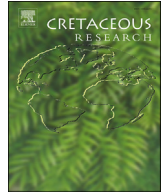




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New brachyrostran remains (Theropoda, Abelisauridae) from La Invernada fossil site (Bajo de la Carpa Formation, Upper Cretaceous), northern Patagonia, Argentina

Ariel H. Méndez ^{a, *}, Leonardo S. Filippi ^b, Federico A. Gianechini ^c,
Rubén D. Juárez Valieri ^d

^a CONICET, Instituto de Investigación en Paleobiología y Geología (CONICET-UNRN), Av. Roca 1242, 8332, General Roca, Río Negro, Argentina

^b Museo Municipal "Argentino Urquiza", Jujuy y Chaco s/n, 8319, Rincón de los Sauces, Neuquén, Argentina

^c CONICET, Instituto Multidisciplinario de Investigaciones Biológicas (CONICET-UNSL), Chacabuco 917, 5700, San Luis, Argentina

^d Secretaría de Cultura de la Provincia de Río Negro, 8332, General Roca, Río Negro, Argentina

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ABSTRACT

Several remains of an abelisaurid theropod including a nearly complete sacral complex articulated with both ilia, the distal boot of the pubes, the furcula, teeth, and fragments of transverse processes of caudal vertebrae was discovered in the La Invernada fossil site, northern Patagonia from the Bajo de la Carpa Formation (Santonian). The sacrum exhibit features typical of abelisauroids as narrowing of the middle sacral centra, fused neural spines forming a continuous sheet and ventral bow of the sacrum, in lateral view. The furcula represents de first mention of this bone for a South American abelisaurid. The morphology observed in the transverse processes with distal end projected forward and sagittal ridge on the ventral surface allows its taxonomic assignment to the clade Brachyrostra.

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1. Introduction

The vertebrate fossil record of the Bajo de la Carpa Formation, where outcrops appear scattered throughout different areas of northern Patagonia, consists of crocodyliforms (Woodward, 1896; Gasparini, 1982; Bonaparte, 1991; Fiorelli and Calvo, 2007; Martinelli et al., 2012), snakes (Woodward, 1901; Caldwell and Albino, 2002), turtles (Lapparent de Broin and De la Fuente, 2001), non avian dinosaurs (Bonaparte, 1996; Apesteguía, 2004; Porfiri and Calvo, 2006; Martinelli and Vera, 2007; Porfiri et al., 2008; Ezcurra and Méndez, 2009; Filippi et al., 2014, 2016; Méndez et al., 2015), and birds (Alvarenga and Bonaparte, 1992; Chiappe and Calvo, 1994).

Among the theropod fauna, four different small-sized theropod taxa were described, the basal abelisauroid *Velocisaurus unicus*

(Bonaparte, 1996), the alvarezsaurid *Alvarezsaurus calvoi* (Bonaparte, 1996), the enantiornithine *Neuquenornis volans* (Bonaparte, 1996) and the basal bird *Patagopteryx deferrariisi* (Alvarenga and Bonaparte, 1992). In this regard, medium-large sized theropod remains correspond to abelisaurids (Porfiri and Calvo, 2006; Ezcurra and Méndez, 2009; Filippi et al., 2014, 2016; Méndez et al., 2015), and tetanurans (Porfiri et al., 2008; Méndez et al., 2015). In this manner, the specimen described here constitutes the second record of abelisaurid theropod recovered from the Bajo de la Carpa Formation in the La Invernada area (Fig. 1). The materials described here were found in an area of 4 m² (Fig. 2), and do not overlap with those from the holotype of *Viavenator*, so that cannot be assigned to this taxon.

Abelisaurid theropods are the best known carnivorous dinosaurs of Gondwana with more than a dozen species nominated (Bonaparte, 1985; Bonaparte and Novas, 1985; Martínez et al., 1986; Coria and Salgado, 1998; Sampson et al., 1998; Coria et al., 2002; Kellner and Campos, 2002; Wilson et al., 2003; Calvo et al., 2004; Coria, 2001; Sereno and Brusatte, 2008; Canale et al., 2009; Novas et al., 2010; Tortosa et al., 2013; Filippi et al., 2016). However, the sacrum is only well known in *Carnotaurus* (Bonaparte et al., 1990;

* Corresponding author.

E-mail addresses: arielmendez@yahoo.com.ar (A.H. Méndez), lsfilippi@gmail.com (L.S. Filippi), smilodon.80@gmail.com (F.A. Gianechini), rubendjuarez@gmail.com (R.D. Juárez Valieri).

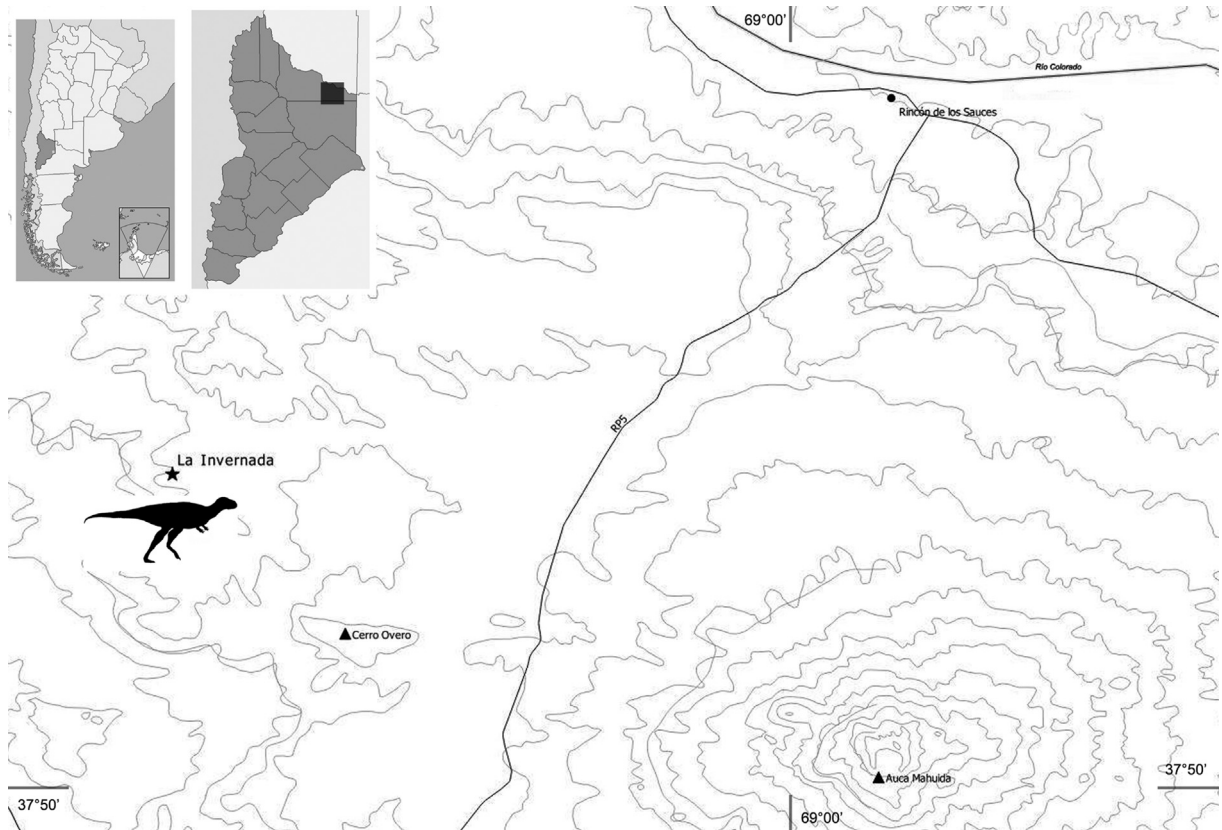


Fig. 1. Map showing the La Invernada fossil site, Northern Patagonia (Bajo de la Carpa Formation) where the specimen MAU Pv LI 547.

Méndez, 2010) and partially in *Majungasaurus* (O'Connor, 2007), *Rajasaurus* (Wilson et al., 2003) and MCF-PVPH-237 (Coria et al., 2006), and the furcula is only known in *Majungasaurus* (Burch and Carrano, 2012). These new findings allow find out more details of the anatomy that so far is poorly understood.

The studied material is deposited at the Museo Municipal “Argentino Urquiza” (MAU), Rincón de los Sauces, Neuquén, Argentina.

2. Systematic paleontology

Theropoda Marsh, 1881
 Ceratosauria Marsh, 1884
 Abelisauridae Bonaparte and Novas, 1985
 Brachyrostra Canale et al., 2009
 Brachyrostra gen. et sp. indet.

Material. MAU Pv LI 547/5 furcula, MAU Pv LI 547/8 proximal third of ceratobranchial bone, MAU Pv LI 547/1 sacrum plus ilia, MAU Pv LI 547/2 distal half of fused pubes, MAU Pv LI 547/6–7 two isolated teeth, MAU Pv LI 547/10–14 distal end of caudal transverse processes. Museo Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén, Argentina.

Horizon and locality. Bajo de la Carpa Formation (Santonian, Upper Cretaceous), Río Colorado Subgroup, Neuquen Group (Garrido, 2010). La Invernada fossil site, located 50 km southwest of the Rincón de los Sauces City, Neuquén Province, Patagonia, Argentina.

3. Description

Furcula (Fig. 3). This element lacks the left proximal end. It was recovered together with the carrier sediment in which the material impression was marked, whereby its shape and full size is known.

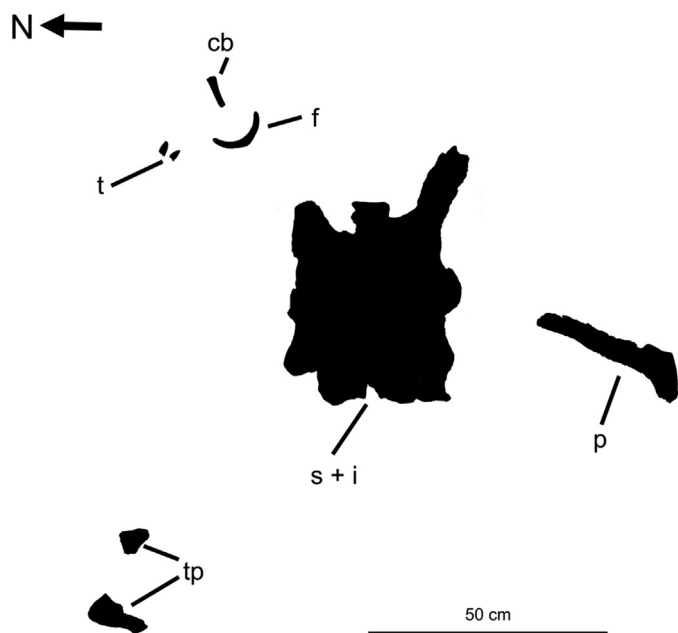


Fig. 2. Quarry map showing the spatial arrangement of the specimen MAU Pv LI 547.

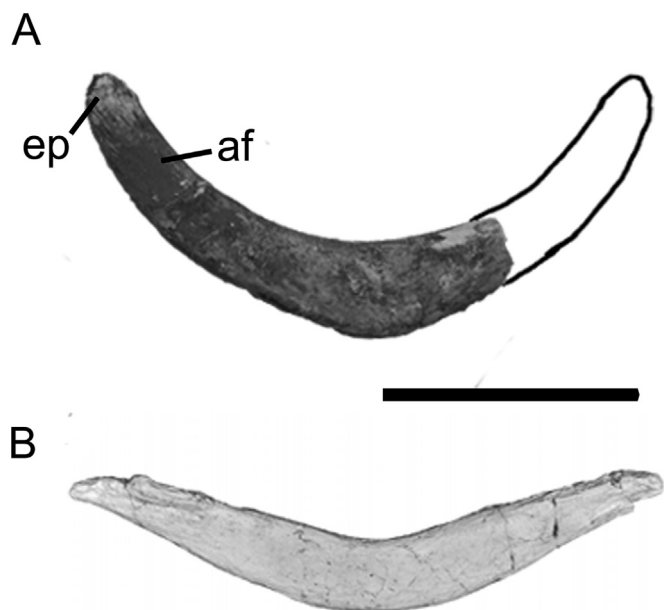


Fig. 3. Furcula of (A) MAU Pv LI 547 and (B) *Majungasaurus crenatissimus* (modified from Burch and Carrano, 2012) in anterior view. Abbreviations: ep, epicleideal process; af, acromial facet. Scale 5 cm.

The furcula has a semilunar shape with recurved rami and differs markedly from the morphology displayed in the furcula of *Majungasaurus* (Burch and Carrano, 2012) which is boomerang-like shaped, with the rami nearly straight. This gives it a shape similar to a wide U, instead of a V, but without being so curved as in some tyrannosaurids or deinonychosaurs (Nesbitt et al., 2009). The length between both ends of epicleideal processes is 11.2 cm, with an interclavicular angle of 120° . The dorsoventral height is 1.8 cm, notably greater than the 0.5 cm that the boné presents in anteroposterior direction. The symphysis does not present any type of hypocleideal process or bulging. The anterior surface is convex, with the center of curvature positioned more dorsally, while the posterior surface is concave. On the proximal end of the preserved epicleideal process there is a series of striations that correspond to the anchoring of the musculature that links the furcula with the scapula. Transversally, it can be seen that the ventral part is slightly wider than the dorsal one and that it is constituted by massive bone.

Sacrum (Fig. 4). Four vertebral elements have been preserved, probably from s2 to s5, and a part of s6 which are firmly fused together. This fusion is observed both in the vertebral bodies and in the neural arches. In lateral view, the vertebral bodies form a ventrally concave arch, less marked than in *Carnotaurus* (Bonaparte et al., 1990) but present in other abelisauroids like *Skorpiovenator* (Canale et al., 2009), *Eoabelisaurus* (Pol and Rauhut, 2012), *Rajasaurus* (Wilson et al., 2003), *Rahiolisaurus* (Novas et al., 2010) and *Masiakasaurus* (Carrano et al., 2002, 2011). The sacrum is transversely narrow as in *Skorpiovenator*, *Eoabelisaurus*, and *Rajasaurus*, although it is less so than in *Aucasaurus* (Coria et al., 2002), *Carnotaurus*, MCF-237 (Coria et al., 2006) or *Majungasaurus*. In ventral view, the sacral centra 3 and 4 are transversely narrower and shorter than the more external elements of the sacrum, a condition observed in *Carnotaurus*, MCF-237, *Rajasaurus*, and *Rahiolisaurus*. There is no evidence of pneumatic openings in any of the vertebral centra.

The main connection between the sacrum and the ilia is through the transverse processes, which are laterally oriented. The neural arches are characterized by the fusion of the neural spines forming a spinal lamina that presents a straight dorsal margin, similar to observed in *Carnotaurus* and *Majungasaurus*. The preserved

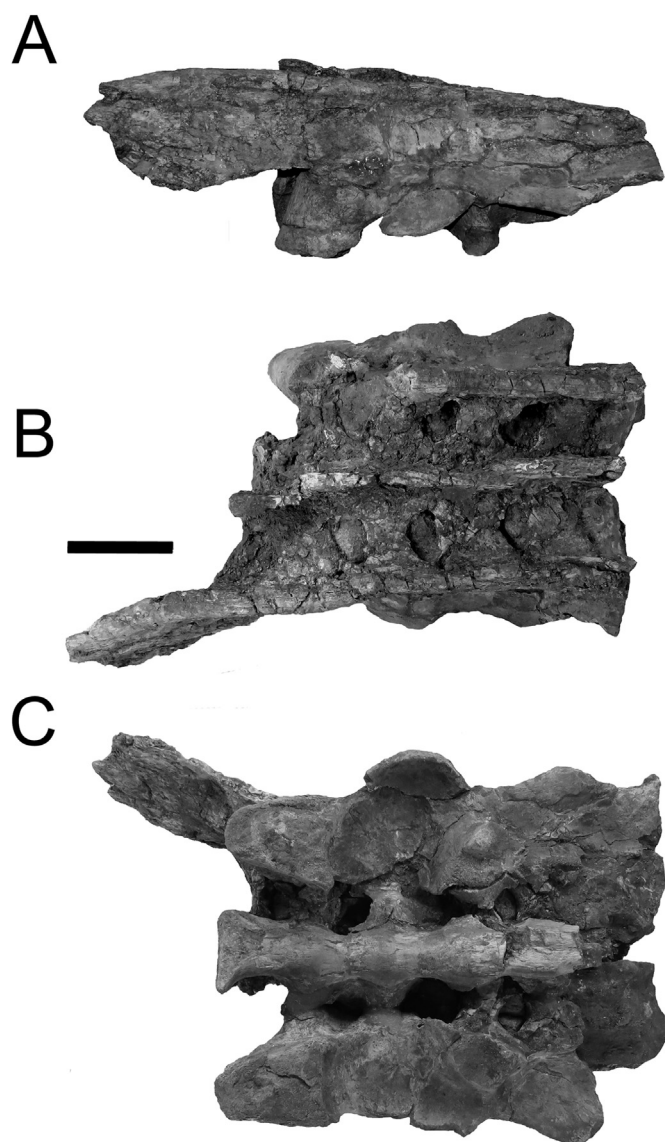


Fig. 4. Sacral complex of MAU Pv LI 547. (A) left lateral, (B) dorsal, and (C) ventral views. Abbreviations: Scale 10 cm.

transverse processes are all located almost at the same height and have the same inclination. The state of preservation of the material does not allow a correct recognition of the possible location of the intervertebral foramina.

Ilia (Fig. 4). The left ilium is almost complete while the right ilium lacks the anterior and posterior ends. The ilium is low (12 cm in the preacetabular area) and elongated (51 cm). In lateral view, it is observed that the dorsal edge is almost straight, as in *Carnotaurus*, *Aucasaurus*, *Rahiolisaurus*, MCF-237 and *Masiakasaurus* and contrary to the dorsal convexity exhibited in the iliac blade of *Eoabelisaurus*, *Skorpiovenator* and to a lesser extent in *Majungasaurus*. The preacetabular portion of the iliac lamina shows a characteristic ventral elongation observed in *Masiakasaurus*, *Eoabelisaurus*, *Skorpiovenator*, *Majungasaurus*, *Rahiolisaurus* and *Carnotaurus*. The postacetabular process is not observed, due to the preservation of the material. The pubic pedicel is very broad in relation to the ischiadic pedicel, similar to that observed in *Carnotaurus*, *Majungasaurus* and *Skorpiovenator*.

Pubes (Fig. 5). The distal ends of partially fused pubes were preserved. The distal boot is about 10 cm wide. The morphology of

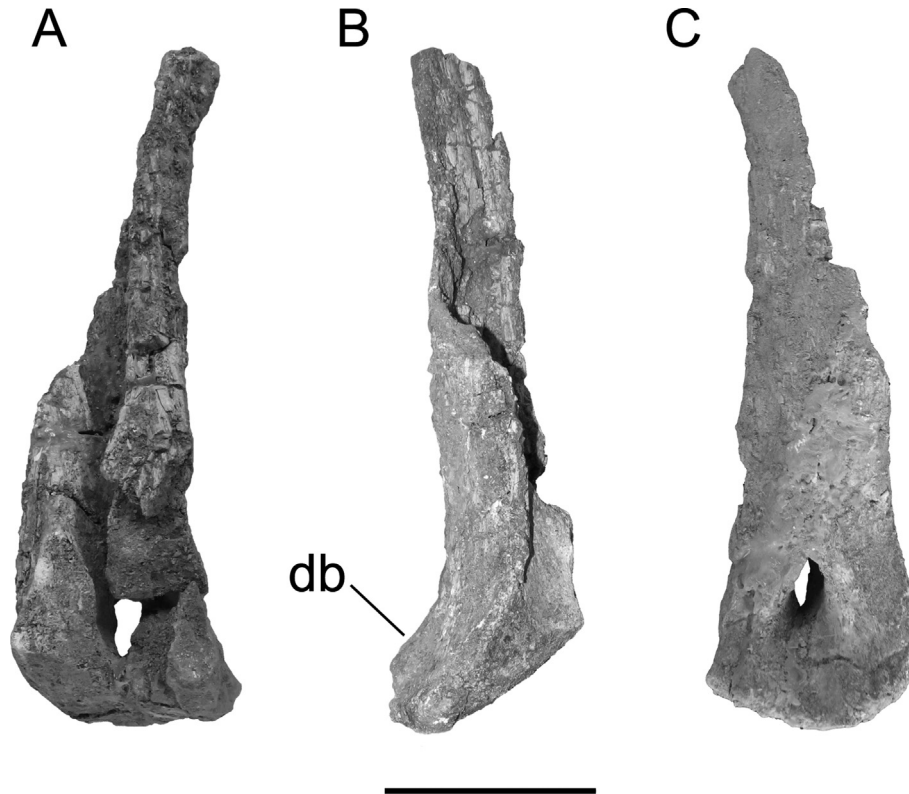


Fig. 5. Pubes of MAU Pv LI 547 in (A) anterior, (B) lateral, and (C) posterior views. Abbreviation: db, distal boot. Scale 10 cm.

the preserved part is very similar to that of *Carnotaurus* and *Aucasaurus*, and differs, in distal view, from the form exhibited in *Masiakasaurus*. The fusion of the bones is observed more firmly in the posterodistal sector of the distal boot and the pubic shaft, exhibiting a sector with an unfused space between both pubes as in *Carnotaurus* (Bonaparte et al., 1990).

Ceratobranchial bone (Fig 6). The proximal end of one of the ceratobranchial bones that are part of the hyoid apparatus was recovered. This is similar to that described for *Carnotaurus* (Bonaparte et al., 1990) and *Viavenator* (Filippi et al., 2016). It presents the kidney-shaped joint surface and a series of striations

crowning this portion of the bone. Also a marked ridge on the dorsal surface is observed.

Teeth (Fig. 7). Two isolated teeth were recovered. The largest tooth presents a poor state of preservation, with several fractures and lacking the apical end, while the smaller tooth is better preserved. They only preserve the dental crown, lacking the roots, and thus they most likely correspond to shed teeth. Both teeth have a basal part of the crown poorly preserved, and the smaller tooth presents one of the sides of the base much fractured. Besides these conditions the general form of the crowns seems not to be altered by taphonomic processes. Both crowns are distally curved,

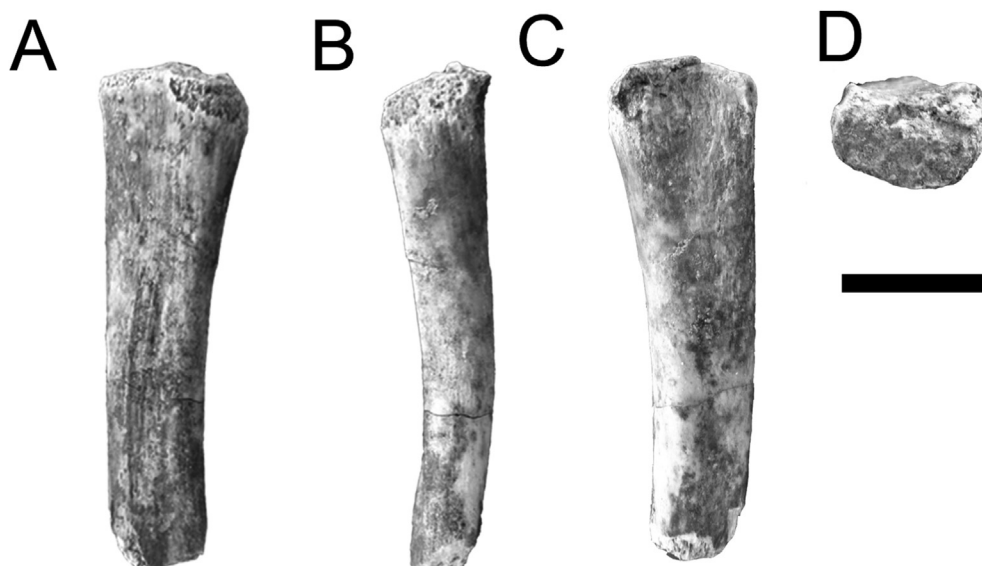


Fig. 6. Ceratobranchial of MAU Pv LI 547 in (A) dorsal, (B) lateral, (C) ventral, and (D) proximal views. Scale 2 cm.

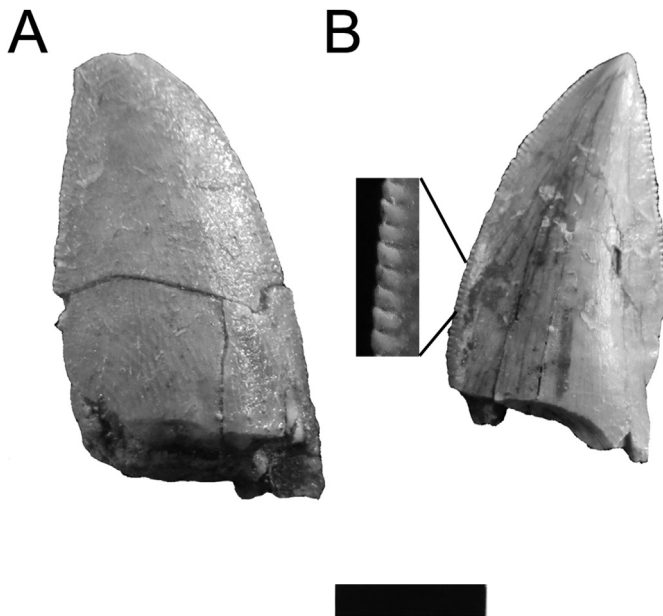


Fig. 7. Teeth of MAU Pv LI 547. Scale 1 cm.

although the distal margin is nearly straight, so the apex of the crown not exceeds the most distal point of the base in lateral view. Unfortunately, the distal carina of both teeth has not preserved its basal portion, because fracture. Mesial and distal carinae present denticles in all their extension. The smaller tooth has sub-quadrangular distocentral mesial denticles (sensu the terminology proposed by Hendrickx et al., 2015), without a significant change in the morphology along the carina. The mesial carina bears 14 denticles per 5 mm at the tip, and 13 at the mid-crown and near the cervix (MAVG = 13.33). The denticles of the distal carina are weakly apically hooked and they are 14 per 5 mm at the tip and 12 per 5 mm at the mid-crown. Although the basal portion of the distal carina is not preserved likely the denticle count at this part was approximately 13 per 5 mm, taking into account the scarce variation in size along the carina. Thus it can be estimated a DAVG of 13. In this way the DSDI is around 1. The larger tooth has sub-quadrangular distocentral and proximodistally subrectangular distocentral mesial and distal denticles, respectively. The mesial carina bears 12 denticles per 5 mm at the tip and 11 per 5 mm at the mid-crown and near the cervix (MAVG = 11.33). The distal carina has 11 denticles per 5 mm at the tip and the mid-crown, and possibly the same was near the cervix, so DAVG likely is 11. Thus, the DSDI for this tooth is also around 1. Interdenticular sulci are observed between the distal denticles of the smaller tooth, which are short and without apical or basal inclination. In the larger tooth also seems to be interdenticular sulci, although the poor preservation precludes corroborating this. The larger tooth has labial and lingual surfaces equally convex and the crown base is lenticular in cross-section (sensu the terminology of Hendrickx et al., 2015). On the other hand, the smaller tooth has one side with concave zones near the carinae, which is interpreted as the lingual side. This interpretation is also based in the displacement of the mesial carina, which commonly is lingually displaced in theropod teeth (Hendrickx et al., 2015). The cross-section of the crown base is parlinon-shaped (sensu Hendrickx et al., 2015), with a more marked concavity close to the mesial carina. The degree of curvature of the apex of the crown and the contour of the base of the crown, would position the smaller tooth as more rostral and the larger as more caudal.

Based on the observed features of the teeth, i.e., straight distal margin, mesial and distal carinae completely serrated from base to tip, denticles with interdenticular sulci, distal denticles apically pointed, and a DSDI close to 1, these teeth can be assigned to Abelisauridae (Hendrickx and Mateus, 2014).

Transverse processes (Fig. 8). Several fragments belonging to the transverse processes of the caudal vertebrae were recovered. They exhibit the typical morphology of abelisaurids (e.g., *Aucasaurus*, *Carnotaurus*, *Viavenator*, *Ekrixinatosaurus*, *Skorpiovenator*, *Pycnomosaurus*), as the presence of conspicuous centrodiapophyseal lamina on the ventral surface of transverse processes and the expanded distal end with an anterior projection. A sagittal ridge is also observed in the ventral side of the transverse process, which is present in brachyrostrans like *Aucasaurus*, *Carnotaurus*, *Viavenator* and *Ekrixinatosaurus* (Ezcurra and Méndez, 2009; Méndez, 2014; Filippi et al., 2016).

4. Discussion

Several authors have recognized diagnostic characters of Abelisauroida (Rowe, 1989; Bonaparte, 1991; Coria and Salgado, 1998; Sereno, 1999; Rauhut et al., 2003; Ezcurra and Méndez, 2009) that are present in the materials described here to perform an unequivocal taxonomic assignment of this specimen. Moreover features belonging to less inclusive clades (e.g., Abelisauridae, Brachyrostra) can be observed in the recovered bones of MAU Pv LI 547.

The furcula is the only element that makes it difficult to compare since only this bone is known in *Majungasaurus*, and between both, they present notable differences, something that coincides with the current view that the majungasaurin abelisaurids and the brachyrostran abelisaurids followed different evolutionary paths possibly from the separation of Africa and South America during the fragmentation of Gondwana.

The morphology of the sacrum is typical of the members of Abelisauridae. The narrowing of the complex sacrum in its middle as well as the ventral arch of the sacral series are characters that are present in several members of Abelisauroida, whereas the narrowing and shortening of the middle sacral centra seems to be present only in members of the family Abelisauridae. The strong fusion of sacral neural spines forming a continuous lamina is also an abelisauroid feature.

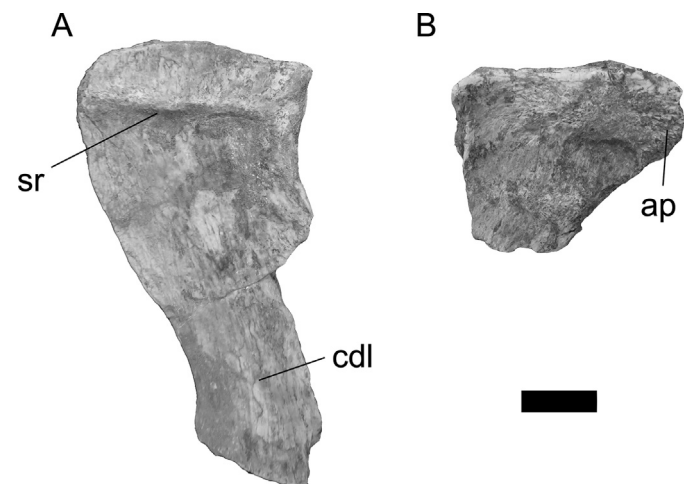


Fig. 8. Transverse processes of MAU Pv LI 547 in (A) ventral, and (B) dorsal views. Abbreviation: ap, anterior projection of transverse process; cdl, centrodiapophyseal lamina; sr, sagittal ridge. Scale 2 cm.

The morphology of the ilia is variable within Abelisauroidea, and MAU Pv LI 547 shares characters observed in members of Abelisauridae as well as of Noasauridae.

The shape of the pubic foot is very similar to that of derived brachyrostrans like *Aucasaurus* and *Carnotaurus*.

Dental morphology with straight distal margin, mesial and distal carinae serrated from base to tip, denticles with interdenticular sulci, and distal denticles apically pointed are features shared by members of the family Abelisauridae.

The presence of a marked centrodiaepophyseal lamina on the ventral surface of the transverse processes in the anterior caudal vertebrae is characteristic of members of Brachyrostra although this feature seems to be present also in *Majungasaurus* but much less marked. The anterior projection of the distal end of the transverse processes and the presence of the sagittal ridge on the ventral surface of the distal end of the transverse process are features documented in several South American members of Abelisauridae, particularly in those that belong to the Brachyrostra clade.

5. Conclusions

It is noteworthy that for the first time, a brachyrostran furcula is documented, being the second record for the family Abelisauridae, which provides a better knowledge of the anatomy of this group of South American abelisaurids and their differences with the majungasaurin abelisaurids.

Based on the morphological evidence of the material described here, it can be assigned without doubt to the family Abelisauridae and most likely to the Brachyrostra clade. No autapomorphies were identified in the available elements that might allow us to diagnose a new genus and species within Abelisauridae.

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