

The cervical vertebrae of the Late Cretaceous abelisaurid dinosaur *Carnotaurus sastrei*

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The cervical vertebral series of *Carnotaurus sastrei* from Argentina is described in detail, and compared with *Majungasaurus crenatissimus* from Madagascar, both Late Cretaceous (Maastrichtian) in age. Notable differences in the morphology of the cervical vertebrae, especially in the shape and development of the epiphysis and the neural spines, are observed between these two genera. These differences show a neck much more robust in *Carnotaurus* than in *Majungasaurus*, may be linked to the evolution of the clade in relation to the divergence time since the two genera shared a common ancestor, and functionally may relate to the feeding function associated to the extreme reduction of the forelimbs.

Key words: Dinosauria, Abelisauridae, *Carnotaurus*, *Majungasaurus*, neck, cervical vertebrae, morphology, Cretaceous, Argentina, Madagascar.

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Introduction

The record of Abelisauridae, with over 10 recognized species, represents the best-known carnivorous dinosaur group from Gondwana and includes two of the anatomically best-known dinosaurs, *Carnotaurus sastrei* from the La Colonia Formation (Maastrichtian) of Argentina (Bonaparte 1985) and *Majungasaurus crenatissimus* from the Maevarano Formation (Maastrichtian) of Madagascar (Sampson et al. 1998).

Vertebral anatomy of Gondwanan theropod dinosaurs has received increased attention over the past 25 years. Several workers (e.g., Martínez et al. 1986, 2004; Bonaparte et al. 1990; Carrano et al. 2002, 2011; O'Connor 2007; Méndez 2010) have detailed axial anatomy and provided valuable information about the vertebrae and ribs of Abelisauroida, documenting a number of features that distinguish members of this group from other theropods (i.e., hypertrophied cervical epiphyses, extremely elongate cervical ribs, increased fusion of elements into the sacral complex, caudal vertebrae with long transverse processes, expanded distal ends of transverse processes in caudal vertebrae). In 1990, Bonaparte, Novas, and Coria fully described the vertebral morphology in *Carnotaurus sastrei*, documenting for the first time these features in abelisaurids, which were hitherto unknown

in other theropods. After this initial description, *Carnotaurus* has received little detailed attention. O'Connor (2007) added to our knowledge of abelisaurid axial morphology with a detailed description of vertebral remains of *Majungasaurus crenatissimus*, and data on vertebral morphology within Abelisauridae slowly accumulated following constant discoveries of new, but less complete specimens. Preliminary descriptions of two fairly complete abelisaurids, *Aucasaurus garridoi* (Coria et al. 2002) and *Skorpiovenator bustingorryi* (Canale et al. 2009), were also presented, although complete osteological descriptions remain to be completed.

In this work I provide a detailed comparison of the cervical series of *Carnotaurus sastrei* (MACN-CH 894) with that of *Majungasaurus crenatissimus* (UA 8678). The goal of the present work is to document different structural patterns exhibited by members of Abelisauridae and to emphasize those features of the cervical vertebral column that would enable a more precise analysis and allocation of new abelisaurid remains that are based on incomplete cervical series.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; UA, Université d'Antananarivo, Antananarivo, Madagascar.

Description and comparison

Carnotaurus and *Majungasaurus* share the same number of vertebrae in the cervical series (10). Throughout, *Carnotaurus sastrei* exhibits morphological differences in these vertebrae. Vertebral centra are longer than high from the axis to the 6th cervical vertebra, and then the 7th becomes shorter relative to its height (Table 1). In *Majungasaurus*, only the last three vertebrae in the neck are less rectangular in outline. When the posterior articular surface of the centrum is oriented perpendicularly, the ventral margin of the anterior articular surface is equal to the mid-height of the posterior surface at the axis, whereas it does not exceed this level in any other vertebrae of the neck. In *Majungasaurus*, the pattern is different: the ventral edge of the anterior surface of the axis is well below the mid-height of the posterior surface; the next six cervical vertebrae show a much more intense antero-posterior slope, with the ventral edge of the anterior face one-half or more of the vertebral height above the ventral margin of the posterior face. Only in the last two cervical vertebrae of *Majungasaurus* is the articular surface offset similarly to *Carnotaurus*. The ventral concavity observed in lateral view is most pronounced in the 10th cervical vertebra of *Carnot-*

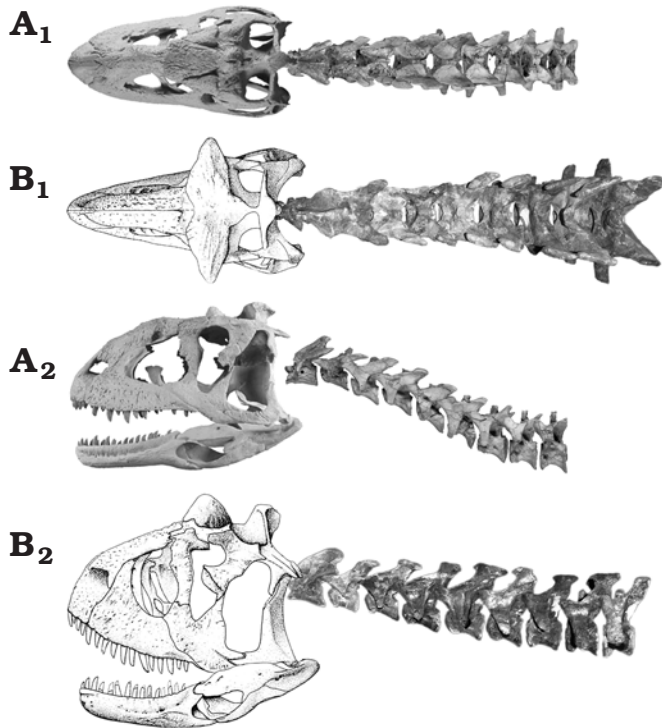


Fig. 1. Comparison of cervical series and skull of two abelisaurid dinosaurs. **A.** *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. **B.** *Majungasaurus crenatissimus* Sampson, Witmer, Forster, Krause, O'Connor, Dodson, and Ravoavy, 1998 (UA 8678), Madagascar, Maevarano Formation, Maastrichtian, Upper Cretaceous. Dorsal (A₁, B₁) and lateral (A₂, B₂) views. Skull of *C. sastrei* was modified from Bonaparte et al. 1990, and skull of *M. crenatissimus* from Sampson et al. 1998. Not to scale (for measurements see Table 2).

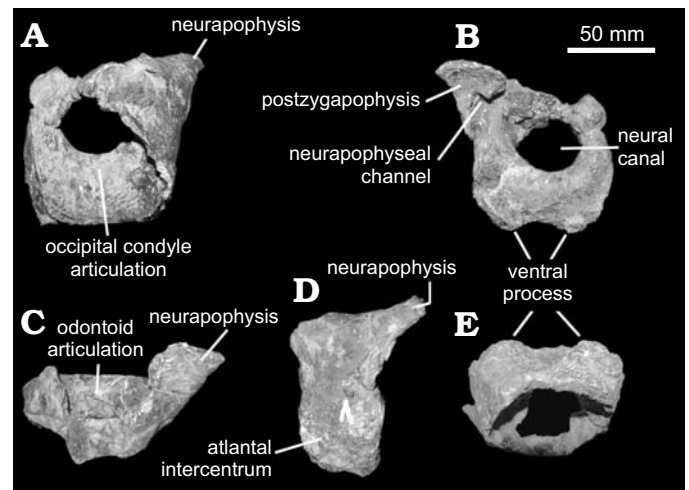


Fig. 2. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894, Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous). Atlas in anterior (A), posterior (B), dorsal (C), left lateral (D), and ventral (E), views.

aurus, whereas it is more developed from the middle to the end of the series in *Majungasaurus* (Fig. 1).

Atlas.—The atlas of *Carnotaurus* consists of an intercentrum and a neural arch preserving a slightly deformed left neurapophysis (Fig. 2). The intercentrum exhibits a concave surface for articulation with the occipital condyle. This surface is transversely pronounced and anterodorsally oriented.

The articular surface for the axis is large, transversely oriented, and crescentic in outline. There is no evidence of a prezygapophysis, so we infer the absence of a proatlas. The neurapophysis is directed posterolaterally, rather than dorsally, and is less elongated than the neurapophysis of *Majungasaurus*. The postzygapophysis is small and triangular in outline. The articular surface is ventromedially directed, similar to the situation of *Majungasaurus*. The postzygapophysis is projected from the medial part of neurapophysis, forming a channel between the inner side of the latter and the ventral end of the postzygapophysis. Incomplete preservation of the atlantal neurapophysis in *Carnotaurus* precludes a characterization of its distal end (e.g., it is unclear if it has a sickle-shaped epiphysis like that of *Majungasaurus*; O'Connor 2007). The ventral surface of the intercentrum has two small lateral processes, separated by a wide groove.

Axis.—This element is complete and very well preserved in *Carnotaurus* (Fig. 3). The vertebral body is long and low (ratio length/height is 2.4, see Table 1), and increases in height towards the posterior end. A thick ventral rim is present on the posterior articular surface, contributing to the visible height difference between anterior and posterior intervertebral surfaces. There is a clear and firmly conjoined line of fusion between the axial centrum and intercentrum. The latter is broad and almost flat ventrally.

The odontoid process projects forwards beyond the lower end of the axial intercentrum. In *Majungasaurus* the odontoid reaches but does not pass this edge. Noticeable is the

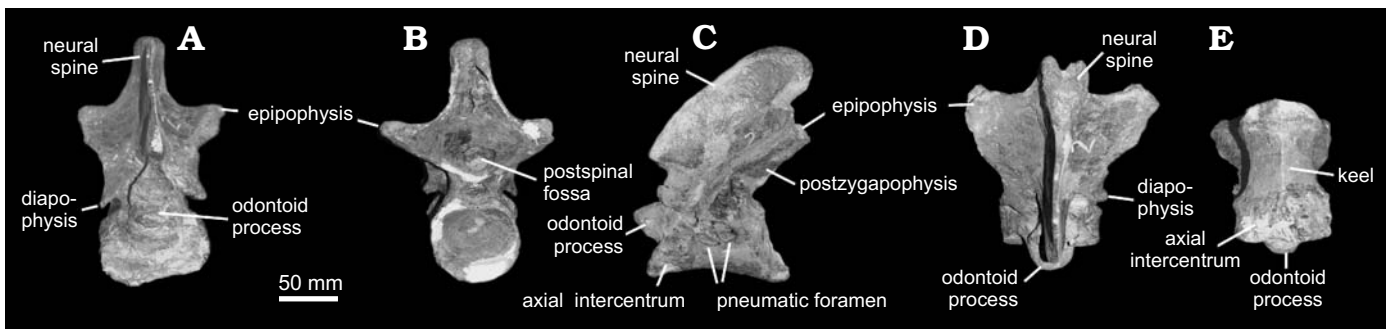


Fig. 3. Abelisaurid dinoasaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Axis in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

high grade of opisthocoelia, similar to *Majungasaurus*. In *Carnotaurus*, the centrum bears two small pneumatic foramina on both sides. On the right side the anterior one is drop-shaped (with the apex oriented caudally), while the posterior one is subcircular. On the left side, both are elliptic. *Majungasaurus* shows only one circular pneumatic foramen on each side. However, a second specimen of *Majungasaurus* (FMNH PR 2293, MAD95-14 locality) exhibits two pneumatic foramina on the side of the centrum (O'Connor 2007). The posterior articular surface is exposed at an angle of 70° (considering the base of the neural channel as the horizontal plane). In *Majungasaurus*, this surface shows a minimum tilt, being almost perpendicular to the horizontal plane. On the ventral surface of the axial centrum, there is a keel extending from the junction of the axial intercentrum to the rear

end of the vertebra, being more pronounced in the middle of the centrum length. Although present, this ventral keel is less developed in *Majungasaurus*. The parapophysis is not very pronounced in *Carnotaurus*; it is located at the anteroventral end of the neural arch, projecting laterally. In *Majungasaurus*, the parapophysis is located in the same place but higher (at mid height), and also directed laterally. The *Carnotaurus* axis is characterized by great development of the neural arch, being twice the centrum height.

The diapophysis is small and anteroventrally projected. However, in *Majungasaurus*, the diapophysis is more developed, and lateroventrally oriented. The prezygapophysis of *Carnotaurus* is small, positioned behind the anterior end of the neural spine. *Majungasaurus* also exhibits a small prezygapophysis, but its anterior end reaches the same position as

Table 1. Measurements (in cm) of cervical series. Abbreviations: °AAS, angle of anterior articular surface; ACH, height of anterior articular surface; ACW, width of anterior articular surface; EH, height of epiphysis; CL, maximum length of centrum; MCW, width of medial part of centrum; NSH, height of neural spine; NSL, length of neural spine; NSW, width of neural spine; °PAS, angle of posterior articular surface; PCH, height of posterior articular surface; PCW, width of posterior articular surface; TH, total height; TH/CL, total height/maximum length of centrum.

	CL	ACW	ACH	PCW	PCH	TH	TH/CL	NSH	NSL	NSW	°AAS	°PAS	MCW	EH
<i>Carnotaurus sastrei</i>														
Atlas	4.2	6.2	3.8	8.3	3.0	10.0	2.38	–	–	–	–	–	–	–
Axis	8.1	7.4	5.5	7.4	6.6	19.4	2.39	5.9	15.4	3.2	73°	68°	5.4	0.3
C3	10.7	6.5	4.4	8.0	6.4	16.9	1.58	4.0	1.9	3.5	71°	84°	5.5	3.3
C4	12.8	7.1	5.0	8.6	6.7	18.9	1.47	2.8	3.7	2.8	69°	75°	5.4	5.8
C5	11.4	8.1	5.6	9.2	6.7	19.7	1.73	2.8	3.4	3.2	69°	81°	6.3	6.7
C6	11.7	8.9	6.3	10.0	7.8	20.0	1.71	2.8	3.0	3.4	74°	88°	7.1	6.9
C7	11.0	9.7	7.1	10.3	8.4	22.5	2.04	2.6	2.9	3.8	82°	86°	7.5	6.8
C8	10.8	10.5	8.6	11.2	8.9	23.6	2.18	–	1.3	3.4	81°	95°	7.9	6.8
C9	10.2	11.4	9.5	12.1	10.8	25.8	2.50	3.2	2.4	4.0	89°	87°	8.2	6.8
C10	9.4	11.8	10.5	11.2	10.0	24.2	2.57	3.9	3.1	3.6	87°	92°	8.2	5.1
<i>Majungasaurus crenatissimus</i>														
Atlas	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Axis	5.0	–	–	5.3	4.4	11.2	2.24	2.2	8.2	–	82°	86°	3.9	0
C3	6.0	5.3	4.2	5.4	3.8	9.5	1.58	3.1	3.3	0.3	66°	74°	3.9	2.2
C4	6.2	–	–	4.6	4.3	10.9	1.76	–	2.3	0.7	60°	74°	3.1*	–
C5	6.3	4.5	3.0	5.3	4.3	10.5	1.67	1.5	2.7	0.6	53°	75°	4.0	2.4
C6	6.6*	–	–	6.1	4.1*	10.3*	1.56	–	2.0	0.7	57°	59°	4.6	–
C7	6.0*	–	–	5.8*	–	11.5*	1.92	–	1.5	1.0	68°	69°	3.6*	–
C8	5.6*	–	–	6.0	5.6	12.3	2.20	–	1.3	1.3	82°	76°	4.1	–
C9	5.8	–	–	6.1	6.1	13.2	2.28	–	1.3	1.5	84°	85°	4.0*	–
C10	5.8	5.4	5.6	5.7	6.2	13.6	2.34	2.4	1.2	1.9	88°	85°	3.7*	0.5

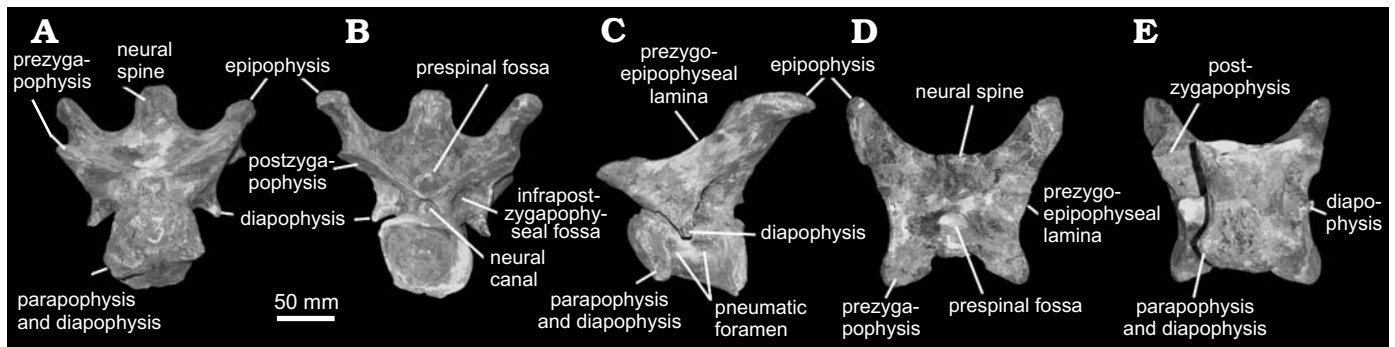


Fig. 4. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 3 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

the anterior end of the neural spine. The postzygapophysis is large and has an elliptical shape in *Carnotaurus*, with the major axis mediolaterally directed, occupying $\frac{1}{4}$ of the total width of the neural arch. In *Majungasaurus*, the morphology of the postzygapophysis is quite similar, except for the orientation of the articular surfaces (horizontal in *Majungasaurus*, and anteroposteriorly directed in *Carnotaurus*). The epipophysis almost reaches half the height of the neural spine, which also occurs in *Majungasaurus*. Below the postzygapophysis, there is a subcircular infrapostzygapophyseal fossa, as also in *Majungasaurus*.

The neural spine is well developed (it is twice the height of the centrum), with a strongly convex anterior margin and posteriorly directed, in lateral view. On the other hand, *Majungasaurus* shows a less developed neural spine, with a straight anterior margin. The distal tip of the neural spine in *Carnotaurus* is slightly convex, with a visible bifurcation on the posterior edge, showing dorsal rugosities axially oriented, that could correspond to the sites of attachment of soft tissues (i.e., tendons, muscle fibres). The bifurcation of the posterior margin of the spine is also visible in *Majungasaurus*, although it does not show any roughness in this sector. A very deep postspinal fossa is present in *Carnotaurus*, and this exhibits a pair of cavities on the sides that appear to be the relics of attachments of the interspinous ligament. This is also observed in *Majungasaurus* (O'Connor 2007). In dorsal view, the general morphology of the axis of *Carnotaurus* resembles an isosceles triangle, as in *Majungasaurus* (O'Connor 2007). Nevertheless, in *Carnotaurus*, the posterior ends of the epipophysis do not exceed to the posterior margin of the neural spine, as in *Majungasaurus*.

Cervical 3.—This vertebra shows a great development of the neural arch, being twice wider than the centrum (Fig. 4). The surface that articulates with the axis describes an approximate angle of 70° (with respect to the horizontal base of the neural channel), is markedly convex and has a trapezoidal outline. In *Majungasaurus*, the inclination of this surface is similar but the outline is clearly subcircular. The posterior articular surface is wider than tall, oval, with an angle somewhat smaller than 90° , as in *Majungasaurus*, except that, in the latter, the outline is subcircular with the dorsal edge flattened.

The centrum is markedly opisthocoelous, with the geometric centre displaced dorsally, as in *Majungasaurus*. On the lateral surface of vertebral body, two pneumatic foramina are present, which are further apart and smaller than in the axis. The anterior one is smaller than the posterior, and subcircular in outline while the posterior one is oval with its major axis anteroposteriorly directed. In *Majungasaurus*, there is only one pneumatic foramen, and it resembles in shape and position, the posterior one described for *Carnotaurus*. The ventral surface of this vertebra in *Carnotaurus* is flat, with a small sketch of a keel, which is more noticeable in the rear of the vertebral body. In *Majungasaurus*, a ventral keel, poorly developed, is seen only in the third cervical vertebra. The parapophysis is located in the anteroventral corner of the centrum, in lateral view. It is directed laterally, in contrast with the parapophysis of *Majungasaurus* which projects ventrolaterally, although it matches its ovoid shape and the orientation (anterodorsal to posteroventral) of the major axis.

The diapophysis is smaller than the parapophysis and inclines ventrolaterally. It is located over the middle length of the centrum, at the level of the neurocentral suture. This makes the distance between the capitulum and tuberculum of the rib greater than in *Majungasaurus* because, in the latter, the diapophysis is placed above the parapophysis, in lateral view. The prezygapophysis is well developed, with the articular surface directed dorsomedially and the major axis transversely. In dorsal view, it is wedge-shaped. In *Majungasaurus*, the prezygapophysis extends beyond the front of the centrum, is anterodorsally inclined, keeping the major axis in the same direction as in *Carnotaurus*. The postzygapophysis, oval in outline, is very wide and tilted laterally and posteroventrally, while in *Majungasaurus*, even if the form is similar, the lateral inclination is less marked. The epipophysis exhibits a great development, reaching the height of the neural spine, hiding it in lateral view. On the contrary, in *Majungasaurus* the epipophysis does not reach the height of the neural spine. The bulky distal end of the epipophysis of *Carnotaurus* is located behind the line of the posterior articular surface of the centrum, as in *Majungasaurus*. The width of the epipophysis is slightly smaller than the neural spine in *Carnotaurus*, while in *Majungasaurus* the width

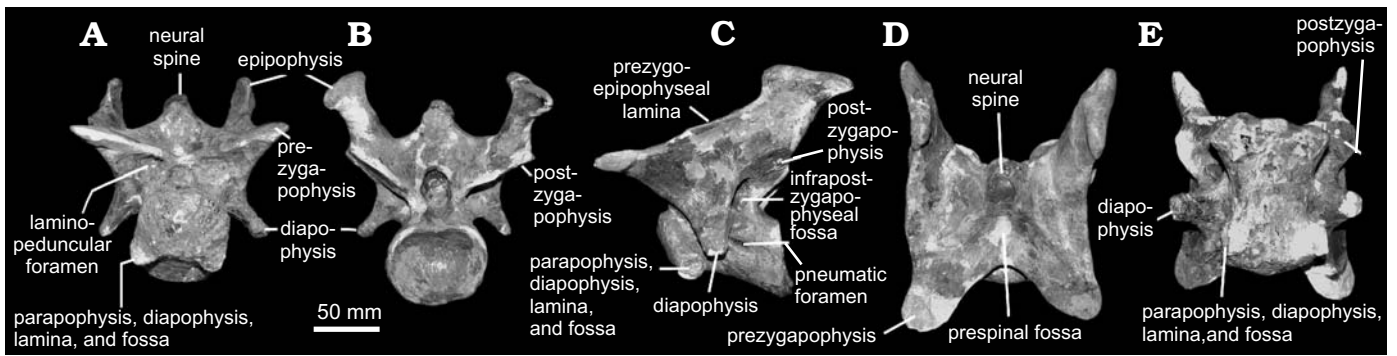


Fig. 5. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 4 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

is the same. In this vertebra of *Carnotaurus*, a conspicuous lamina connects the epipophysis with the prezygapophysis, clearly defining the lateral and dorsal parts of the neural arch. In lateral view, this prezygoepipophyseal lamina is inclined 45° . In *Majungasaurus*, this lamina is slightly more horizontal, with a slope of approximately 30° . In posterior view, the lateral inclination of the epipophysis is just over 45° ; this angle is somewhat lower in *Majungasaurus*.

The neural spine in the third cervical of *Carnotaurus* is transversely wide and short, located on the posterior half of the neural arch, whereas in *Majungasaurus*, the neural spine is short and narrow, placed as in *Carnotaurus* on the posterior half of the centrum. A prespinal fossa is formed between the laminae that connect the neural spine with the prezygapophyses as in *Majungasaurus*. Two small foramina (cranial peduncular foramina; Britt 1993) are located on either side of the neural channel, bounded by the centroprezygapophyseal lamina and another lamina that connects the prezygapophyses, just as in *Majungasaurus*. The postspinal fossa is wide and has rugosities which could be the osteological correlate of the interspinous ligament insertions.

Cervical 4.—The fourth cervical vertebra of *Carnotaurus* is a little larger than the preceding, with the neural arch almost twice as high and twice as wide as the centrum (Fig. 5). The centrum is almost flat ventrally, as in *Majungasaurus*. However, in lateral view, the ventral projection of the parapophysis makes it look concave. There is no evidence of a ventral keel. This vertebrae is more opisthocoelous than the anterior ones. However, in *Majungasaurus*, the centrum of cervical 4 is also opisthocoelous, although the degree of concavity does not differ from anterior vertebrae. As in the previous vertebrae, the anterior articular surface of the centrum is not so dorsoventrally high as the posterior, and it is also convex in lateral view. On the contrary, in *Majungasaurus* this surface is rather flat. The anterior surface (approximately inclined 65°) is slightly more sloped than the posterior, as in *Majungasaurus*.

The parapophysis in this vertebra of *Carnotaurus*, is better defined, located as in the preceding cervical vertebra (protruding from the ventral edge of the centrum), with its contact surface pointing out. In *Majungasaurus*, the parapophysis

is located in the anteroventral corner of the centrum, and it is ventrolaterally oriented. Of the two pneumatic foramina in cervical 4 of *Carnotaurus*, the anterior one is not clearly distinguishable, and the posterior one is smaller compared to that in the preceding vertebra, as well as being oval, with the major axis anteroposteriorly oriented. In *Majungasaurus*, the only pneumatic foramen is in the same position as the posterior one of the fourth cervical of *Carnotaurus*, with a longitudinal major axis.

The diapophysis of *Carnotaurus* is more robust in this vertebra, being ventrolaterally directed. In *Majungasaurus* it is also robust, but laterally instead of ventrally oriented. The infrapostzygapophyseal fossa is broader than in the preceding cervical. As in the cervical 3 of *Carnotaurus*, two anterior foramina are present on the sides of the neural canal, an unreported condition in *Majungasaurus*. The prezygapophysis of this vertebra in *Carnotaurus* exhibits an articular facet more rounded than that in the third cervical, with an anterior projection much higher. In *Majungasaurus*, the morphology of the prezygapophysis is different, with a transverse major axis, located closer to the anterior end of the centrum. The prezygapophyseal facet of this vertebra is more dorsally inclined than the medial (in cervical 3, the medial component was more pronounced), opposite to the condition in *Majungasaurus*, where it is more dorsal in cervical 3, and more medial in cervical 4. The postzygapophysis is larger than in the preceding vertebra of *Carnotaurus* and has a ventrolateral inclination (as in *Majungasaurus*), and slightly posterior. The epipophysis is axially larger with a well-defined posterior process, while the anterior one is still incipient (as in the third cervical). The longitudinal development of the epipophysis in *Majungasaurus* is smaller, without anterior projection.

The neural spine is lower than in cervical 3, being much lower than the epipophysis. It is still wide, located in the posterior half of the neural arch. In contrast, in *Majungasaurus* the neural spine is laterally compressed and its maximum height is equal to that of the epipophysis, and is confined, as in *Carnotaurus*, to the posterior half of the neural arch. There is a depression or prespinal fossa, located ahead the neural spine, and flanked by the dorsal projections of the epipophyses, as in the anterior cervical. The same morphology is

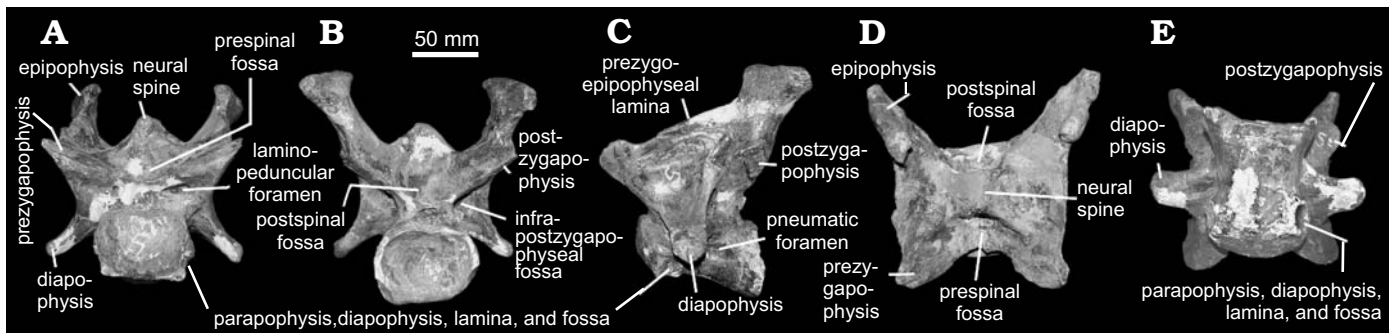


Fig. 6. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 5 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

observed in *Majungasaurus*. A well-developed prezygoepipophyseal lamina is present and clearly demarcates dorsal and lateral surfaces of the neural arch, being less concave in dorsal view than in cervical 3. This is similar to the comparison between cervical 3 and 4 of *Majungasaurus*. The posterior centrodiaepophyseal lamina of *Carnotaurus*, as in *Majungasaurus*, joins the vertebral centrum around its mid-length. The postspinal fossa is much more developed than in the cervical 3.

Cervical 5.—This vertebra is well preserved (Fig. 6). It is bigger than the fourth cervical, in particular the centrum. The development of the neural arch is notable, especially in the height, which is twice that of the centrum. The anterior articular surface inclines about 70° , while the posterior surface begins to become more vertical, with respect to the base of the neural canal. This arrangement is also observed in the fifth cervical of *Majungasaurus*. The opisthocoely of this vertebra in *Carnotaurus* is as marked as in the preceding vertebra, and this is true also of the fifth cervical of *Majungasaurus*. The parapophysis does not change its location, keeping on the ventrolateral edge of the centrum, as in *Majungasaurus*. In *Carnotaurus*, both pneumatic foramina are located high on the vertebral centrum. The posterior one is elliptical with a longitudinal major axis, and continues to be more conspicuous than the anterior. In *Majungasaurus* the unique pneumatic foramen is located in a posterior position, and its shape is oval (but the opening seems to be almost circular). There is no evidence of a ventral keel in either genus.

In the neural arch of cervical 5 of *Carnotaurus*, the prezygapophysis remains fairly well developed, with a dorso-medial inclination, whereas in *Majungasaurus* the prezygapophysis is oriented more dorsally than medially. The postzygapophysis of *Carnotaurus* faces ventrolaterally, and is subelliptical in outline. In *Majungasaurus*, the postzygapophysis seems to be posteriorly inclined. This vertebra of *Carnotaurus* shows a diapophysis that is more robust and more separated from the centrum, and more anteriorly located, than in cervical 4. This is the case also in *Majungasaurus*. Anterior and posterior projections of the epipophysis are better defined in this vertebra of *Carnotaurus* than in the previous vertebra. The axis of this distal expansion of the epipophysis is now inclined from medial (anterior) to

lateral (posterior). In addition, there are some rugosities on the distal tips of the epipophysis. *Majungasaurus* exhibits less development of the epipophysis, with only a small posterior projection.

The neural spine of cervical 5 of *Carnotaurus* is much lower in comparison with the epipophysis, besides being poorly developed anteroposteriorly. It is shaped like a dome, whereas the neural spine in *Majungasaurus* is similar in height to the epiphyses. In this vertebra of *Carnotaurus*, there is a deep postspinal fossa; another fossa is located below the postzygapophysis. On the right side, this fossa seems to divide into two, by the presence of a small septum. Below the diapophysis, a small foramen is located at the level of the neurocentral suture, and this also seems to be present in *Majungasaurus*.

Cervical 6.—This vertebra (Fig. 7) is slightly larger than the preceding vertebra, and it seems to have a broader centrum. The angle of the anterior articular surface is about 75° , whereas that of the posterior surface is close to 90° . This differs from *Majungasaurus*, where both surfaces are much more inclined (less than 75°). The medial constriction of the vertebral body (in ventral view) appears to be greater even than in the previous cervical vertebrae of *Carnotaurus*. The pair of pneumatic foramina are still present, in the same position as in fifth cervical vertebra. *Majungasaurus* seems to exhibit only one pneumatic foramen, located in the posterior half of the centrum, with an elliptical outline.

The epipophysis of this vertebra is well developed. Its anterior projection is directed medially such that, in anterior view, it seems to be closing over the neural spine. In *Majungasaurus*, on the other hand, the epipophysis is less developed and exhibits only a slight posterior projection. The infradiapophyseal fossa is larger than in the preceding vertebra. The prezygapophysis is well separated, projecting forward nearly 30% of the length of the centrum. In *Majungasaurus*, the projection of the prezygapophysis is even higher (approximately 40%), and morphologically similar. The diapophysis in *Carnotaurus* is located just ahead of the midline of the centrum and slightly above the level of the parapophysis. Instead, the diapophysis of the sixth cervical of *Majungasaurus* is located in a more anterior position, and its distal end partially covers the position of the parapophy-

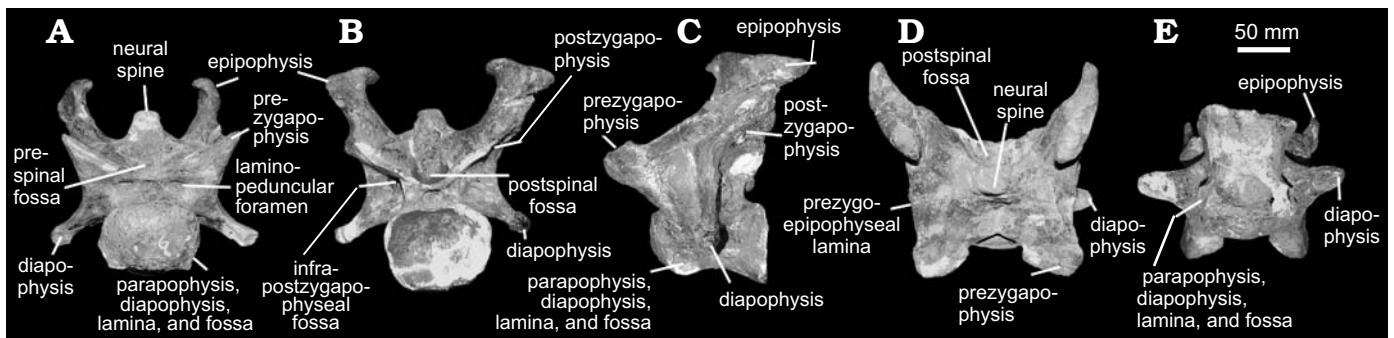


Fig. 7. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 6 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

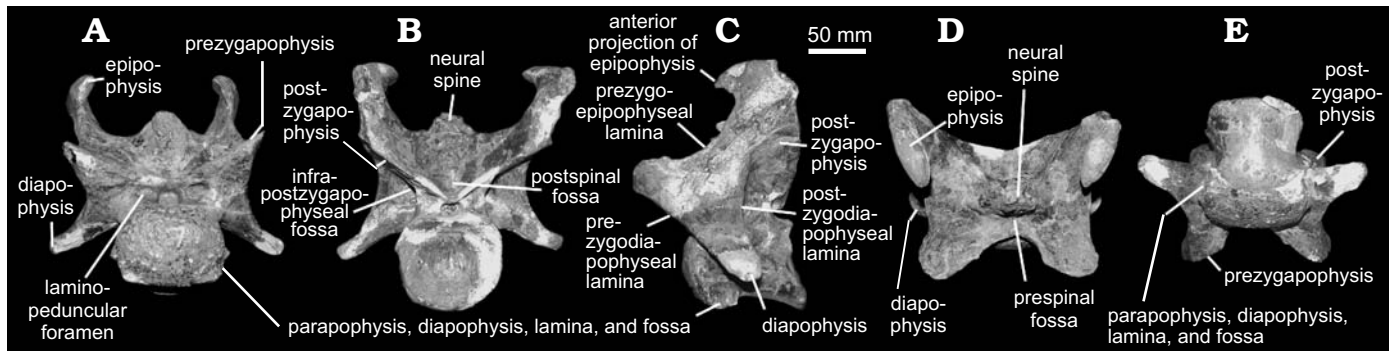


Fig. 8. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 7 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

sis, in lateral view. Anterior (these are bigger) and posterior lamino peduncular foraminae are present, on each side of the neural channel.

The neural spine, located in the middle of the length of centrum, is much smaller than the epipophyses. The postspinal fossa is highly developed.

Cervical 7.—The seventh cervical vertebra (Fig. 8) continues the trend seen throughout the series, being more robust than the preceding vertebra. The length of the centrum is almost equal to its width, and this proportion is also seen in cervical 7 of *Majungasaurus*. The anterior articular surface has an angle close to 80° in *Carnotaurus*, and the posterior surface about 85° . The morphology of the centrum in the seventh cervical vertebra of *Majungasaurus* is very different, with the anterior surface almost perpendicular to the horizontal, whereas the posterior surface is slightly tilted, less than 80° . The posterior surface of the articulation in the *Carnotaurus* centrum presents a subcircular outline. In lateral view, there is a slight concavity on the ventral side of the vertebral body, contrasting with *Majungasaurus*, where the curvature is very pronounced. There is a pronounced constriction of the vertebral body in the middle, as in *Majungasaurus*.

The parapophysis is rounded and laterally oriented, whereas in *Majungasaurus* this is ovoid and ventrolaterally inclined. The pair of pneumatic foramina is located at the top of the vertebral body. The poor preservation of this

vertebra in *Majungasaurus* does not allow any comparison of this feature. The epipophysis is highly developed in *Carnotaurus*, and is more than twice as high as the neural spine, but in *Majungasaurus* the height of both structures is almost the same. The infradiapophyseal fossa is larger even than in cervical 6 of *Carnotaurus*. The prezygapophysis, as in *Majungasaurus*, is medially inclined at an angle steeper than the previous vertebrae. The anterior projection of the prezygapophysis is over 30% of the length of the centrum, whereas in *Majungasaurus* this projection is slightly less. The diapophysis is now much more separated and posteroventrally projected, and its end is still above the height of the parapophysis. In *Majungasaurus*, on the other hand, the projection of the diapophysis is ventrolaterally directed, and its end covers the parapophysis, in lateral view. Anterior and posterior lamino peduncular foraminae are still present in this vertebra of *Carnotaurus*.

The neural spine is located at half the length of the centrum, and despite being smaller than the epipophysis, it is possible to observe it slightly, in lateral view. In *Majungasaurus* the position of the neural spine is similar. The neural arch exhibits a large development of the postspinal fossa.

Cervical 8.—This vertebra (Fig. 9) is more robust and higher than the seventh. The vertebral centrum is narrower in the posterior half. As in *Majungasaurus*, the centrum is slightly concave ventrally and devoid of a keel. The degree of opisthoceoly is smaller than in the preceding vertebrae. Both

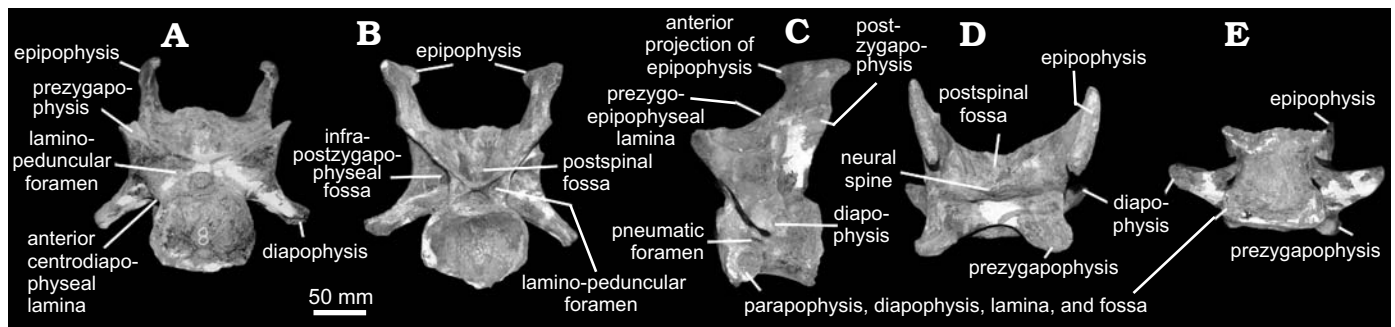


Fig. 9. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 8 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

pneumatic foramina are now further apart. *Majungasaurus* also shows two pneumatic foramina, with a spatial arrangement similar to cervical 8 of *Carnotaurus*.

The prezygapophyses are further apart, and less projected forward than in the preceding vertebrae. In contrast, in *Majungasaurus*, although not completely preserved, the prezygapophysis is more developed and located closer to the midline. Its anterior projection is more marked than in cervical 8 of *Carnotaurus*. The surface of the postzygapophysis is ventrolaterally oriented in *Carnotaurus*, the same as in *Majungasaurus*. The foramina on the sides of the neural canal are present, both anterior and posterior, in *Carnotaurus*. These foramina have not been reported in *Majungasaurus*. The epiphysis is even higher and presents a series of rugosities at the end, which could be evidence of the attachment site for muscles and/or tendons. The diapophysis has a higher position with respect to the centrum, besides being furthest from the vertebral body, and therefore also of the parapophysis. To a lesser degree than in *Carnotaurus*, the diapophysis of cervical 8 of *Majungasaurus* is high and separated, revealing the position of the parapophysis, in lateral view. The infrapostzygapophyseal fossa of *Carnotaurus* is very well developed, as in *Majungasaurus*, and it is accompanied by a smaller one under the prezygodiapophyseal lamina.

The neural spine in *Carnotaurus* is virtually non-existent, quite opposite to *Majungasaurus*, in which the neural spine is much more developed, reaching the same height as the epiphyses.

Cervical 9.—This vertebra (Fig. 10) is larger than cervical 8, especially the centrum, which is as long as high and slightly wider. This is very similar to *Majungasaurus*. The degree of opisthocoely is significantly reduced relative to preceding vertebrae. In ventral view, the centrum presents a marked constriction in the middle of its length. Anterior and posterior articular surfaces are circular in outline. The angles of both articular surfaces are slightly less than 90°. In all these respects *Majungasaurus* is similar. Ventrally, a rounded keel can be observed, which is more noticeable in the mid-posterior part of the centrum. However, in *Majungasaurus* this is not observed. The parapophysis is located in the same place

as throughout the entire cervical series, on the anteroventral edge of the centrum.

The diapophysis is located higher and is more robust, and ventrolaterally oriented, as in *Majungasaurus*. A small part of the prezygapophysis extends past the anterior end of the centrum. This is unlike *Majungasaurus*, where the anterior projection of the prezygapophysis is still remarkable. Although in *Carnotaurus* the epiphysis is very well developed (and it is higher than the neural spine), in *Majungasaurus* it is less substantial (and it is lower than the neural spine). The foramina and/or fossae in the neural arch are the same as in the previous vertebra, but larger, as in *Majungasaurus*. Anterior and posterior lamino peduncular foramina are present in both genera.

The neural spine regains prominence in this vertebra, being more developed than in cervical 8, just as in *Majungasaurus*.

Cervical 10.—This vertebra, the last of the cervical series, is complete and well preserved (Fig. 11). The shape of both intervertebral joints is circular, although in *Majungasaurus*, at least the posterior surface appears to be higher than wide. Both joint surfaces are almost perpendicular to the horizontal plane, observed also in *Majungasaurus*. The opisthocoely is much less than in the preceding vertebra, and is comparable to *Majungasaurus*. In the centrum of the tenth cervical of *Carnotaurus* the medial constriction is very marked, in both lateral and ventral view, similar to *Majungasaurus*. It also presents an inconspicuous ventral keel, perhaps resembling the “sagittal crest” of the cervical 10 of *Majungasaurus* (O’Connor 2007). In *Carnotaurus*, pneumatic foramina present on the side of the centrum are more widely spaced than in preceding vertebrae, and both have an elliptical shape with the major axis anteroposteriorly oriented. In contrast, *Majungasaurus* exhibits only one foramen in an anterior position, which appears to be circular in outline.

In the neural arch, the diapophysis is higher and longer than in the ninth cervical, as also in *Majungasaurus*. The anterior end of the prezygapophysis of *Carnotaurus* is just ahead of the anterior surface of the centrum, while the projection in *Majungasaurus* is more pronounced. The medial and lateral inclination of the prezygapophyseal and postzy-

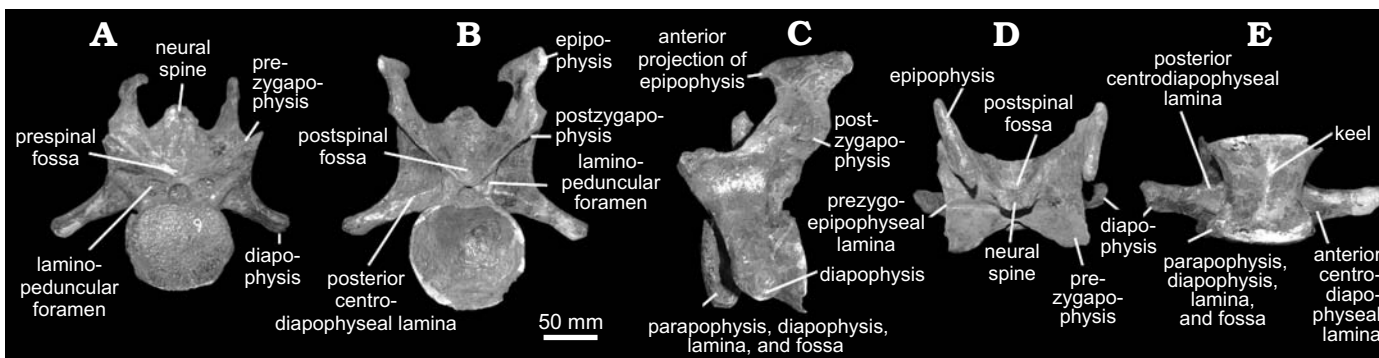


Fig. 10. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 9 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

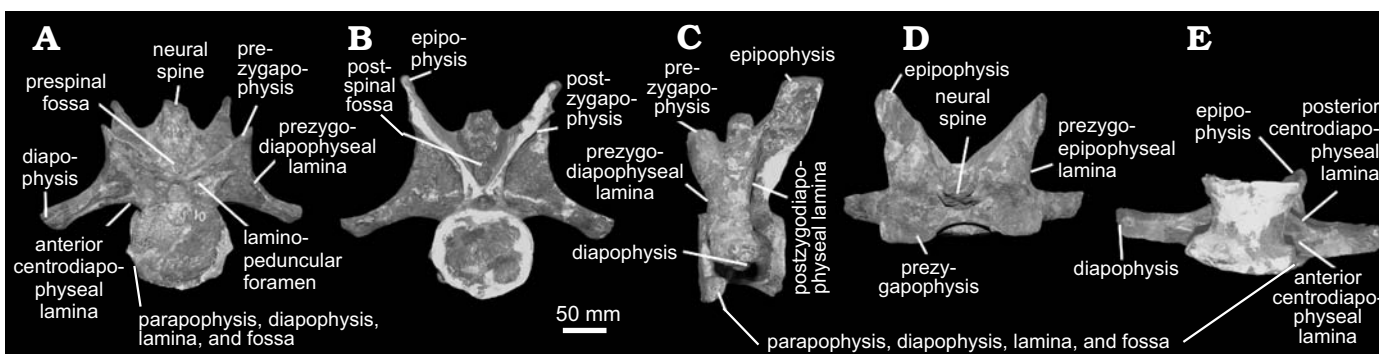


Fig. 11. Abelisaurid dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894), Argentina, La Colonia Formation, Maastrichtian, Upper Cretaceous. Cervical 10 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views.

gapophyseal facets, respectively, is the most marked in the whole series. The epipophysis of this vertebra is smaller and lacks the anterior and posterior processes seen in previous vertebrae. In both genera, lamino peduncular foramina are present in the anterior aspect, but absent in posterior view. The infraprezygapophyseal fossa is very conspicuous in both genera. The infradiapophyseal fossa is well developed and its outline is semicircular. The infrapostzygapophyseal fossa is slightly divided in two, with a circular foramen in the dorsal position, and the other, with elliptical shape, placed ventrally.

The neural spine is relatively higher compared to the epipophyses, but still below the height of these. This differs significantly from the tenth cervical of *Majungasaurus*, where the neural spine is visibly higher than the epipophyses (more so than in the ninth cervical). The posterior margin of the neural spine has strong rugosities, maybe a mark of the insertion site of the interspinous ligament.

Discussion

Neck and skull dimensions.—These two abelisaurids differ in the proportions of skull and neck. For comparisons, we used the complete cervical series of one subadult specimen of *Majungasaurus crenatissimus* (UA 8679); accordingly, its size was increased by 20% following O'Connor (2007) in or-

der to associate this cervical series with the skull of an adult specimen of *Majungasaurus* (FMNH PR 2100; see Table 2). By comparing the cervical series of *Carnotaurus* with that of *Majungasaurus* it is possible to observe substantial differences in dorsal view (Fig. 1A). In *Carnotaurus*, the width of the axis represents almost 40% of skull width, whereas in *Majungasaurus* the axis is less than 30%. The anterior cervical vertebrae of *Carnotaurus* are approximately 52% of the width of the skull, whereas those of *Majungasaurus* are approximately 31%. In *Carnotaurus*, the middle cervicals amount to 60% of head width, but slightly less than 50% in *Majungasaurus*. The last cervical of *Carnotaurus* is as wide as the skull, whereas in *Majungasaurus* it is estimated (due to

Table 2. Measurements (in cm) of skull and cervical vertebrae.

	<i>Carnotaurus sastrei</i>	<i>Majungasaurus crenatissimus</i>
Length between premaxila and occipital condyle	53.8	53.1
Width between quadratojugals	27.8	33.2
Width axis (maximum)	11	7.9 (+20% = 9.5)
Width anterior cervical (maximum)	14.5	8.7 (+20% = 10.4)
Width median cervical (maximum)	16.8	13.4 (+20% = 16.1)
Width posterior cervical (maximum)	28	13.6 (+20% = 16.3)

breakage) at approximately 50%. Thus we see that the South American form has a cervical series that is proportionally wide in the anterior section and increases posteriorly. By contrast, the Malagasy form exhibits vertebrae that are not conspicuously wide in the anterior part of the series, nor are the mid-cervical vertebrae significantly different from the posterior cervicals (Méndez 2010).

The length of the cervical series in *Carnotaurus*, taking into account only centra from the axis to the tenth cervical, is estimated at approximately 96 cm. This articulates with a skull, measured from the anterior end of the premaxilla to the end of occipital condyle, of almost 54 cm. Thus, the length of the cervical series is 1.8 times the length of the skull. The cervical series of *Majungasaurus* is approximately 64 cm, resulting in a neck that is equivalent to 1.2 times the length of the skull (53 cm). When articulated, it is clear that the two cervical series exhibit varying degrees of curvature, being straighter in *Carnotaurus*, with a greater sigmoidal curvature in *Majungasaurus* (Fig. 1B).

This could indicate that the relationship between the skull and cervical series differs in *Carnotaurus* and *Majungasaurus* and other basal theropods that have a similar size ratio between head and neck (e.g., *Ceratosaurus*, *Allosaurus*). This difference in the general morphology of the cranio-cervical complex of both genera may have functional implications. The robustness of this region in abelisaurids has been associated with the reduced size of the forelimbs (Tykoski and Rowe 2004). The less gracile appearance of *Carnotaurus* compared to *Majungasaurus* may indicate greater specialization in carnosaurines, not only related to feeding habits (possibly scavengers), but perhaps also with intraspecific confrontations.

Abelisaurid cervical characters.—Several of the characters in the cervical series of *Carnotaurus* are shared by other members of the clade Ceratosauria (*Ceratosaurus* + Abelisauroidae): axial pneumatic foramina located behind the position of the diapophysis (*Ceratosaurus*, *Masiakasaurus*, *Rahiolisaurus*, *Majungasaurus*); anterior peduncular foramina in posterior cervicals (*Ekrixinatosaurus*, *Majungasaurus*, and *Ceratosaurus*); posterior peduncular foramina in posterior cervicals (*Majungasaurus*, *Masiakasaurus*, and *Ceratosaurus*); pre- and postzygapophysis more separated from the midline, surpassing the lateral edge of the centrum (*Majungasaurus*, *Ekrixinatosaurus*, *Ilokelesia*, MPM-99, *Noasaurus*, *Masiakasaurus*, and *Ceratosaurus*).

The following characters are shared by most of the taxa that comprise the clade Abelisauroidae (Noosauridae + Abelisauridae): lateral surface of cervical centrum excavated or depressed (*Elaphrosaurus*, *Masiakasaurus*, *Ilokelesia*, *Ekrixinatosaurus*, *Carnotaurus*, and MPM-99); reduced cervical neural spines (*Elaphrosaurus*, *Masiakasaurus*, *Noasaurus*, *Carnotaurus*, *Majungasaurus*, *Ekrixinatosaurus*, *Ilokelesia*, and MPM-99).

Cervical vertebrae of *Carnotaurus* share several characters with other members of the family Abelisauridae: length

of centrum in anterior and mid cervicals, longer than the axial centrum and the presence of ventral keel on the axis (*Majungasaurus*); hypertrophied epiphysis in post-axial cervicals (*Majungasaurus*, *Ekrixinatosaurus*, *Ilokelesia*, MPM-99); neural spines located on the posterior half of the neural arch in anterior cervicals (*Majungasaurus* and *Ilokelesia*); presence of a well-developed prezygoepiphysal lamina (*Ekrixinatosaurus*, *Majungasaurus*, *Ilokelesia*, *Rahiolisaurus*, MPM-99); pre- and postzygapophysis equidistant from the midline of the axis (*Majungasaurus*).

The height and orientation of the cervical epiphysis directed dorsolaterally and being higher than the neural spine, is a feature shared between *Carnotaurus* and several members of the clade Brachyrostra (*Ekrixinatosaurus*, *Ilokelesia*, and MPM-99).

Function of the abelisaurid neck.—The morphology of the cervical series of *Carnotaurus* probably gave it some unusual properties, not noted before. The distribution of vertebral centra with offset articular surfaces largely determines the sigmoid arching or curvature of the neck. In the neck of *Carnotaurus* such centra are restricted to the area between the axis and the fifth cervical, resulting in a neck that only minimally exhibits the typical lateral “S”-curve that is characteristic of theropods. In addition, the articulated cervical series shows a marked widening of the neck posteriorly.

In comparing the cervical series of *Carnotaurus* and *Majungasaurus*, I have identified additional characters that differentiate these two forms; these morphological differences in no way question the assignment of the Malagasy taxon to Abelisauridae, but potentially highlights a morphological differentiation within the clade as proposed by Canale et al. (2009).

Abelisaurids have a set of specialized vertebral features, which probably had a close functional relationship, both to allow movement of the head and to maintain the body balance. The unique morphology of the vertebral structures in the neck of *Carnotaurus* may suggest a rearrangement of the muscles. The absence of a well-developed neural spine for muscle attachment and the extreme development of the epiphyses, may have favoured the greater development of some cervical muscles at the expense of others, thus modifying the capability of *Carnotaurus* to perform certain movements.

The robust neck of *Carnotaurus* seems to have been the anterior extension of the long and quite stiff axis, continued by a dorsal sector whose vertebrae have accessory articulations (hyposphene–hypantrum) to increase structural rigidity, a sector composed of sacral vertebrae fused firmly, and an anterior caudal region with vertebrae that, in addition to accessory articulations (hyposphene–hypantrum), exhibits a particular expansion of the transverse processes that would have provided increased rigidity in this sector of the column. All these modifications result in a vertebral axis with little flexibility between the base of the neck and the first third of the caudal appendage.

Conclusion

The neck appears to be more robust in *Carnotaurus* than in *Majungasaurus*. This robustness is also widespread in the rest of the vertebral column of the Patagonian genus (e.g., greater development of the hyposphene–hypantrum complex in dorsal vertebrae, extreme fusion of vertebral components of the sacrum, specialization of the proximal segment of the tail providing more rigidity). Perhaps the differences observed in the vertebral structures could result in differential development of certain groups of muscles present in the neck of these dinosaurs. For example, in *Carnotaurus*, the extreme reduction of the neural spines and the remarkable development of the epiphysis should have led to a restructuring of the cervical muscles, much more than in *Majungasaurus*. Future study of the neck in *Aucasaurus*, another carnosaurin, should allow a better assessment of whether these interpretations apply more widely within the clade, or merely to *Carnotaurus*.

This detailed study of cervical morphology has revealed diagnostic characters of the family Abelisauridae, and also for less inclusive clades, such as Brachyrostra. This region presents a particular morphology that distinguishes it clearly from other theropods.

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