recently proposed for Abelisauria?

### *Abelisaurids recorded in the Bajo Barreal Formation*

Abelisaurid materials at present recorded in this unit consist of the holotype of *Xenotarsosaurus bonapartei* (UNPSJB-PV 184 and 612; Martínez *et al.*, 1986), an isolated maxilla referred as to Carnotaurini (UNPSJB-PV247; Lamanna *et al.*, 2002), and the vertebral remains described here. Unfortunately, the bones preserved for these three specimens do not overlap each other, thus the reference of them to a single species (or, conversely, to different taxa) is a task not possible for the moment. The only elements that can be partially compared are the available dorsals of MPM 99 (e.g., dorsal 1) and the holotype of *Xenotarsosaurus bonapartei* (e.g., dorsal 2). However, the vertebra of this taxon is badly preserved, with few structures amenable to comparison. They are: dorsal 2 of *Xenotarsosaurus* with cranial articular surface concave, instead of being flat as in dorsal 1 of MPM 99; presence of a single pleurocoel in

*Xenotarsosaurus*, contrasting with the two of MPM 99; in *Xenotarsosaurus* the parapophyses occupy a higher position on centrum, and the triangular cavity that is ventral to the diapophyses is shallower than in MPM 99; the “supraneural cavities” present on the base of the neural arch, as well as the excavations present between the prezygapophyses and the diapophyses, are much greater in *Xenotarsosaurus* than in MPM 99. We can not dismiss that such differences may reflect the position of each piece in the vertebral column rather than any relevant taxonomic differences. In this regard, it is important to emphasize the remarkable change in morphology between the first and second dorsals in the holotype of *Carnotaurus sastrei*. However, because no modification from an opisthocoealous to a procoelous condition is present in the cervico-dorsal region in *Carnotaurus*, we assume that MPM 99 can not be referred to *Xenotarsosaurus*.

### *Synapomorphies of Abelisauroidea and Abelisauridae present in MPM 99*

Although most of the postcranial abelisaurian synapomorphies enumerated in the literature correspond to the vertebral column, few efforts were addressed to understand the morphological variation of the vertebral column in this theropod clade. There are some traits that are unevenly distributed among members of Abelisauroidea and less inclusive groups (e.g., Abelisauridae, Carnotaurini, Noasauridae). Derived features present in MPM 99 that may constitute synapomorphies of Neoceratosauria (e.g., the common ancestor of *Ceratosaurus*, *Carnotaurus*, and all its descendants) include the presence of paired pleurocoels on the cervical and dorsal vertebrae, and the presence of cranial peduncular foramina on the cervical and anterior dorsal vertebrae. Diagnostic features of Abelisauroidea (e.g., the common ancestor of *Ligabueino*, *Carnotaurus*, and all its descendants) present in MPM 99 are: cervical vertebrae transversely wide, hypertrophied epipophyses on cervical vertebrae, presence of a ridge connecting the epipophyses with the prezygapophyses, cervical neural spines reduced, and cervical prespinal fossa broad. Some derived traits present in the caudal vertebrae of MPM that are shared with members of Abelisauridae (e.g., the common ancestor of *Abelisaurus*, *Carnotaurus*, and all its descendants) include: transverse processes distally fan-shaped, and presence of a slender anterior projection on the transverse processes that contacts with the transverse process of the preceding caudal. With regard to this last feature, it is important to note that it is present in MPM 99, *Carnotaurus*, *Aucasaurus*, *Pycnonemosaurus*, and presumably also in the basal abelisauroid *Ilokelesia*. However, an anterior prong on



the transverse processes of caudal vertebrae is absent in *Majungatholus* (M. Carrano, pers. comm.). Moreover, distribution of such features remains unknown in other abelisauroids (e.g., *Abelisaurus*, *Noasaurus*, *Masiakasaurus*, *Laevisuchus*).

### Recent phylogenetic hypothesis

The suite of characters enumerated before for MPM 99 (e.g., presence of well developed epipophyses on posterior cervicals, posterior cervicals and "pectorals" with deep and transversely expanded neural arches, and mid-caudal vertebrae with fan-shaped transverse processes), suggests that this specimen may belong to a derived subgroup within Abelisauridae, being more closely related to *Carnotaurus* than to other abelisauroids. However, this interpretation must be taken with caution because our current knowledge about character distribution among abelisauroids is far from being complete.

We must briefly refer to recent taxonomic arrangements that divide Abelisauridae into less inclusive units. Sereno (1999) was first in recognizing the abelisauroid subgroup Carnotaurinae, to join *Carnotaurus* and *Majungatholus* with the exclusion of *Abelisaurus*, a phylogenetic hypothesis later adopted by Carrano *et al.* (2002) and Lammana *et al.* (2002). Moreover, Coria *et al.* (2002) coined the term Carnotaurini for a subgroup of Carnotaurinae, to include *Carnotaurus* and the new recently discovered *Aucasaurus*, with the exclusion of *Majungatholus*. Two synapomorphies were recognized by Coria *et al.* (2002) in support of their Carnotaurini: presence of hyposphene-hypantrum articulation in the proximal and middle sections of the caudal series, and cranial processes in the epipophyses of the cervical vertebrae (MPM 99 has mid-caudal vertebrae with extra articulations, but its cervical 10 does not show a cranial projection on the epipophyses).

We recommend reviewing the features supporting the monophyly of Carnotaurini for the following reasons: first, the analysis performed by Coria *et al.* (2002) does not include *Noasaurus*, the cervical vertebra of which certainly exhibits craniocaudally extended epipophyses with an acute and protruding cranial process (Bonaparte and Powell, 1980; Bonaparte, 1991); second, the presence of hyposphene-hypantrum articulations in the proximal and middle portions of caudal series is unknown in *Abelisaurus*, *Xenotarsosaurus*, and noasaurids, as well as in basal neoceratosaurs (e.g., *Elaphrosaurus*), except for the available caudal of *Ilokelesia* (presumably corresponding to a portion of the tail distal to caudal 15<sup>th</sup>) which does not show hyposphene-hypantrum articulations (Coria and Salgado, 2000). Finally, an incongruence

emerges when the tree topology and definition of taxa presented by Coria *et al.* (2002) are compared with the systematic arrangement of Abelisauridae and Carnotaurinae depicted by other authors (e.g., Sereno, 1999; Lammana *et al.*, 2002; Carrano *et al.*, 2002): *Majungatholus* is placed by Coria *et al.* (2002) as emerging from an unresolved node (e.g., Abelisauridae) also including *Ilokelesia*, *Abelisaurus*, and Carnotaurini (= *Carnotaurus* + *Aucasaurus*). By doing this, the monophyly of Carnotaurinae Sereno 1999, is consequently collapsed.

For the reasons exposed above, we interpret that the phylogenetic relationships of Abelisauridae require review, and that proliferation of names applied to poorly supported nodes create instability in current systematic interpretations.

### Conclusions

The new finding offers support that the main abelisauroid derived features in the vertebral column had already been acquired, at least, by the beginning of the Late Cretaceous (Cenomanian), and that the morphology of the cervical, pectoral, and caudal vertebrae remained almost unchanged in some abelisauroid representatives through Maastrichtian times (e.g., *Carnotaurus*).

The derived condition of the vertebral remains here described are in congruence with skull remains suggesting that derived abelisauroids (e.g., Carnotaurinae) were present at the time of deposition of the Bajo Barreal Formation (Lammana *et al.*, 2002). Available evidence coming from this sedimentary unit dismisses previous assumptions that abelisauroids radiated at the end of the Late Cretaceous (Sampson *et al.*, 1998).

Abelisaurid remains from the Cenomanian Bajo Barreal Formation are among the oldest known, along with ungual phalanges found in Cenomanian beds from the Río Limay Formation (Novas and Bandyopadhyay, 2001) and Kem Kem, Morocco (Dalla Vecchia *et al.*, com. pers.), as well as material from the Cenomanian of Niger (Sereno *et al.* 2002).

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