

The caudal vertebral series in abelisaurid dinosaurs

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Méndez, A.H. 2014. The caudal vertebral series in abelisaurid dinosaurs. *Acta Palaeontologica Polonica* 59 (1): 99–107.

The caudal vertebrae of abelisaurid theropods show notable variations in the shape of the transverse process, among other characters, and these distinguish the two subclasses Brachyrostra and Carnotaurini. The vertebrae in the proximal third of the tail in abelisaurids, especially derived taxa, show adaptations that provide considerable rigidity, when compared to other theropod dinosaurs, especially Maniraptora, which have highly flexible tails. This continues the considerable rigidity in the neck, trunk, and sacral region in abelisaurids, and is consistent with the hypothesis that South American abelisaurids evolved in isolation from those that inhabited India and Madagascar.

Key words: Dinosauria, Theropoda, Abelisauridae, tail morphology, caudal vertebrae, functional morphology.

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Received 24 August 2012, accepted 5 December 2012, available online 20 December 2012.

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Introduction

Abelisaurid theropods are the best-known carnivorous dinosaur group from Gondwana. The record of this clade includes more than 10 recognized species, some of which are exceptionally well preserved, like *Carnotaurus sastrei* (Bonaparte 1985), *Majungasaurus crenatissimus* (Sampson et al. 1998), *Aucasaurus garridoi* (Coria et al. 2002), and *Skorpiovenator bustingorryi* (Canale et al. 2009).

Although much of the detailed morphological description on the clade thus far has focused on cranial morphology, vertebral anatomy has received increased attention. Several researchers (e.g., Bonaparte et al. 1990; Coria et al. 2002; O'Connor 2007; Méndez 2010, in press) have detailed axial anatomy and provided valuable information regarding vertebral morphology in Abelisauridae, documenting a number of features that differentiate members of this group from other theropods. Included among these features are: hypertrophied cervical epiphyses, elongated cervical rib shafts, increased fusion of elements into the sacral complex, caudal vertebrae with long transverse processes, and expanded distal ends of transverse processes in caudal vertebrae (Bonaparte et al. 1990; Bonaparte 1991; Coria and Salgado 1998; Coria et al. 2002; Rauhut et al. 2003; O'Connor 2007; Méndez 2010, in press).

Bonaparte, Novas, and Coria (1990) described the vertebral morphology of *Carnotaurus sastrei*, documenting for the first time the remarkable features of abelisaurids, that were hitherto unknown in other theropod dinosaurs. Sub-

sequent to this work, additional discoveries of abelisaurids from South America (Coria and Salgado 1998; Coria et al. 2002; Kellner and Campos 2002; Calvo et al. 2004; Martínez et al. 2004; Rauhut et al. 2003; Novas et al. 2008; Canale et al. 2009; Ezcurra and Méndez 2009) and other former Gondwanan landmasses such as Madagascar (Sampson et al. 1998; O'Connor 2007), and India (Wilson et al. 2003; Novas et al. 2010) added significantly to our knowledge of abelisaurid vertebral morphology.

In this work I provide a detailed comparison of the caudal vertebral series of abelisaurids. The aim is to document the different morphologies present in the tail of abelisaurids in relation to other theropods, in addition to denoting the trends and specific differences observed within the group. I further highlight the phylogenetic value of certain of these features.

Institutional abbreviations.—DGM, Departamento Nacional da Produção Mineral, Rio de Janeiro, Brasil; FMNH, Field Museum of Natural History, Chicago, USA; GSI, Geological Survey of India, Kolkata, India; ISIR, Geology Museum, Indian Statistical Institute, Kolkata, India; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCF, Museo Municipal “Carmen Funes”, Plaza Huinca, Neuquén, Argentina; MMCH, Museo Municipal “Ernesto Bachmann”, Villa El Chocón, Neuquén, Argentina; MPEF, Museo Paleontológico “Egidio Feruglio”, Trelew, Chubut, Argentina; MPM, Museo Regional Provincial “Padre Manuel Jesús Molina”, Santa Cruz, Argentina; MUPC, Museo de la Universidad Nacional del Comahue,

Neuquén, Argentina; UA, Département de Paléontologie, Université d'Antananarivo, Antananarivo, Madagascar.

Other abbreviations.—CL, length of the vertebral centrum; TPL, transverse processes.

Material and methods

Caudal vertebral remains of the following specimens were compared: *Aucasaurus garridoi* (MCF-PVPH-236), *Carnotaurus sastrei* (MACN-PV-CH 894), *Ekrixinatosaurus novasi* (MUCPV-294), *Ilokelesia aguadagrandensis* (MCF-PVPH-35), *Majungasaurus crenatissimus* (UA 8678; FMNH PR 2100), *Pycnonemosaurus nevesi* (DGM 859-R), *Rahiolisaurus gujaratensis* (ISIR 408–429, 518–545), *Rajasaurus narmadensis* (GSI 21141), *Skorpiovenator bustingorryi* (MMCH-PV 48), and three specimens of Abelisauridae indet. (MPM-99, MPEF V 1699, and MACN-PV-RN 1012).

Description and comparisons

There are no complete caudal series from any known abelisaurid, although several specimens preserve at least partial remains. Articulated caudal vertebrae are present in *Carnotaurus* (caudals 1–7), *Majungasaurus* (caudals 1–5 and 5–29; following O'Connor 2007), *Aucasaurus* (caudals 1–13) and *Skorpiovenator* (caudals 1–13, although this material still remains to be completely prepared for a detailed comparison). The tail has been divided into three sections, anterior (caudals 1 to 10), middle (caudals 11 to 16), and posterior (caudals 17 to the end). This division is arbitrary and is based on certain modifications that are observed along the caudal series. Its validity may only extend to the abelisaurids.

Anterior caudal vertebrae (Fig. 1).—The anterior caudal vertebrae are most common (ten caudal vertebrae in *Majungasaurus*, *Aucasaurus*, and *Skorpiovenator*, eight in *Carnotaurus*, three in *Ekrixinatosaurus* and Abelisauridae indet. (MPM-99), two in *Pycnonemosaurus* and Abelisauridae indet. (MPEF-V-1699), and one in *Rajasaurus*, *Rahiolisaurus*, and Abelisauridae indet. (MACN-RN-1012).

The vertebral centra are amphicoelous, almost higher than long, medially compressed, thus presenting the typical spool-shape. In lateral view, the first four caudal vertebrae

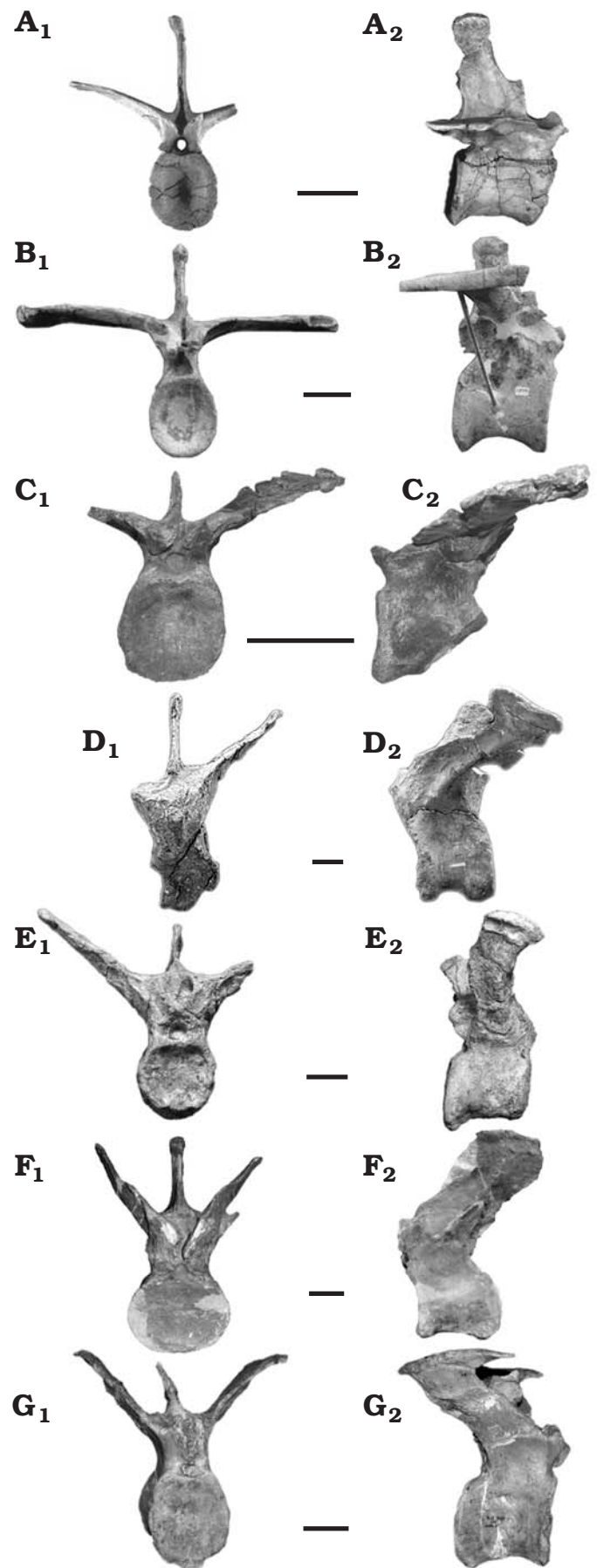


Fig. 1. Anterior caudal vertebrae of abelisaurids. **A.** *Majungasaurus crenatissimus* Déperet, 1896 (UA 8678) from Maastrichtian; Madagascar. **B.** Abelisauridae indet. (MPM-99) from Turonian; Patagonia. **C.** Abelisauridae indet. (MPEF-V 1699) from Hauterivian–Barremian; Patagonia. **D.** *Ekrixinatosaurus novasi* Calvo, Rubilar-Roger, and Moreno, 2004 (MUCPV 294) from Cenomanian; Patagonia. **E.** Abelisauridae indet. (MACN-PV-RN 1012) from Santonian; Patagonia. **F.** *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894) from Maastrichtian; Patagonia. **G.** *Aucasaurus garridoi* Coria, Chiappe, and Dingus, 2002 (MCF-PVPH 236) from Campanian; Patagonia, in anterior (A₁–G₁) and lateral (A₂–G₂) views. Scale bars 5 cm.

exhibit a slightly concave anterior margin, whereas the posterior one is convex, as seen in *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Ekrixinatosaurus*, *Rajasaurus*, *Rahiolisaurus*, MPEF-V-1699, MPM-99, and MACN-RN-1012 (Fig. 1). The remainder of the anterior caudal vertebrae (caudals 5–10) exhibit straight margins.

The ventral surface of anterior caudal vertebrae of *Aucasaurus*, *Majungasaurus*, MPM-99, MPEF-V-1699, and MACN-RN-1012 exhibit a longitudinal groove, whereas in *Ekrixinatosaurus* and *Rajasaurus* the ventral surface of the centrum exhibits a keel. In *Carnotaurus*, the ventral surface is too damaged to recognize either of the above mentioned features. The sides of the anterior caudal centra do not have any pneumatic features, although in *Carnotaurus*, *Aucasaurus*, and *Ekrixinatosaurus* they do exhibit a slight depression.

Regarding the neural arch, transverse processes exhibit both size and shape features that are characteristic of abelisaurids. For example, Rauhut et al. (2003) observed that the length of the transverse processes (TPL) relative to the length of the vertebral centrum (CL) exhibits a higher ratio than in other groups of carnivorous dinosaurs. The TPL/CL ratio is greater than 1.3 in *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Skorpiovenator*, *Ekrixinatosaurus*, MPM-99, MPEF-V-1699, and MACN-RN-1012 (Table 1). This ratio is less than 1.3 in *Masiakasaurus* and *Ceratosaurus*, and is close to unity in *Allosaurus*. The ventral surface of the transverse processes of anterior caudal vertebrae of abelisaurids (e.g., *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Rahiolisaurus*, MPM-99, MPEF-V-1699, MACN-RN-1012) exhibit a centrodiaepophyseal lamina (Fig. 2A). This lamina is present in *Masiakasaurus* (Carrano et al. 2002), but not in *Allosaurus* or *Ceratosaurus*. There is also a bony ridge on the ventral surface of the distal end of the transverse processes (Fig. 2B) that run in an anteroposterior direction. This ridge is present in *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, MACN-RN-1012, and possibly in *Skorpiovenator*, although in the latter the state of preservation does not allow absolute confirmation (Juan Canale, personal communication 2012). This structure was identified by Ezcurra and Méndez (2009) and might be the same as that proposed by Carrano et al. (2011) and used by Persons and Currie (2011) to differentiate the transverse process from the caudal rib. The distal end of the transverse processes presents a remarkable fan-shaped expansion in most abelisaurids, including *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Pycnonemosaurus*, *Skorpiovenator*, MPM-99, MPEF-V-1699, and MACN-RN-1012. In *Rahiolisaurus* the distal ends are broken so it is unknown if these exhibit the expanded condition. In *Majungasaurus*, the transverse processes are not distally expanded, a condition similar to that in *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*. In relation to the distal expansion of the transverse processes, an anterior projection (Fig. 2C) can be observed in *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, MPM-99, and MACN-RN-1012. In MPEF-V-1699 this feature is not visible due to the poor state of preservation of this part of the transverse process.

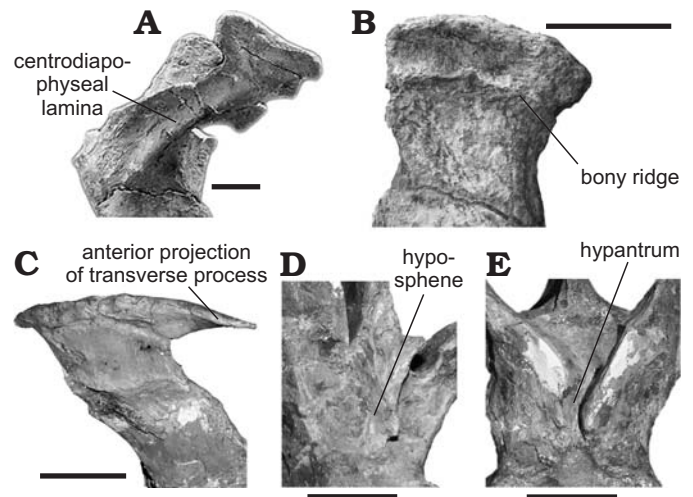


Fig. 2. Detail of several features of abelisaurid caudal vertebrae. **A.** Centrodiaepophyseal lamina of *Ekrixinatosaurus novasi* Calvo, Rubilar-Roger, and Moreno, 2004 (MUCPv 294) from Cenomanian; Patagonia. **B.** Bony ridge in ventrodistal end of transverse process of MACN-PV-RN-1012 from Santonian; Patagonia. **C.** Expanded distal end of transverse process with anterior projection of *Aucasaurus garridoi* Coria, Chiappe, and Dingus, 2002 (MCF-PVPH 236) from Campanian; Patagonia. **D.** Hyposphene (**D**) and hypantrum (**E**) of *Carnotaurus sastrei* Bonaparte, 1985 (MACN-CH 894) from Maastrichtian; Patagonia. Scale bars 5 cm.

The external margin of the transverse processes is convex in *Carnotaurus*, *Aucasaurus*, and MACN-RN-1012, and straight in *Majungasaurus*, *Ekrixinatosaurus*, *Pycnonemosaurus*, and MPM-99.

The position of the transverse processes with respect to the horizontal plane is another distinctive feature of certain abelisaurids. In *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, and MACN-RN-1012 the angle is greater than 40° . In *Pycnonemosaurus*, *Skorpiovenator*, MPEF-V-1699, and MPM-99 the degree of inclination is $\sim 30^\circ$, whereas in *Majungasaurus* and *Rahiolisaurus* it is lower at $\sim 20^\circ$. Another outstanding feature of anterior caudal neural arches is the presence of the accessory hyposphene-hypantrum articulations (Fig. 2D, E), a characteristic of *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Pycnonemosaurus*, MPM-99, and MACN-PV-RN-1012. This feature is not present in the anterior caudal vertebrae of *Majungasaurus* nor in the basal tetanuran *Allosaurus*, although it is present in *Masiakasaurus* (Carrano et al. 2011) and *Ceratosaurus* (Madsen and Welles 2000).

Middle caudal vertebrae (Fig. 3).—Vertebrae belonging to the middle section of the tail are preserved in *Majungasaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Ilokelesia*, and *Rahiolisaurus*. The mid-caudal vertebrae of these abelisaurids are distinguished by having amphicoelous and elongated centra (almost twice the height of the centrum), with subcircular articular surfaces, as well as facets to articulate with the haemal arches and a clearly marked ventral concavity in lateral view. These features are also present in the mid-caudal vertebrae of *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*, except that in the first two genera the articular surfaces are slightly ovoid. The transverse processes of the mid-caudal vertebrae

Table 1. Measurements of caudal vertebrae in Abelisauridae (in cm). Abbreviations: CL, maximum length of centrum; ACW, width of anterior articular surface; ACH, height of anterior articular surface; PCW, width of posterior articular surface; PCH, height of posterior articular surface; TH, total height; CL/PCH, maximum length of centrum/ height of posterior articular surface; NSH, height of neural spine; NSL, length of neural spine; NSW, width of neural spine; TPL, transverse process length; TPL/CL, transverse process length/maximum length of centrum; MCW, width of medial part of centrum; * measures underestimated by damage or deformation; – missing data. ¹ The measurements of *Majungasaurus* were taken from O'Connor (2007).

Caudal vertebrae	CL	ACW	ACH	PCW	PCH	TH	CL/PCH	NSH	NSL	NSW	TPL	TPL/CL	MCW
<i>Carnotaurus sastrei</i> (MACN-PV-CH 894)													
CD1	12.7	13.8	12.7	14.1	12.8	34.1	0.90	14.0	–	1.7	18.5	1.46	9.3
CD2	12.3	14.0	–	13.2	–	–	–	13.5	–	–	17.5	1.42	–
CD3	12.6	13.3	12.1	–	–	32.8	–	13.0	–	1.6	9.0*	0.71*	–
CD4	13.2	–	–	9.2	11.0	34.7	1.20	14.0	–	1.8	18.5	–	–
CD5	–	–	–	–	–	–	–	13.5	–	1.5	16.6	1.40	–
CD6	–	–	–	–	–	–	–	11.9*	–	1.7	16.5	–	–
CD7	–	–	–	–	–	–	–	11.5	–	–	17.5	–	–
CD9	9.9	6.0	7.3	7.2	7.6	–	1.30	–	–	–	–	–	5.0
<i>Majungasaurus crenatissimus</i> (FMNH PR 2100 / UA 8678) ¹													
CD1 (FMNH PR 2100)	8.5	–	–	7.0	7.4	23.5	1.15	–	4.4	0.9	–	–	3.4*
CD2	9.6	–	–	6.8	7.7	23.3*	1.25*	–	–	–	–	–	3.4
CD3	9.8	–	–	6.2	7.0	23.0*	1.40*	–	–	–	–	–	3.3
CD4	9.8	–	–	5.8	6.5	22.8	1.51	–	3.4	1.1	–	–	3.1
CD5	9.7	–	–	5.8	6.3	21.8*	1.54*	–	–	0.9	–	–	2.9
CD6	9.3*	–	–	5.7	5.9	21.0	1.58*	–	2.3	1.3	–	–	2.7*
CD7	9.6	–	–	–	–	19.4	–	–	2.3	1.6	–	–	–
CD8	9.7	–	–	5.3*	5.3*	18.6	1.83*	–	2.2	1.3	–	–	2.8
CD9	9.6	–	–	4.8	5.3*	17.8	1.81*	–	2.1	1.2	–	–	–
CD10	9.4	–	–	4.5	5.1	17.2	1.84	–	2.2	1.2	–	–	2.5
CD11	9.1	–	–	5.1	5.0	15.6	1.82	–	2.1	1.0	–	–	3.7
CD12	9.2	–	–	4.8	5.0	14.5	1.84	–	1.9	1.2	–	–	3.8
CD13	9.0	–	–	4.8	5.0	13.9	1.80	–	1.7	1.1	–	–	3.6
CD14	9.1	5.2	4.8	5.1	4.9	12.3	1.86	5.7	1.9	1.0	1.7	0.19	3.8
CD15	9.1	–	–	4.9	5.1	11.1	1.78	–	1.6	0.8	–	–	3.6
CD16	8.9	–	–	4.7	5.0	10.0	1.78	–	1.5	0.6	–	–	3.4
CD17	8.7	–	–	4.6	4.8	9.6	1.81	–	1.7	0.6	–	–	3.3
CD18	8.4	–	–	4.4	4.7	9.3	1.79	–	1.7	0.6	–	–	3.2
CD19	8.2	–	–	4.3	4.4	8.7	1.86	–	1.5	0.6	–	–	3.3
CD20	7.9	–	–	4.2	4.2	8.1	1.88	–	1.4	0.5	–	–	3.3
CD21	7.9	–	–	3.8	4.1	8.0	1.93	–	1.5	0.4	–	–	3.2
CD22	7.7	–	–	3.7	4.0	7.2	1.93	–	–	–	–	–	3.0
CD23	7.5	–	–	3.4	3.6	6.7	2.08	–	–	–	–	–	3.1
CD24	7.1	3.6	3.4	3.0	3.2	5.7	2.22	1.2	–	–	–	–	2.8
CD25	6.8	–	–	2.6	2.7	4.7	2.52	–	–	–	–	–	1.5
CD1(UA 8678)	7.1	–	–	5.2	5.9	17.6	1.20	–	2.8	0.8	–	–	3.0
CD2	7.0	–	–	5.0	5.6	17.4	1.25	–	2.9	0.7	–	–	2.9
CD3	7.1	–	–	4.5	5.2	–	1.37	–	2.5	0.7	–	–	2.5*
CD4	7.3	5.9	6.4	4.5	4.9	16.0	1.49	8.1	2.2	0.6	9.8	1.34	3.1
CD5	7.5	–	–	4.3	4.8	–	1.56	–	–	–	–	–	2.6
<i>Aucasaurus garridoi</i> (MCF-PVPH 236)													
CD1	9.8	9.7	10.4	8.3	9.8	28.0	1.00	9.6	–	1.6	12.7	1.30	6.1
CD2	9.8	8.7	10.0	8.0	9.4	23.0	1.04	6.4*	–	1.3	11.8	1.20	4.0
CD3	9.6	7.9	9.1	7.3	8.8	23.0	1.09	4.8*	–	–	11.6	1.21	3.3
CD4	9.2	6.8	8.4	6.7	8.4	21.6	1.10	9.2	–	0.9	11.6	1.26	3.1
CD5	6.6	7.4	8.5	–	–	23.4	–	8.8	–	0.9	10.0	1.51	3.3
CD6	6.3	–	–	6.0	7.7	22.8	0.82	8.8	–	1.0	–	–	2.8
CD7	8.7	5.8	7.2	5.4	6.6	20.0	1.32	8.2	–	0.8	10.4	1.20	2.1
CD8	9.2	5.4	6.5	5.2	6.3	19.3	1.46	8.7	–	0.7	11.9	1.29	2.3

Caudal vertebrae	CL	ACW	ACH	PCW	PCH	TH	CL/PCH	NSH	NSL	NSW	TPL	TPL/CL	MCW
CD9	9.3	5.6	5.9	5.4	5.9	18.3	1.58	—	—	—	12.3	1.32	2.4
CD10	8.9	5.6	5.4	5.6	5.3	14.2	1.68	—	—	—	11.4	1.28	3.1
CD11	8.4	5.4	5.1	5.2	5.2	9.2	1.62	—	—	—	12.6	1.50	2.9
CD12	8.2	5.5	4.7	4.9	5.0	10.4	1.64	—	—	—	11.0	1.34	3.2
<i>Ekrixinatosaurus novasi</i> (MUPCv 294)													
Anterior caudal	11.9	11.8	9.9	10.8	13.9	30.1	0.86	11.9	—	1.5	16.7	1.40	1.4
Mid caudal	9.7	9.4	—	8.3	9.4	—	1.03	—	—	—	—	—	5.5
Mid caudal	9.4	6.1	6.7	5.3*	6.3*	14.4*	1.49*	3.6	—	1.4	7.9	0.84	3.4
Mid caudal	9.0	6.1	5.5	5.4	5.5	11.2*	1.64	3.0	—	0.7	9.0	1.00	3.4
Posterior caudal	8.9	5.2	5.0	4.6	4.9	8.1*	1.82	—	—	—	4.5*	0.51*	3.5
<i>Ilokelesia aguadagrandensis</i> (MCF-PVPH 35)													
Mid caudal	9.2*	6.2	4.1*	6.0*	5.3*	9.3*	1.74*	3.1	—	0.7	10.0	1.09*	3.9
Mid caudal (fusionated)	8.4	5.2	4.6	—	—	8.5	—	—	—	—	7.7	0.92	3.4
Mid caudal (fusionated)	8.3	—	—	—	—	—	—	—	—	—	6.8	0.82	3.4
Mid caudal (fusionated)	8.2	—	—	—	—	—	—	—	—	—	5.7*	0.70*	3.2
<i>Pycnonemosaurus nevesi</i> (DGM 859-R)													
Anterior caudal	—	10.7	9.6	—	—	22.5	—	6.4	1.3	—	7.6*	—	—
Anterior caudal	—	8.1	9.9	—	—	20.5	—	—	—	—	5.5*	—	—
<i>Rajasaurus narmadensis</i> (GSI 21141)													
Anterior caudal	11.4	7.5	8.8	—	—	—	—	—	—	—	—	—	4.1
<i>Skorpiovenator bustingorryi</i> (MMCH-PV 48)													
CD1	10.7	—	—	—	—	—	—	—	—	—	—	—	—
CD2	11.0	—	—	—	—	—	—	—	—	—	12.7*	1.15*	—
CD3	10.2	—	—	—	—	—	—	—	—	—	15.0	1.47	—
CD4	10.1	—	—	—	—	—	—	—	—	—	14.0	1.39	—
CD5	10.2	—	—	—	—	—	—	—	—	—	12.5	1.23	—
CD6	10.0	—	—	—	—	—	—	—	—	—	10.3	1.03	—
CD7	9.9	—	—	—	—	—	—	—	—	—	—	—	—
CD8	10.0	—	—	—	—	—	—	—	—	—	—	—	—

in *Aucasaurus*, *Ekrixinatosaurus*, and *Ilokelesia* are well developed and, as in the anterior caudals, have expanded ends. *Rahiolisaurus* also exhibits well-developed transverse processes without expanded distal ends. In *Majungasaurus* the transverse processes are less developed than in preceding vertebrae with distal ends that taper.

The distal expansion in *Aucasaurus* exhibits the same anterior projection observed in the anterior caudals, whereas *Ekrixinatosaurus* and *Ilokelesia* exhibit distal expansion in both anterior and posterior directions. In contrast to preceding caudal vertebrae, where the base of the transverse process is nearly as wide as the length of the centrum, the transverse processes are narrower. The position of the transverse process along the anteroposterior axis of the neural arch also varies, being located in the middle part of the vertebra in *Aucasaurus*, *Ekrixinatosaurus*, *Ilokelesia*, *Ceratosaurus*, and *Allosaurus*. The transverse process is positioned more posteriorly in *Majungasaurus* (and *Masiakasaurus*) being located

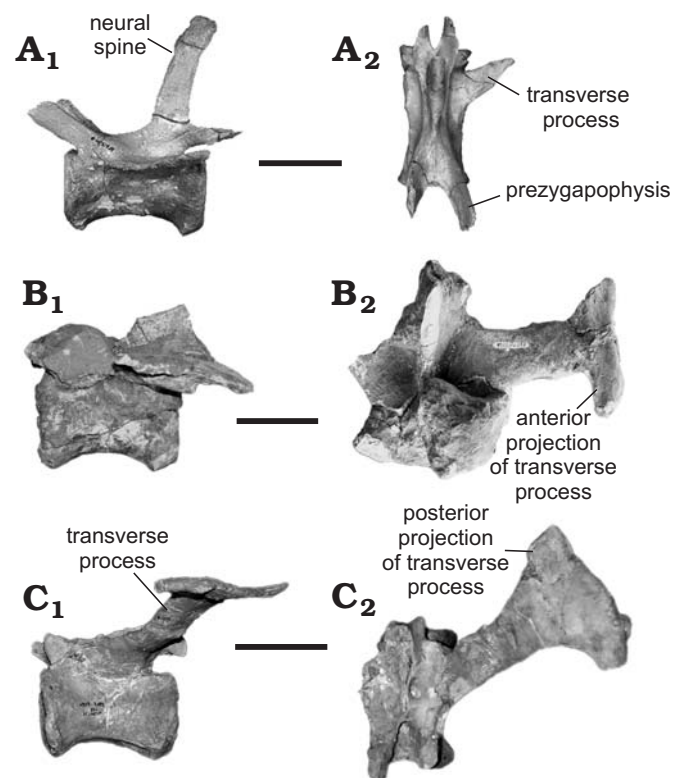


Fig. 3. Middle caudal vertebrae of abelisaurids. **A.** *Majungasaurus crenatissimus* Déperet, 1896 (FMNH PR 2100) from Maastrichtian; Madagascar. **B.** *Ekrixinatosaurus novasi* Calvo, Rubilar-Roger, and Moreno, 2004 (MUCPv 294) from Cenomanian; Patagonia. **C.** *Aucasaurus garridoi* Coria, Chiappe, and Dingus, 2002 (MCF-PVPH 236) from Campanian; Patagonia, in lateral (A_1 – C_1) and dorsal (A_2 – C_2) views. Scale bars 5 cm.

in the posterior half of the vertebra. The prezygapophysis in the mid-caudals is slightly elongated and extends beyond the anterior edge of the centrum, less than 1/4 of its length, as in *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*. It is also quite robust and gently sloping dorsally. The postzygapophysis in *Majungasaurus*, *Aucasaurus*, *Ekrixinosaurus*, and *Ilokelesia*, as in *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*, is located on the posterior margin of the centrum and its posterior projection is not very pronounced. In all abelisaurids the neural spine is located in the posterior half of the vertebra, as is in the mid-caudals of *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*.

Posterior caudal vertebrae (Fig. 4).—Posterior caudal vertebrae have been described only in *Majungasaurus* (O'Connor 2007) and *Rahiolisaurus* (Novas et al. 2010). These vertebrae are amphicoelous, with very elongated centra. The length is twice the height, this ratio being even higher in the more posterior caudals, and the articular surfaces are sub-circular in outline. The ventral facets that articulate with the haemal arches remain distinctive, as they were in previous caudal vertebrae. In *Majungasaurus*, there is a slight ventral ridge that cannot be called a well-defined keel, whereas in *Rahiolisaurus* the ventral surface is flat. On the lateral surface of the vertebral body, there is a depression just below a longitudinal ridge that appears to be a vestige of the transverse process. Most of these features of the centrum are also observed in the vertebral centra of the posterior caudals of *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus*, suggesting

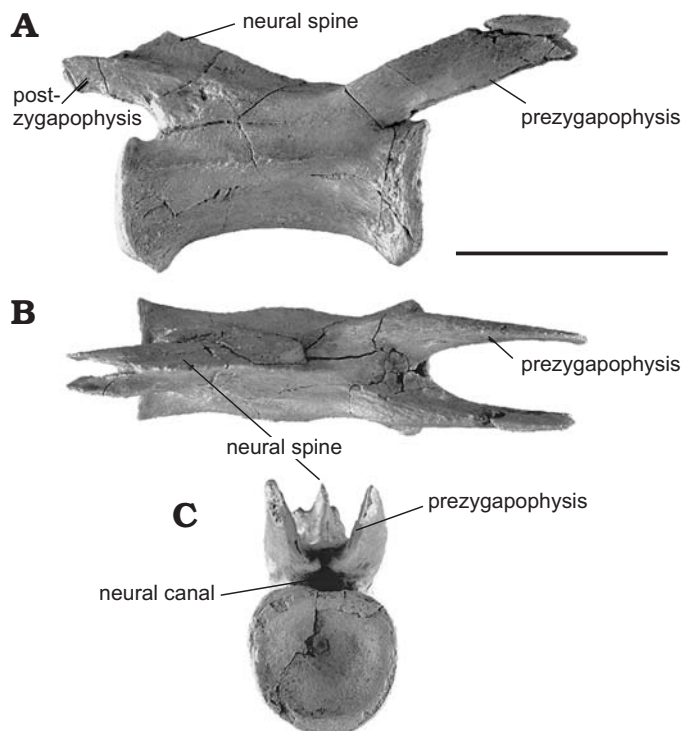


Fig. 4. Posterior caudal vertebra of *Majungasaurus crenatissimus* Déperet, 1896 (FMNH PR 2100) from Maastrichtian; Madagascar, in lateral (A), dorsal (B), and anterior (C) views. Scale bar 5 cm.

that this part of the caudal appendage retains more plesiomorphic characters than the anterior and middle portion of the tail, although in *Masiakasaurus* the elongation of the centrum is three times the height.

The development of the neural arch in the posterior caudal vertebrae of *Majungasaurus* begins at approximately 1.5 times the height of the centrum and decreases to half that height in the last caudal segments. The prezygapophysis is projected anterodorsally, surpassing the anterior margin of the vertebral body by 50% of its length (O'Connor 2007), similar to that in *Masiakasaurus* (Carrano et al. 2002), and *Allosaurus* (Madsen 1976). The facet of the prezygapophysis is located anterior to the anterior margin of the centrum in the posterior caudals, unlike the condition in the mid-caudals, where the prezygapophyseal facet is located on the front edge of the centrum (O'Connor 2007). This morphology is very different from the posterior caudals of *Ceratosaurus* in which the anterior projection of the prezygapophysis and the prezygapophyseal facet are positioned immediately dorsal to the anterior margin of the centrum. The postzygapophysis is projected posteriorly between 15 to 25% of the length of the centrum, whereas in *Masiakasaurus*, *Ceratosaurus*, and *Allosaurus* this projection is almost nonexistent. The neural spine in the posterior caudal vertebrae of *Majungasaurus* is laminar as in *Ceratosaurus*, and decreases in height more caudally along the series. In the posterior region of the tail, the neural spine becomes gradually elongate and short, such that it spans approximately half the length of the centrum. This is also observed in *Masiakasaurus* and differs from the posterior caudals of *Ceratosaurus* and *Allosaurus* in which the neural spine is positioned over the posterior half of the centrum.

Discussion

Abelisaurid caudal characters

Previous authors have recognized several apomorphies in the caudal vertebrae of abelisauroids (Bonaparte 1991; Bonaparte et al. 1990; Coria and Salgado 1998; Coria et al. 2002; Rauhut et al. 2003; Canale et al. 2009; Ezcurra and Méndez 2009). However, at least within Theropoda, vertebral characters are not yet decisive for phylogenetic analyses. The detailed review of morphological features in the caudal vertebrae indicated diagnostic features of Abelisauridae and less inclusive clades (e.g., Brachyrostra, Carnotaurini). The few phylogenetic analyses that have included the clade Abelisauridae (Carrano and Sampson 2008; Canale et al. 2009) improved their resolution when data from detailed morphological analysis of the vertebral column were included (Méndez 2010, unpublished data). In this regard, derived features of Abelisauroidea, and lesser inclusive clades are discussed below.

Length of the transverse process in anterior caudal vertebrae.—The length of the transverse process in relation to

the length of their respective vertebral body is a character proposed by Rauhut et al. (2003). In representative theropods (e.g., *Dilophosaurus*, *Allosaurus*) the TVP/CL ratio ranges from 1 to 1.1. TVP/CL increases in *Ceratosaurus* (Madsen and Welles 2000) to values ranging between 1.1 and 1.3. Finally, the abelisaurids *Carnotaurus*, *Majungasaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Pycnonemosaurus*, MPM-99, MACN-PV-RN-1012, and MPEF-V-1699 exhibit much longer transverse processes in relation to the centrum, this ratio being greater than 1.3 (see Table 1).

Centrodiapophyseal lamina in anterior and mid-caudal vertebrae.—This feature was first proposed by Rauhut et al. (2003). The presence of a centrodiapophyseal lamina in anterior and mid-caudal vertebrae is a character shared by *Carnotaurus*, *Majungasaurus* (O'Connor 2007), *Aucasaurus* (Coria et al. 2002), *Ekrixinatosaurus* (Calvo et al. 2004), *Skorpiovenator* (Canale et al. 2009), *Ilokelesia* (Coria and Salgado 1998), *Pycnonemosaurus* (Kellner and Campos 2002), MPM-99 (Martínez et al. 2004), MACN-PV-RN-1012 (Ezcurra and Méndez 2009) and MPEF-V-1699 (Rauhut et al. 2003). Carrano et al. (2002) also identify this lamina in *Masiakasaurus*. This feature has not been documented in any other group of theropods and could be considered a synapomorphy of Abelisauroidae.

Accessory articulation hyposphene-hypantrum in anterior and mid-caudal vertebrae.—This feature was first proposed by Coria et al. (2002). The presence of a well defined hyposphene in anterior and middle caudal vertebrae is a feature exhibited by the abelisaurids *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Pycnonemosaurus*, MPM-99, MACN-PV-RN-1012, and MPEF-V-1699. However, this feature is not present in other abelisaurids such as *Ilokelesia* and *Majungasaurus*, nor in the abelisauroid *Elaphrosaurus*, the tetanuran *Allosaurus* and *Herrerasaurus*. It should be noted that the hyposphene-hypantrum articulation is not a unique feature within Abelisauridae since it is also present in *Masiakasaurus*, *Ceratosaurus*, and *Dilophosaurus*.

Expansion and projection of the transverse processes in anterior and mid-caudal vertebrae.—This feature was first proposed by Coria and Salgado (1998). The transverse processes in the anterior and mid-caudals of the abelisaurids *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Pycnonemosaurus*, MPM-99, MACN-PV-RN-1012, and MPEF-V-1699 are characterized by a marked expansion of the distal end and an anterior projection of same. In *Ilokelesia* this expansion is present but the projection is not only anterior but also posterior. This expansion and projection of the distal end of the transverse process is not present in *Majungasaurus* or in other theropods.

Ventrodiscal bony ridge in the distal end of the transverse processes in anterior caudal vertebrae.—This feature was first proposed by Ezcurra and Méndez (2009). The ventral surface of the transverse processes in the abelisaurids *Car-*

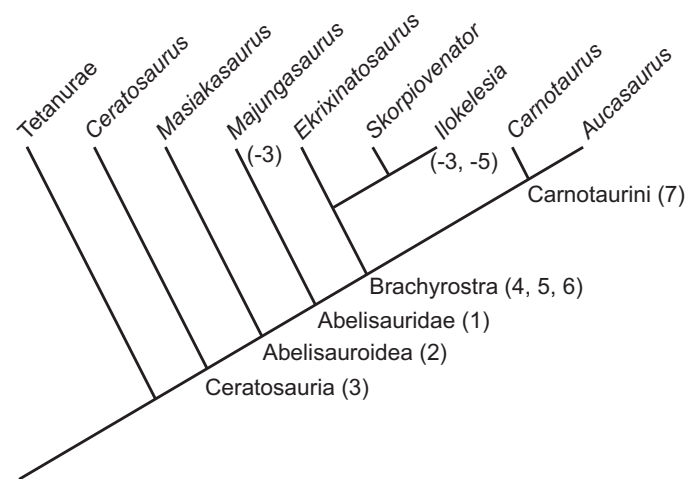


Fig. 5. Distribution of selected caudal vertebral characters in recent phylogenetic analysis (Modified from Canale et al. 2009).

notaurus, *Aucasaurus*, *Ekrixinatosaurus*, and MACN-PV-RN-1012 presents a bony ridge at its distal end. This character has not been observed in the abelisaurids *Majungasaurus*, *Ilokelesia* and *Pycnonemosaurus*, nor in any other theropod (e.g., *Ceratosaurus*, *Elaphrosaurus*, *Masiakasaurus*, *Allosaurus*, *Dilophosaurus*).

Orientation angle of the transverse processes with respect to the horizontal in anterior caudal vertebrae.—This feature was proposed by Bonaparte et al. (1990). The transverse processes in caudal vertebrae tend to be located on the horizontal plane in *Herrerasaurus* and *Dilophosaurus*, which could be considered the ancestral condition for this character. In other theropods (e.g., *Allosaurus*, *Ceratosaurus*) the transverse processes of anterior caudal vertebrae exhibit a slight dorsal inclination not exceeding 20°, as in *Majungasaurus*. Other abelisaurids present a dorsal inclination of the transverse processes of approximately 30° (i.e., *Pycnonemosaurus*, *Skorpiovenator*, MPM-99, MPEF-V-1699). However, in the anterior caudal vertebrae of *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, and MACN-PV-RN-1012, this feature becomes more extreme, reaching inclinations of at least 40°.

External margin of the transverse processes on caudal vertebrae.—This feature was proposed by Canale et al. (2009). The external edge of the transverse processes of caudal vertebrae is straight in basal theropods (e.g., *Dilophosaurus* and *Ceratosaurus*) and also in the noosaurid *Masiakasaurus* (Carrano et al. 2002) and the abelisaurids *Majungasaurus*, *Ekrixinatosaurus*, *Pycnonemosaurus*, and MPM-99, in what could be considered the plesiomorphic condition of this character. *Ilokelesia* shows a particular morphology of the external edge of the transverse process, being notably concave. On the other hand, a convex external margin seems to be distinctive of Carnotaurini (i.e., *Carnotaurus*, *Aucasaurus*, MACN-PV-RN-1012).

Most of the characters present in the abelisaurid caudal series allow an accurate identification of the less inclusive

groups Brachyrostra (Canale et al. 2009) and Carnotaurini (Coria et al. 2002: fig. 5). This would imply a greater degree of specialization in this sector of the vertebral column within more derivatives abelisaurids.

Function of the abelisaurid tail

The peculiar morphology of the caudal series of abelisaurid theropods probably gave it functional properties that have not been observed in other theropods. As observed by Méndez (2010), and Persons and Currie (2011), the first third of the caudal appendage of the abelisaurids, in particular the most derived (e.g., *Carnotaurus*, *Aucasaurus*), is characterized by features that promote the structural rigidity of this region of the tail (i.e., presence of accessory articulation hyposphene-hypantrum, expanded distal end of transverse processes, presence of centrodiapophyseal lamina). The presence, in most members of this group, of a slender anterior projection on the transverse processes that contacts, at least in *Carnotaurus* and *Aucasaurus* with the transverse process of the preceding caudal vertebra is also linked with this stiffness. Moreover, in *Aucasaurus* the cranial projections of the transverse processes of caudal 1 contact the caudal ends of both ilia (Coria et al. 2002). Although not preserved in the holotype of *Carnotaurus*, moulds of its transverse processes associated with skin patches indicate that the condition described before for *Aucasaurus* is also present in *Carnotaurus* (Coria et al. 2002). In *Aucasaurus* the awl-like projections of its transverse processes laterally embrace the ilia. Although these projections are not preserved in the first caudals of *Carnotaurus*, notches for their reception are visible on the lateral surface of the dorsocaudal corner of the ilia (Coria et al. 2002). This evolutionary trend contrasts with the theropods on the line to birds. In derived maniraptorans (e.g., dromaeosaurids and birds) the base of the tail was highly movable and the distal 2/3 was stiffened by longitudinal tendons (Gatesy 2001).

Abelisaurids have a set of specialized vertebral features that probably had a close functional relationship. The rigidity proposed for the anterior third of the tail of the more derivatives abelisaurids, would be the culmination of a long and quite stiff axis that starts with a robust neck dominated by hypertrophied epiphyses and well-developed cervical ribs (O'Connor 2007; Méndez in press). This is followed by a dorsal sector whose vertebrae have accessory articulations (hyposphene-hypantrum) to increase structural rigidity, and a sacral region composed of firmly fused vertebrae. 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 (Méndez in press).

The unique morphology of the vertebral structures in the tail of abelisaurids may suggest a rearrangement of the muscles (Persons and Currie 2011). The increase of the available space below the transverse processes for muscle attachment, and the extreme development of the transverse processes, may have favoured greater development of some muscles (e.g., *M. caudofemoralis* and *M. ilio-ischiocaudalis*) at the

expense of others (e.g., *M. spinalis* and *M. longissimus*), thus modifying the capability to perform certain movements. (Persons and Currie 2011).

Conclusion

The tail of abelisaurid theropods evolved differently from the rest of carnivorous dinosaurs. This region presents a particular morphology that distinguishes it clearly from other theropods. This evolutionary strategy could result in a functional benefit by allowing further development of the musculature associated with cursoriality, providing an adaptive advantage to compete with other contemporary meat-eaters (i.e., carcharodontosaurids, coelurosaurians). This detailed study of caudal morphology has revealed diagnostic characters of the family Abelisauridae, and also of less inclusive clades, such as Brachyrostra and Carnotaurini.

Acknowledgements

I thank Fernando Novas (MACN) and Juan Canale (MMCH) for providing invaluable comments; Alejandro Kramarz (MACN), Ariana Carabajal (MCF), Juan Porfiri (Centro Paleontológico Lago Barreales, Neuquén, Argentina), and Juan Canale for allowing the study of material under their care; and Patrick O'Connor (Ohio University, Ohio, USA), Fernando Novas, and Rubén Martínez (Universidad San Juan Bosco, Comodoro Rivadavia, Argentina) for providing photographs of *Majungasaurus*, *Pycnonemosaurus*, and MPM-99, respectively, Cristina Garat (Bariloche, Argentina) and Michael J. Benton (School of Earth Sciences, University of Bristol, Bristol, UK) who kindly helped me with the writing in English. I thank Patrick O'Connor and Rodolfo Coria (Universidad Nacional de Río Negro, General Roca, Argentina) for the useful comments that improved the quality of this contribution. This work represents part of my Ph.D. thesis completed at the Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. I thank CONICET for providing financial support.

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