An Early Cretaceous, medium-sized carcharodontosaurid theropod (Dinosauria, Saurischia) from the Mulichinco Formation (upper Valanginian), Neuquén Province, Patagonia, Argentina

Rodolfo A. Coria, Currie, Philip J. Currie, Francisco Ortega, Mattia A. Baiano

PII: S0195-6671(19)30395-7

DOI: https://doi.org/10.1016/j.cretres.2019.104319

Reference: YCRES 104319

To appear in: Cretaceous Research

Received Date: 11 September 2019

Revised Date: 10 October 2019

Accepted Date: 11 November 2019

Please cite this article as: Coria, R.A., Currie, Currie, P.J., Ortega, F., Baiano, M.A., An Early Cretaceous, medium-sized carcharodontosaurid theropod (Dinosauria, Saurischia) from the Mulichinco Formation (upper Valanginian), Neuquén Province, Patagonia, Argentina, *Cretaceous Research*, https://doi.org/10.1016/j.cretres.2019.104319.

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- 2 Saurischia) from the Mulichinco Formation (upper Valanginian), Neuquén Province,
- 3 Patagonia, Argentina
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- 5 Rodolfo A. Coria<sup>a</sup>, Currie, Philip J. Currie<sup>b</sup>, Francisco Ortega<sup>c</sup>, Mattia A. Baiano<sup>a,d</sup>
- 6 <sup>a</sup> CONICET Museo Carmen Funes, Av. Córdoba 55, (8318) Plaza Huincul, Neuquén,
- 7 Argentina. <u>rcoria@unrn.edu.ar;</u> mbaiano@unrn.edu.ar
- 8 <sup>b</sup> University of Alberta, Biological Sciences CW405, Edmonton, Alberta T6G 2E9, Canada.
- 9 pjcurrie@ualberta.ca
- <sup>c</sup> UNED, Fac. de Ciencias. Senda del Rey 9, 28040. Madrid, Spain. fortega@ccia.uned.es
- <sup>d</sup> CONICET-IIPG, Av. Roca 1242 (8322), General Roca, Río Negro, Argentina
- 12
- 13
- 14 Corresponding author: R.A. Coria <u>rcoria@unrn.edu.ar</u>
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#### Abstract 17

18

19	A new carcharodontosaurid taxon, Lajasvenator ascheriae gen. et sp. nov. is described. The new
20	taxon is based on two specimens: MLL-PV-Pv-005 is a partial skeleton represented by a portion of the
21	snout, partially articulated presacral vertebral series, four articulated caudal vertebra and fragments of the
22	pelvic girdle; MLL-PV-Pv-007 includes the anterior ends of both dentaries, a quadratojugal, and
23	fragments of cervical vertebrae, ribs and a possible tarsal bone. Lajasvenator is unique in having anterior
24	projections on cervical prezygapophyses, lip-like crests on the lateral surfaces of cervical
25	postzygapophyses, and bilobed anterior processes on cervical ribs. Lajasvenator material was collected
26	from the terrestrial sandstones of the Valanginian Mulichinco Formation. It is the oldest
27	carcharodontosaurid record from South America. This medium sized theropod was found associated with
28	remains of the dicraeosaurid sauropod Pilmatueia, indeterminate diplodocid remains, and a yet
29	unidentified iguanodontian-like ornithopod.
30	
31	Keywords: Lajasvenator; Carcharodontosauridae; Theropoda; Valanginian; Patagonia
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#### 33 **1. Introduction**

34

During the second half of the 20th Century, knowledge about South American dinosaur faunas
was primarily built upon a wealth of discoveries from the Mesozoic outcrops of Argentina (see Coria,
2016; Ezcurra and Novas, 2016; Salgado and Calvo, 2016, and references therein). Notwithstanding, most
dinosaur taxa are known from the latest levels of the Cretaceous, given the scarcity of Lower Cretaceous
outcrops.

In a global context, fossil-bearing localities from the lowest levels of the Cretaceous -- the
Berrasian and Valanginian -- are either scarce or have uncertain stratigraphic identification (Weishampel
et al., 2004). A handful of Valanginian dinosaur species are known from Asia, Australia and Europe,
although the phylogenetic status of many of these species is currently uncertain (Broom, 1904; Buffetaut
et al., 2009a and b; Carpenter and Ishida, 2010; Christiansen and Bonde, 2003; Galton, 2009; Harrison
and Walker, 1973; de Klerk et al., 2000; Norman, 2010, 2012; Pereda-Suberbiola et al., 2012; Rauhut and
Xu, 2005; Taylor and Naish, 2007; You et al., 2005).

In Argentina, the Valanginian is well exposed in the Neuquén Basin, where it is represented by
marine and terrestrial deposits of the Mulichinco and Bajada Colorada formations (Gulisano et al., 1984;
Zavala, 1999, 2000), which are considered to be synchronous, at least at some of their levels. The
Mulichinco Formation includes older beds composed mostly of marine deposits, whereas the upper
terrestrial sediments are unconformably overlain by the marine sediments of the Agrio Formation (upper
Valanginian–lower Barremian) (Zavala et al., 2005).

Since 2009, annual expeditions have collected fossil vertebrates at the locality of Pilmatué,
located 9 km northeast from Las Lajas, Neuquén Province. Here, the terrestrial levels of the Mulichinco
Formation are extensively exposed over many square kilometers. Through the years, numerous dinosaur
remains have been collected, including articulated or semiarticulated skeletons of dicraeosaurid
sauropods, ornithopods and theropod dinosaurs (Coria et al., 2010, 2012, 2017, 2019; Paulina Carabajal et

al., 2018), many of which are associated with fossil plants (Martinez et al., 2012; Gnaedinger et al., 2017).

59 Furthermore, recent collections of vertebrate fossils from the synchronous Bajada Colorada Formation

- 60 produced what could be a similar dinosaur association (Gallina et al., 2014, 2019; Canale et al., 2017),
- 61 suggesting that the fossils from both formations could represent the same ecosystem.

62 During the 2010 field season at Pilmatué locality, a partial, semiarticulated skeleton of a medium 63 sized theropod (MLL-Pv-005) was collected (Fig.1). A second, less complete specimen (MLL-Pv-007) was recovered 50 meters southeast from the same stratigraphic level during the 2012 field season, which 64 65 although very incomplete, it preserved the proximal end of a cervical rib that is undistinguishable from 66 the seventh cervical rib of the specimen MLL-Pv-005. A new theropod taxon - Lajasvenator ascheriae gen. et sp. nov. – is based on these materials, which constitutes the first theropod remains reported for the 67 68 Valanginian Cretaceous of Patagonia (Coria et al., 2010) and the first described Theropoda taxon from the Mulichinco Formation (Fig.1). 69

*Lajasvenator* shows clear features that link it with the Carcharodontosauridae, a clade of meateating dinosaurs commonly known by large, heavily built, Late Cretaceous forms like *Giganotosaurus*, *Carcharodontosaurus, Mapusaurus* and *Tyrannotitan* (Coria and Salgado, 1995; Coria and Currie, 2006;
Novas et al., 2005; Sereno et al., 1995). However, little is known from the early stages of the evolution of
the clade, which could be represented by medium size species like the one here described. *Lajasvenator* is
the oldest Cretaceous carcharodontosaurid from South America and a key element to understand the
evolutionary history of this clade, which could be older than thought for this continent.

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#### 2. Institutional abbreviations:

79 IVPP, Institute od Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCF-PVPH, Museo
80 Municipal Carmen Funes, Vertebrate Paleontology, Plaza Huincul, Neuquén Province, Argentina; MLL81 PV, Museo Municipal de Las Lajas, Las Lajas, Neuquén Province, Argentina; MPCA PV, Museo

82 Provincial Carlos Ameghino, Vertebrate Paleontology, Cipolletti, Río Negro Province, Argentina;

83 MUCPv-CH, Museo de la Universidad Nacional del Comahue, El Chocón Collection, Neuquén City,

Qroo

84 Argentina; USNM, United States National Museum, Washington DC, USA.

85

86 **3.** Systematic Paleontology

87

88 Theropoda Marsh, 1881

89 Tetanurae Gauthier, 1986

90 Allosauroidea Currie and Zhao, 1993

91 Carcharodontosauridae Stromer, 1931

92

93 *Lajasvenator ascheriae* gen. et sp. nov.

Etymology: *Lajas*, referring the city of Las Lajas, within the jurisdiction of which the specimen
was found; *venator*, Latin, hunter; *ascheriae*, after Susana Ascheri, for her kindness in allowing
us to work on her land.

97 Holotype: MLL-PV-005, an incomplete but partially articulated skeleton that includes a partial 98 skull represented by the almost complete left premaxilla with one tooth, anterior portion of the 99 right premaxilla with two teeth, most of the main body of the left maxilla, anterior section of the 100 main body of the right maxilla, distal half of the left dentary, posterior ramus of the left splenial, 101 complete last four cervical vertebrae (articulated with each other and their cervical ribs), almost 102 complete first dorsal vertebra, a series of nine articulated dorsal centra (the centra are incomplete 103 at the anterior and posterior ends of the series), fragment of sacrum with three incomplete

104	vertebrae attached to a fragmentary ilium, a series of four articulated mid caudal vertebrae (two of
105	which are complete), five almost complete posterior dorsal ribs with heads, three dorsal rib shaft
106	fragments, four fragments of possible gastralia, incomplete right ilium, and proximal end of the
107	right pubis.
108	Referred material: MLL-PV-007, a right quadratojugal, symphysial ends of both dentaries,
109	fragmentary series of four cervical transverse processes, proximal end of seventh right cervical
110	rib, proximal half of a left, anterior dorsal rib, and a possible distal tarsal.
111	Locality and horizon: Pilmatué Locality, 9 km northeast of Las Lajas, Neuquén Province,
112	Patagonia, Argentina. Mulichinco Formation (upper Valanginian, Lower Cretaceous). GPS
113	positions: MLL-PV-005, S38° 29' 59.5", W70° 15' 51.1", Elevation 732 masl; MLL-PV-007,
114	S38° 29' 59.6", W70° 15' 48.0", same elevation as MLL-PV-005. (Figs. 2 and 3).
115	Diagnosis: medium-sized theropod with the following autapomorphies: anterior projection on
116	cervical prezygapophyses, lip-like crest on lateral surface of cervical postzygapophyses, and
117	cervical ribs with bilobed anterior process. The phylogenetic analysis shows that Lajasvenator
118	has the following unique combination of features: premaxilla ventral to external naris has a
119	height/length ratio less than 0.5 (character 2); paradental plates with striated or ridged surfaces
120	(character 140); relatively small premaxillary teeth (character 152); cervical vertebrae with a
121	distinct rim on each anterior articular surface (character 175) (all characters are also present in
122	some megalosaurs); and ilium with straight dorsal margin (also in some basal theropods).
123	

#### 4. Description 124

125 The holotype (MLL-PV-005) consists in an adult individual based on the complete fusion of neural arches with their respective central along the preserved vertebral elements. The partial 126 skull was lying on its left side and was upside down in relation to the hips and posterior dorsal 127

vertebrae. The neck was twisted downwards so that the distal elements of the cervical vertebrae
and their ribs were recovered in articulation. The hips and posterior part of the abdomen were
lying on the right side when the animal was buried, and most of the left side of this region was
destroyed by erosion. This suggests that the animal was articulated when buried, and was in a
modified death pose. It was collected from a heavily indurated, coarse-grained sandstone layer,
and had been eroding for a long time before it was discovered and excavated.

Premaxilla. The left premaxilla is complete, whereas the right one lacks the supranarial
process and the posterior end (Fig. 4). Both premaxillae were recovered in contact but were not
fused with each other, or with the maxillae.

137 The external surface of the left premaxilla is somewhat weathered, but that of the right 138 premaxilla is relatively smooth other than pitting for nutrient foramina (Fig. 4A). The subnarial 139 body of the premaxilla is somewhat taller (43 mm) than long (41 mm anteroposteriorly, 43 mm 140 obliquely between the front and back of the alveolar margin). There are four alveoli in each premaxilla. The last alveolus is positioned under the front of the external naris. The supranarial 141 142 process arches high above the external naris and the posterior end is 90 mm above the alveolar 143 margin of the maxilla. The external naris was clearly large (about 30 by 60 mm) with a posterodorsally inclined axis. On the left side, the premaxilla has a tapering, elongate 144 145 posterodorsal, subnarial process, which is more clearly seen in medial view. It separates the 146 maxilla from the narial margin and probably contacted the subnarial process of the nasal.

Maxilla. The anteroventral region of the left maxilla is preserved with the first seven
alveoli (Table 1) (Fig. 4). The external surface of the bone is heavily weathered in most places. In
areas where the outer surface is well-preserved, there are anteroventrally trending canals and
deeply rugose texture that are characteristic of carcharodontosaurids like *Giganotosaurus*(MUCPv-CH-01) and *Mapusaurus* (MCF-PVPH-108), and abelisaurids like *Aucasaurus* (MCF-

152 PVPH-236). The anterior ramus is as long as it is deep, and extends beneath the posterior region 153 of the external naris. Neither the posterodorsal (lacrimal) process nor the interfenestral region is 154 preserved. However, depressions in the dorsal surface of the palatal shelf show that there were 155 pneumatic excavations in the anterior ramus. A curved edge on the medial surface of the anterior border of the antorbital fossa presumably marks the position of the promaxillary fenestra. 156 157 However, because the posteromedial margin of the promaxillary fenestra is not preserved, it is impossible to know if the fenestra was exposed in lateral view. The ventral margins of the 158 antorbital fossa and fenestra seem to coincide in the posterior region of the preserved part of the 159 160 left maxilla. The interdental plates are texturally distinct from the medial alveolar margin, and 161 have patterns of vertical ridges and grooves. The first interdental plate is small and low (9 mm), but subsequent ones increase progressively in height. The tallest plate (25 mm) is between the 162 163 fourth and fifth alveoli. Posterior to this one, they are fused into a continuous plate that decreases 164 steadily in height. The fused interdental plates resemble those of Acrocanthosaurus (Eddy and Clark, 2011), Carcharodontosaurus (Stromer, 1931), Eocarcharia (Sereno and Brusatte, 2008), 165 166 Giganotosaurus (MUCPv-CH-1), Mapusaurus (MCF-PVPH-108, Coria and Currie, 2006) and other carcharodontosaurids, but also abelisaurids (Lamanna et al., 2002; Sampson and Witmer, 167 168 2007), Allosaurus (Madsen, 1976), Ceratosaurus (Madsen and Welles, 2000), dromaeosaurids 169 (Currie, 1995), Torvosaurus (Britt, 1991) and many other theropods.

170 Quadratojugal. MLL-Pv-007 includes a nearly complete right quadratojugal (Fig. 5).

171 It has an "L" shape, with dorsal and anterior rami forming a 90° angle. The dorsal ramus 172 lacks the distal end, but it is more slender and thinner than that in *Allosaurus* (Madsen, 1976). 173 The posterior side of the dorsal ramus has a shallow depression that would have formed the 174 anterolateral border of a large quadratic fenestra. On the medial surface of the quadratojugal, 175 below the quadratic fenestra, is a tall, rugose facet that would have contacted the lower end of the 176 quadrate (Fig. 5C). The ventroposterior end of the quadratojugal is shallowly convex with a small

177 notch that would have exposed a small ventrolateral surface of the quadrate. The anterior ramus is 178 wide at its base and tapers anteriorly to a single point that would have been wedged between two 179 posterior prongs of the jugal as in Acrocanthosaurus (Currie and Carpenter, 2000) and Sinraptor 180 (Currie and Zhao, 1993). However, unlike the latter, there was no contact for the third, medial quadratojugal process of the jugal. The sutures for the two prongs of the jugal clearly show that 181 182 the upper prong was restricted to the front of the quadratojugal on the dorsal edge, whereas the lower prong would have been largely overlapped laterally by the quadratojugal but extended 183 184 almost to the quadrate suture.

185 Vomers. The anterior parts of the vomers are fused to form a thick midline ridge (17 mm
186 tall) on the roof of the mouth (Fig. 4D). They contact the premaxillae on the midline anteriorly,
187 and are held in place posteriorly by the anteriorly tapering anteromedial processes of the maxillae.
188 The width of the vomer is 12 mm and seems to be constant throughout the preserved part of the
189 bone. This suggests that the narial region of the animal was narrow.

Dentary. Partial dentaries are preserved in the two known specimens of *Lajasvenator*.
MLL-Pv-007 includes the anterior ends of both dentaries, although the right side is slightly more
complete (Fig. 6).

193 The symphysial ends of Lajasvenator have the typical squared-off profile of 194 carcharodontosaurids, and each has an anteroventral chin-like process (Brusatte and Sereno, 195 2007; Calvo and Coria, 2000; Currie and Carpenter, 2000; Eddy and Clarke, 2011). The lateral 196 surfaces of the dentaries are lightly sculptured by grooves and foramina. The first three 197 neurovascular foramina are close to the dorsolateral edge of the lateral surface, but are not within 198 a neurovascular groove as they are in Acrocanthosaurus (Eddy and Clarke, 2011). However, there 199 is an anteroposteriorly oriented groove on the ventral edge of the lateral side. It is suspected that 200 the anterior end of the dorsal neurovascular groove may have been behind the fourth alveolus as it

201	is in Giganotosaurus (Calvo and Coria, 2000). In medial view, the proximal end of the Meckelian
202	groove (Figs. 6D and E) reaches the level between the second and third dentary teeth. The first
203	three interdental plates are triangular and did not contact each other (Fig. 6E). However, this may
204	have been an age- or size-specific character because the anterior interdental plates of one of the
205	smaller specimens of Mapusaurus (MCF-PVPH-108.125, Coria and Currie 2006, fig. 8D) and
206	Giganotosaurus (MUCPv-CH-01) are also unfused. Only external sections of three dentary tooth
207	crowns (second to fourth) are preserved with the right dentary, although the root of the first
208	dentary tooth can be seen in the broken anterodorsal corner of the bone. Only part of the first
209	tooth crown is represented on the left dentary, although at least two more alveoli are present with
210	broken tooth roots.
211	MLL-Pv-005 includes the posteroventral end of the left dentary (Fig. 7). The fragment is
212	a mediolaterally thin and dorsoventrally deep lamina that is invaded by a distinct oval anterior
213	extension of the mandibular fenestra on the ventroposterior border. Below the mandibular
214	fenestra, the ventral border of the dentary is gently convex, wrapping around the ventral edges of
215	the splenial and probably the angular.
246	
216	Splemal. Part of the posterior ramus of the left splemal of MLL-Pv-005 is
217	preserved in articulation with the medial side of the dentary, which bears a forked end for the
218	articulation with the angular (Fig. 8).

The long slender shape of the posteroventral process is similar to that of *Mapusaurus* (MCF-PVPH-108.179), which also forks (Coria and Currie 2006, fig. 9), although at a relatively more anterior level. The elongate, distally forked process is also found in *Acrocanthosaurus* (Eddy and Clarke, 2011). The posterodorsal process is rather square in contrast with the triangular process seen in most theropods. seven maxillary teeth (Table 1).

224

Three premaxillary teeth are preserved in their sockets; two in the right premaxilla, which occupy the third and fourth positions, and one in the left premaxilla that occupies the fourth position. Each is lateromedially compressed and gently curved. However, each of the three teeth is oval in basal outline.

Predepositional weathering has made details of the carinae and denticulation hard to see. 230 231 The anterior carina of the third premaxillary tooth on the right side is offset to the medial side of the crown (so that the tooth is J-shaped in cross-section) and extends at least half the height of the 232 233 crown. Under high magnification, barely discernible denticulation suggests there were 2.7 234 anterior denticles per millimeter in the apical third of the tooth. The posterior carina has about three low denticles per millimeter. The enamel of the crown is smooth, and lacks any longitudinal 235 ridging, striations or crenulations. The alveoli suggest that the first premaxillary tooth was the 236 smallest, followed by the second. The third premaxillary tooth was the largest, and the fourth is 237 only slightly smaller. Alveolar size shows that the first maxillary tooth was about the size of the 238 239 posterior premaxillary teeth, and that the fifth maxillary tooth would have been the largest tooth. 240 Maxillary teeth must have been quite bladelike because the widths of the maxillary alveoli are 241 only about 40% their anteroposterior lengths.

The dentary teeth of MLL-Pv-007 are poorly preserved (Fig. 6B and E). Nevertheless, a few of the serrations can be seen on the posterior carinae of the second and third, right dentary teeth. The third dentary tooth has a base that is longer anteroposteriorly than wide, and is apically curved.

246

247 Postcranial

- 248 The Lajasvenator vertebral column is incomplete and represented by articulated partial
- series of five cervical, nine dorsal, three sacral and four caudal vertebrae (Table 2).

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250	The most anterior are an articulated series of five vertebrae and ribs (Fig. 9). Based on
251	comparisons with Allosaurus (Madsen, 1976) and Neovenator (Brusatte et al., 2008), they correspond to
252	the 6 <sup>th</sup> , 7 <sup>th</sup> , 8 <sup>th</sup> , 9 <sup>th</sup> and 10 <sup>th</sup> presacral vertebrae (which are the last four cervicals and the first dorsal). The
253	dorsal section is represented by an articulated series of the last nine vertebral centra. The sacrum is
254	preserved partially from the second to the fourth sacral centra, whereas the tail is represented by four
255	articulated mid-caudal vertebrae. None of the recovered ribs are fused to the vertebrae.
350	
250	Cervical vertebrae: The four cervical centra have concave (anteroventrally and transversally)
257	ventral surfaces between the parapophyses. They have hemispherical anterior intervertebral articulations,
258	and strongly opisthocoelous posterior articular surfaces. Each of the preserved cervical vertebrae has
259	epipophyses, but they are most prominent in the sixth cervical.
260	The most anterior element of the cervical series is identified as a sixth cervical vertebra (Fig. 10).
261	It is largely destroyed by erosion, but still preserves most of the centrum and tips of both
262	postzygapophyses. The centrum is longer than high and has deeply excavated lateral sides.
263	The parapophyses on the anteroventral margins of the centrum are well developed and extend
264	ventrolaterally on short pedicles to a level lower than the anteromedial edge of the centrum (Fig. 10A and
265	B). In anterior view (Fig. 10B), the broken surface anterior to the left parapophysis reveals that the
266	interior of the centrum is camellate. Above each parapophysis there is an oval pleurocoel. The deeply
267	concave posterior intervertebral articulation of the centrum is wider than high (Table 2). The
268	postzygapophyses are posterodorsally oriented and have well-developed epipophyses represented as small
269	horn-like processes that project posteriorly. The articular facets of the postzygapophyses face
270	ventrolaterally. In dorsal view, the lateral edge of each postzygapophysis projects laterally as a
271	pronounced wing-like process (lappet) with a convex outline. The dorsal surfaces of the
272	postzygapophyses merge towards the midline and presumably there was a well-developed lamina that
273	delimited a deep postspinal fossa that can be seen above the neural canal. There is no hyposphene.

The seventh cervical is virtually complete (Fig. 11). The centrum is slightly shorter than that of the sixth cervical (Table 2), but is wider at the midlength constriction. The pleurocoel above each parapophysis is subdivided by a thick septum into two openings. In anterior view, the prezygapophysial facets face dorsally and slightly anteromedially. The prezygodiapophysial lamina is well developed and extends anteriorly beyond the articular facet as a distinct anterior process. This seems to be an autapomorphic character.

On the left side, the wall of the supporting ridge has collapsed to expose the camellate condition 280 of the prezygapophysis. The articular facet of the prezygapophysis extends both laterally and medially on 281 282 distinct lappets. In anterior view, the prezygodiapophysial lamina merges ventromedially with the centroprezygapophyseal lamina. The prespinal fossa is deep and ventrally limited by 283 284 intraprezygapophyseal laminae, which also roof deep anterior peduncular pleurocoels, one on each side of a midline lamina. In lateral view, the diapophysis is supported by the anterior and posterior 285 centrodiapophysial laminae that separate the infraprezygapophysial, infradiapophysial and 286 infrapostzygapophysial fossae. All three fossae are deep and probably extend into the inside of the bone 287 288 through pneumatopores. In ventral view, there are distinct lateral and medial lappets that extend the 289 articular surfaces of the postzygapophyses. In posterior view, the intrapostzygapophysial laminae form a V-shaped ventral boundary for the postspinal fossa, and roof over a pair of posterior peduncular 290 291 pleurocoels. The interspinal ligament scarring covers distinct facets on the anterior and posterior surfaces of the neural spine. There is neither a hyposphene nor a hypantrum. 292

In most features, the eighth cervical vertebra is similar to the preceding vertebra although is slightly larger in most dimensions (Fig. 12). There are no peduncular pleurocoels. The anterior prong beneath the prezygapophyses is more pronounced and there is a conspicuous hemihyposphene beneath each postzygapophysis.

The ninth cervical centrum is marginally larger than its predecessor (Fig. 13). Like the other preserved cervicals, it has a broad, relatively flat ventral surface that is nevertheless slightly concave between the parapophyses, and slightly convex posteriorly. There is a low, barely conspicuous midline ridge behind the level of the parapophyses. The hypantrum is well-developed between the prezygapophyses, and the interspinous ligament scar extends from the hypantrum to almost the tip of the neural spine.

There is neither a prespinal fossa, nor anterior peduncular pleurocoels. The prezygapophyses 303 only extend a short distance anterior to the transverse processes. The anterior edges of the 304 305 prezygapophyses are not well preserved, but seem to lack the distinctive anterior prongs seen on the two preceding vertebrae. Posteriorly, the interspinous scar occupies most of the posterior surface of the neural 306 307 spine and there is no postspinal fossa. The postzygapophysis on the left side is damaged laterally, but the one on the right side extends laterally with a distinct epipophysial process that is continuous with the 308 lateral lappet. The hyposphene articulations are no longer separate, but are connected near the neural 309 spine by a lamina that is ventrally depressed on the midline. There are no posterior peduncular 310 pleurocoels. 311

312 Only the anterior part of the first dorsal (presacral 10) is preserved, including most of the neural313 arch (Fig. 14).

The postzygapophyses and the posterior half of the centrum are missing. The anterior intervertebral articulation of the centrum is markedly less convex than it is in the preceding cervicals. The parapophyses are midheight on the centrum, and unlike the situation in the cervicals, the ventral edge of the anterior intervertebral articulation is below the rib articulations. There appears to have been a weak hypapophysis on the midline, and it is strongly offset from the lateral sides of the centrum by deep depressions. The hypapophysis extends posteriorly as a ventral, midline ridge. There is a large pneumatopore behind the parapophysis. A ridge on the lateral side of the base of the neural spine extends

321	to the posterodorsal tip of the diapophysis. The latter seems to roof over a complex network of laminae
322	and pneumatic sinuses that extend into the base of the neural spine.
323	The last nine dorsal vertebrae of MLL-Pv-005 are preserved in articulation, although their left
324	sides, the neural arches, and some of the midsections (dorsals 15, 19, 23) of the centra were destroyed by
325	erosion (Fig. 15).
326	The ends of the right diapophyses of the $18^{th}$ to $22^{nd}$ presacrals were preserved in position,
327	although the shafts of transverse processes were all destroyed by erosion. They were, however,
328	represented by impressions in the rock. The amphiplatyan centra of all of these dorsals are strongly
329	waisted, similar to other small allosauroids (Malafaia et al., 2016). This is most extreme in presacrals 16
330	to 18 (Table 2) in which the ventral surfaces of the centra narrow into sharp medial ridges. None of these
331	centra appear to have had pneumatopores. The transverse processes are elongate rectangles that project
332	laterally, dorsally and slightly posteriorly. The ventral surfaces of the distal regions of at least the 19 <sup>th</sup> to
333	21 <sup>st</sup> transverse processes have what are presumed to be pneumatic fossae.
334	Parts of three fused sacral vertebrae were recovered with MLL-PV-005. The anterior and
335	posterior vertebrae of the triad are incomplete. However, the arrangement of transverse processes and
336	sacral ribs suggests that these are the second, third and fourth sacrals. The centrum of the third sacral is
337	approximately 68 mm long, and is pierced on both sides by pneumatopores with diameters of more than a
338	centimeter. The sacral rib attachments between the second/third, and third/fourth centra are fused to the
339	centra, although the sutures are still visible. The transverse processes of the third and fourth sacral
340	vertebrae sweep outwards and backwards. The neural arches are broken, but the bases are thin and
341	bladelike.

342 Four articulated caudal vertebrae were recovered (one represented by only the postzygapophyses343 and part of the neural spine) (Fig. 16).

344	The three well-preserved caudals have conspicuous, wide transverse processes and must be from
345	the middle of the tail. Transverse processes can go far back in caudals of carcharodontosaurids at least
346	30 in Acrocanthosaurus (Harris, 1998) – but the sizes of the transverse processes and the dimensions of
347	the central suggest that the caudals of MLL-Pv-005 are probably from the region of the $15^{\text{th}}$ to $20^{\text{th}}$
348	caudals. Presumably the caudals between the sacrum and this section were present when the animal was
349	buried because their alignment follows a natural curve from the hips that would be appropriate for a
350	typical death pose with the tail curved forwards dorsal to the hips. However, the caudal vertebrae did not
351	continue in the rock beyond this preserved section of four vertebrae. None of the preserved caudal centra
352	has a ventral midline sulcus, nor is there any evidence of pleurocoels. The absence of a sulcus is
353	characteristic of Neovenator and derived carcharodontosaurids (Brusatte et al., 2008), whereas it is
354	present in Veterupristisaurus (Rauhut, 2011) and Concavenator (Ortega et al., 2010). The facets for the
355	haemal arches seem to be equally developed on the front and back of each centrum. The neural arch is
356	indistinguishably fused to the centrum in each of the caudals, and is taller than the height of the centrum
357	(Table 2). The neural spine inclines dorsoposteriorly so that the distal (dorsal) end is positioned above the
358	front of the succeeding vertebra. The midline ridge of the neural spine extends forward until it rises into a
359	small but distinct spinous process (accessory neural spine) as in Acrocanthosaurus (Currie and Carpenter,
360	2000; Harris, 1998; Stovall and Langston, 1950), Allosaurus (Gilmore, 1920), Dubreuillosaurus (Allain,
361	2005), Mapusaurus (Coria and Currie, 2006), Sinosauropteryx (Currie and Chen, 2001) and a few other
362	theropods. However, accessory neural spines have been reported in rauisuchians (Franca et al., 2011) and
363	probably have little taxonomic utility. The prezygapophyses are relatively elongate, and extend somewhat
364	more than a third of the length of the preceding centrum. Articular facets on the zygapophyses are nearly
365	vertical in orientation. The transverse process of the second preserved caudal is split into a double
366	process. It is assumed that this represents a pathological condition because the transverse processes of the
367	following two vertebrae are more typical rectangular plates that are orientated laterally and slightly
368	posteriorly.

369	MLL-Pv-007 has only fragments of four vertebrae that were clearly articulated until they were
370	mostly destroyed by erosion. They appear to be the ends of transverse processes from cervicals or anterior
371	dorsals. The sizes of the processes and the degree of separation suggest they were from an animal about
372	the same size as MLL-Pv-005.
373	The longest of the most anterior pair of preserved cervical ribs of MLL-Pv-005 consists of long
374	and thin rods of bone, of which the one from the left side is 25,5 cm long. It probably represents most of
375	the shaft of the fifth cervical rib. Nothing from the proximal end is preserved.
376	The next cervical ribs of the preserved series correspond to the sixth pair (Fig. 17).
377	The rib from the right side seems to be complete and is 26 cm long. It has a conspicuous, bilobed
378	anterior process that is laterally compressed. In medial view, the articular facet of the capitulum is kidney-
379	shaped and significantly larger than the facet of the tuberculum. Both capitulum and tuberculum are
380	linked by a short lamina. The articular facets of the capitulum and tuberculum are separated by about 25
381	mm, and the anterolateral process extends about 18 mm in front of the capitulum. Although the
382	anterolateral process is prominent, it is considered short because it does not extend anteriorly beyond the
383	level of the lateral margin of the intervertebral articulation of the centrum. The shaft is proximally convex
384	laterally and flattens distally. The shaft tapers distally until the diameter is less than 2 mm. On the mesial
385	surface, ridges extend between the capitulum-anterior processes and the tuberculum-anterior process, but
386	there is no evidence of pneumatopores in the depressions on either side of the body.
387	Each of the seventh pair of cervical ribs of MLL-Pv-005 was at least 25 cm long, based on the
388	more complete right rib. The proximal end is dorsoventrally wider than any of the preceding ribs, and so
389	is the bilobed anterolateral process. The capitulum and tuberculum articular facets are separated by 30
390	mm, and the anterolateral process extends 20 mm forward. Pneumatic recesses or pneumatopores
391	excavate the base of the capitulum on the mesial surface. An incomplete right cervical rib of MLL-Pv-007

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392	seems to be from a seventh cervical rib and shows a clear pneumatic recess behind the ridge joining the
393	capitulum and tuberculum mesially. There is a pneumatopore anterior to that ridge.
394	The eighth cervical ribs are 22 cm long. The anterior process, which has fingerlike processes,
395	projects 22 mm in front of the parapophyseal articulation. The capitulum and tuberculum articular facets
396	are separated by 37 mm, and multiple pneumatopores penetrate the mesial depressions into the otherwise
397	thick region between the two heads. The distal end of the shaft tapers to a diameter of 3 mm. The rib from
398	the left side seems to have been broken and re-healed during life of the specimen.
399	The next pair of ribs is associated with the ninth cervical vertebra The distance between the
400	articular facets of the capitulum and tuberculum is 31 mm on the left side, but is 43 mm on the right side.
401	The ribs are 72 mm in length on the right side and 95 on the left side, but most of their shafts are missing.
402	The anterior process of the right side projects 17 mm in front of the junction with the ventral head of the
403	rib, and is bilobed anteriorly. There is a large pneumatopore on the inside of each of these ribs and
404	another that faces anteriorly near the junction of the capitulum, tuberculum and anterior process.
405	Five of the last six dorsal ribs are preserved on the right side of MLL-Pv-005, and presumably
406	represent presacral ribs 17, 18, 20, 21 and 22 (Fig. 18).
407	Presacral rib 17, which would be dorsal rib 8, is 35 cm long when measured along the outside
408	curve between the tuberculum and distal end. The distal end tapers to 6 mm in diameter. Presacral rib 18
409	was broken but had healed while the animal was still alive. The distance between the capitulum and
410	tuberculum measures about 8 cm. In spite of the fact that the adjacent vertebrae and ribs are in natural
411	articulation, there is no sign of any part of rib 19. One can only assume that it was destroyed at the same
412	time as most of the associated vertebra. Presacral ribs 20, 21 and 22 seem to be complete except possibly
413	for their distal tips, and measure 25 cm, 21 cm and 17 cm respectively (capitulum to distal end in a
414	straight line).

415	Up to a dozen fragments of ribs and several gastralia were recovered with ML-005, but provide
416	little information. The thickest rib fragment, which is 20 cm long, has a minimum shaft diameter of 18
417	mm (mediolateral) by 14 mm (anteroposterior) and probably is from one of the first dorsal ribs.
418	Most of an anterior dorsal rib was recovered with MLL-Pv-007. It is about 24 cm long, and the
419	minimum mediolateral shaft width is 21 mm. The separation between the capitular and tubercular
420	articulations is 48 mm, which is close to what the separation is between the parapophysis and diapophysis
421	of the first dorsal vertebra of MLL-Pv-005.
422	The right ilium is partially preserved, although it was split longitudinally by a crack that had been
423	widened by erosion. Assuming that the two blocks that contained the ilium had not moved in relation to
424	each other, then the distance between the ventral edge of the pubic peduncle and the top of the ilium is
425	220 mm. The upper edge of the bone is relatively straight in lateral view (Fig. 19).
426	As in most theropods, there are conspicuous but small vertical ridges (striations) on the medial
427	surface near the edge of the bone (Fig.19B). A fragment of bone adhering to the medial surface is
428	probably a remnant of the dorsal limit of the third sacral rib. None of the broken surfaces suggest that the
429	bone was pneumatic as in Mapusaurus (Coria and Currie, 2006) or Murusraptor (Coria and Currie,
430	2016), although a relatively small portion of the ilium is preserved. A small fragment anteroventral to the
431	main iliac fragment seems to be part of the preacetabular process, and suggests that it extended at least 17
432	cm in front of the anterior margin of the acetabulum, and well beyond the anterior edge of the pubic
433	peduncle. The pubic peduncle is attached to the head of the pubis, but the contact is visible (especially on
434	the lateral surface) which suggests that they were not coossified. The distal end of the peduncle is 86 mm
435	long, and 41 mm wide. A lateral ridge starts on the edge of the acetabulum 34 mm above the pubic
436	contact, and quickly expands the articular surface of the acetabulum to 54 mm. This is the base of the
437	antitrochanteric shelf, which would have expanded even more broadly over the anterodorsal region of the
438	femoral articulation.

The 18 cm long proximal fragment of the right pubis is attached to the pubic peduncle of theilium (Fig. 20).

It is evident from the orientations of its contacts with the ilium and ischium that the shaft of the 441 bone was almost perpendicular to the longitudinal axis of the ilium as in Aerosteon (Sereno et al., 2008), 442 Murusraptor (Coria and Currie, 2016) and Concavenator (Ortega et al., 2010). In this and other features, 443 444 it resembles the pubis of Megaraptor (Calvo et al., 2004) and Murusraptor (Coria and Currie, 2016). The ischial peduncle is somewhat damaged, but clearly was low (41 mm) and short anteroposteriorly (48 mm 445 from the posterior margin of the pubic shaft). The pubis formed about 4 cm of the acetabular margin, 446 447 where it has a smooth dorsal surface that is 27 mm wide. The anteroposterior diameter of the pubic shaft is 35 mm. The posterodorsal margin of the pubis below the ischial peduncle is similar to the typical 448 449 allosauroid condition and does not enclose an obturator foramen (Brusatte et al., 2008). On the medial surface, the dorsal limit of the pubic apron is 107 mm from the contact with the ilium. 450

- 451 A small fragment of the ischium is attached to the ischial peduncle of the pubis. The puboischial452 contact seems to have been vertical in orientation.
- MLL-Pv-007 also includes fragments of the distal end of a metatarsal and other indeterminate
  fragments. None of these provided any particularly useful information or measurements to this study.
  However, there is also a complete basipodial element (Fig. 21).

In outline and most details, it most closely resembles either the radiale of *Allosaurus* (Gilmore 1920,
fig. 45) or the third right distal tarsal of *Sinraptor* (Currie and Zhao, 1993, fig. 24). The bone is 29 mm
long, 21 mm wide and up to 10 mm thick. Comparison of vertebral measurements suggests that *Lajasvenator* was about half the size of either *Allosaurus* or *Sinraptor*. Given the variability in size of
theropod carpal and tarsal elements, the bone in question has roughly the right size to be either element (it
is 0.71 the size of USNM 4734, an *Allosaurus* radiale, and 0.38 the size of the *Sinraptor* distal tarsal 3 of
IVPP 10600).

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### 5. Discussion

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The phylogenetic relationships of *Lajasvenator* among theropods were analyzed using a character matrix composed of 367 cranial and postcranial features distributed among 67 theropod taxa. The character matrix used was based on that one proposed by Coria and Currie (2016), which in turn was taken, with some modifications, from previous contributions (Carrano et al., 2012; Zanno and Makovicky, 2013). That character set was extended with additional characters and taxa presented by Apesteguía et al., (2016) (see Supplementary Material A and B). The character matrix was analyzed using TNT version 1.5 (Goloboff and Catalano, 2016).

Preliminarily, the analysis resulted in 15200 MPTs with 1147 steps in length, with a CI = 0.372
and RI= 0.660. *Lajasvenator* is clearly nested in a basal position within Carcharodontosauridae, in an
unsolved polytomy with *Concavenator* and *Eocarcharia* (Fig. 22) (Supplementary Material C).

476 Lajasvenator shares with Concavenator the presence of an accessory centrodiapophyseal lamina 477 in each dorsal vertebra (character 182, unknown in *Eocarcharia*). On the other hand, *Lajasvenator* shares 478 with giganotosaurines and Carcharodontosaurus a maxilla with a sculptured external surface (character 479 34). Like most carcharodontosaurids, there is an anteroventrally inclined anterior end of junction between 480 medial wall and paradental plates in the maxilla (character 17, unknown in Concavenator and Tyrannotitan). Lajasvenator also shares several apomorphies with most allosauroids (except Allosaurus), 481 including paradental plates that lack replacement grooves (character 138), camellate internal structure of 482 483 pneumatic centra (character 160), cervical vertebrae that each have an anterior pleurocoel consisting of two openings oriented anteroventrally and posterodorsally (character 169), anteroposteriorly elongate 484 485 cervical pleurocoels (character 170), and a pubic peduncle of the ilium that has a length to width ratio 486 greater than 2 (character 272).

487	The presence of Lajasvenator in the Mulichinco Formation is significant because of the
488	stratigraphic context of this unit. This new form represents the oldest record of Carcharodontosauridae in
489	South America. The family has conspicuous diversity at younger levels of the Cretaceous, when it is
490	represented by large-sized forms like Giganotosaurus, Mapusaurus, Tyrannotitan (Coria and Currie,
491	2006; Coria and Salgado, 1995; Novas et al, 2005) and indeterminate remains from Brazil (de Azevedo et
492	al., 2013). Taurovenator violantei (Motta et al., 2016) is a recently described carcharodontosaurid taxon
493	based on an isolated right postorbital. The autopomorphies proposed to support this taxon consist of the
494	presence of a horn-like prominence on the orbital brow, and a deep excavation on the ventral surface of
495	the postorbital. However, these features are present in Mapusaurus (MCF-PVPH-108.177) and, although
496	less developed, are also in Giganotosaurus (MUCPv-CH-1). The holotype specimen MPCA PV 802 of
497	Taurovenator also exhibits the ventrolateral curved lateral margin of the palpebral (Motta et al., 2016,
498	figs. 4 and 5), a diagnostic feature proposed for Mapusaurus roseae (Coria and Currie, 2006).
499	Considering that the holotype specimen of Taurovenator (MPCA PV 802) was collected at the same
500	stratigraphic level as Mapusaurus (Huincul Formation), and that there are no further autopomorphies in
501	that single postorbital, it seems more reasonably to consider Taurovenator violantei as junior synonym of
502	Mapusaurus roseae.

Other Cretaceous carcharodontosaurid records are known from North America, Europe, Africa 503 504 and Asia (Acrocanthosaurus, Carcharodontosaurus, Concavenator, Eocarcharias, Sauroniops, 505 Siamraptor and Shaochilong) (Brusatte et al., 2009; Cau et al., 2013; Chokchaloemwong et al., 2019; D'Emic et al. 2012; Ortega et al., 2010; Sereno and Brusatte, 2008; Sereno et al., 1996). The Jurassic 506 507 record of this clade is poorly represented by the African form Veterupristisaurus milneri from Tendaguru 508 (Rauhut, 2011), although have been also referred to Carcharodontosauria some specimens collected from 509 the Jurassic of Portugal (Malafaia et al., 2017, 2019), and possibly some teeth from the Middle-Upper Jurassic of the Shishugou Formation of China (Han et al., 2011), and from the Lower Saxony Basin of 510 511 Germany (Gerke and Wings, 2016). Although no carcharodontosaurids have yet been recognized from the

512 Jurassic of South America, it is expected that this clade was present on this continent before the513 Cretaceous.

The faunal association of different dinosaur taxa collected from the Mulichinco Formation 514 includes Lajasvenator, ornithopods, and diplodocid and dicraeosaurid sauropods (Coria et al., 2010, 2019; 515 Gnaedinger et al., 2017). The association is, up to certain point, comparable with that known from the 516 517 Jurassic of Tendaguru (Janensch, 1914; Rauhut, 2011; Remes, 2004). Although the available fossil 518 evidence is not conclusive, it is conceivable that some Jurassic dinosaur associations may have survived 519 into Early Cretaceous times. Such a Cretaceous association - formed by dicraeosaurids, diplodocids, carcharodontosaurid theropods and non-hadrosaurian ornithopods - has to date only been recognized in 520 the Valanginian of Patagonia. An Early Cretaceous dinosaur association with strong Jurassic roots 521 522 preceded the drastic faunal turnover represented by the extinction of these ancient linages and the diversification of titanosaur sauropods and abelisaur theropods occurred in the Turonian of South 523 524 America (Coria and Salgado, 2005). 525

526 6. Concluding Remarks

527

528 The diversity of South American dinosaurs is increased by the first Valanginian record of a

529 carcharodontosaurid theropod, Lajasvenator ascheriae.

530 Lajasvenator is also the oldest South American carcharodontosaurid record, suggesting that the

evolutionary history of the clade likely has older roots than was thought.

532 Carcharodontosaurids are typically associated with large predator forms from the Upper Cretaceous

533 Gondwanan beds, and in some way, were considered as ecological equivalents to the Laurasian

tyrannosauroids. The new taxon, Lajasvenator ascheriae, is based on a medium-sized adult individual,

535 indicating that Carcharodontosauride, as a group, is more diverse than previously considered.

536 Acknowledgments

537	MLL-Pv-005 was found by the first author in 2009, and excavated in 2010 by RAC, PJC plus E.
538	Koppelhus, C. Coy (University of Alberta) and L. Martínez (Museo Argentino de Ciencias Naturales
539	"Bernardino Rivadavia"). L. Garat (Universidad Nacional de Río Negro) found the referred specimen
540	MLL-Pv-007. The specimens were prepared by E. Montes (Museo Carmen Funes, Plaza Huincul),
541	photographed by S. Kagan (University of Alberta), and illustrated by RAC. Fieldwork and research was
542	supported by CONICET Grants #0233, #0683 and UNRN-PI- 40-A-157, 297, 378 to RAC, whereas the
543	expenses of PJC were supported by NSERC (Discovery Grant #203091-06) and the Dinosaur Research
544	Institute (Calgary). We thanks the corrections and suggestions made from two annonimous reviewers and
545	to Dr. Eduardo Koutsoukos, Editor-in-Chief of Cretaceous Research for his assistance and support.
546	Finally, the authors are greatly indebted to the logistic support of the Municipality of Las Lajas, and
547	particularly to the staff of the museum working under R. Faúndez with the support of P. Saldoval.
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766	FIGURE CAPTIONS
767	
768	Figure 1. Restoration of Lajasvenator ascheriae showing which bones have been collected.
769	
770	Figure 2. Location map showing provenance of specimens MLL-PV-005 and MLL-PV-007 (after Coria et
771	al., 2019). Quarries indicated by the arrow.
772	

Figure 3. Stratigraphical section and geological provenance of *Lajasvenator ascheriae* remains (modified
from Coria et al., 2019).

775

- Figure 4. Lajasvenator ascheriae, Holotype, MLL-PV-005. Premaxillae and maxilla in A) left lateral, B)
- right lateral, C) anterior and D) ventral views. Abbreviations: mx, maxilla; pmx, premaxilla; snp,

supranarial process; v, vomers. Scale bar: 10 cm.

779

Figure 05. *Lajasvenator ascheriae*, MLL-Pv-007. Right quadratojugal in A) posterior, B) lateral, and C)
medial views. Abbreviations: ljs, suture for lower prong of jugal; qf, limits of border of quadratic fenestra
formed by quadratojugal; qs, quadrate suture; ujs, range of suture of upper prong of jugal. Scale bar: 10
cm.

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Figure 6. *Lajasvenator ascheriae*, MLL-Pv-007. Anterior ends of dentaries. Left dentary in A) lateral and
D) medial views; right dentary in B) lateral, C) dorsal and E) medial views. Tooth crowns seen on the
right side in dt2 and dt3, wheras broken roots are visible in dt1 and dt4. On the left side, part of the crown
is visible in dt1, and broken roots can be seen in dt2 and dt3. Abbreviations: ch, chin-like process; dt1 to
dt4, dentary tooth positions; id, interdental plate; mg, Meckelian groove. Scale bar: 5 cm.

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Figure 7. *Lajasvenator ascheriae*, Holotype, MLL-Pv-005. Left dentary in lateral view. Abbreviation: mf,
mandibular fenestra. Scale bar: 10 cm.

794	Figure 8. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Left splenial in medial view. Abbreviation: aa,
795	articulation for the angular. Scale bar: 10 cm.
796	
797	Figure 9. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Last four cervical vertebrae, first dorsal
798	vertebra, and ribs in articulation as found in left lateral view. Abbreviations: 6 <sup>th</sup> to 10 <sup>th</sup> , sixth to tenth
799	cervical vertebrae; r5 <sup>th</sup> to r10 <sup>th</sup> , fifth to tenth cervical ribs. Scale bar: 10 cm.
800	
801	Figure 10. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Sixth cervical vertebra in A) left lateral, B)
802	anterior, C) posterior, and D) ventral views. Abbreviations: c, anterior articular surface of centrum; pp,
803	parapophysis. Scale bar: 10 cm.
804	
805	Figure 11. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Seventh cervical vertebra in A-A') left
806	lateral, B-B') anterior, C-C') posterior, D-D') dorsal, and E-E') ventral views. A-E, photographs; A'-E',
807	line drawings. Abbreviations: dp, diapophysis; ep, epipophysis; ns, neural spine; pl, pleurocoel; prz,
808	prezygapophysis; pz, postzygapophysis. Scale bar: 10 cm.
809	
810	Figure 12. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Eight cervical vertebra in A-A') left lateral,
811	B-B') anterior, C-C') posterior, E-E') dorsal, and D-D') ventral views. A-D, photographs; A'-D', line
812	drawings. Abbreviations: as in Fig.11. Scale bar: 10 cm.

- 814 Figure 13. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Ninth cervical vertebra in A-A') left lateral,
- 815 B-B') anterior, C-C') posterior, E-E') dorsal, and D-D') ventral views. A-D, photographs; A'-D', line
- 816 drawings. Abbreviations: as in Fig.11. Scale bar: 10 cm.

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818

- 819 Figure 14. *Lajasvenator ascheriae*, Holotype, MLL-Pv-005. Tenth presacral vertebra (Dorsal 1) in A-A')
- 820 left lateral, B-B') anterior, C-C') posterior, E-E') dorsal, and D-D') ventral views. A-D, photographs; A'-
- 821 D', line drawings. Abbreviations: as in Fig.11. Scale bar: 10 cm.

822

- 823 Figure 15. *Lajasvenator ascheriae*, Holotype, MLL-Pv-005. Articulated series of dorsal centra in right
- 824 ventrolateral view. Abbreviations: 15<sup>th</sup>, fifteenth presacral vertebra; 23<sup>th</sup>, twentyeighth presacral vertebra;

dp, diapophysis. Scale bar: 10 cm.

826

Figure 16. *Lajasvenator ascheriaee*, Holotype, MLL-Pv-005. Mid-caudal vertebrae in A) lateral, and B)
ventral views. Abbreviations: c, vertebral centrum; prz, prezygapophysis; ns, neural spine; sp, spinous
process; tp, transverse process. Scale bar: 10 cm.

830

- 831 Figure 17. *Lajasvenator ascheriae*, Holotype, MLL-Pv-005. Left cervical ribs in lateral view.
- Abbreviations: 6cr-9cr, sixth to ninth cervical rib; bap, bilobed anterior process. Scale bar: 10 cm.

- 834 Figure 18. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Left dorsal ribs in lateral view.
- Abbreviations: 8dr-13dr, eighth to thirteenth dorsal rib. Scale bar: 10 cm.

836

- 837 Figure 19. *Lajasvenator ascheriae*, Holotype, MLL-Pv-005. Pelvic elements in A) right lateral and B)
- right medial views. Abbreviations: ib, iliac blade; is, ischium; p, pubis; pa, pubic apron; ppc, pubic

pedicel; prp; preacetabular process: sr, sacral rib. Scale bar: 10 cm.

840

- 841 Figure 20. Lajasvenator ascheriae, Holotype, MLL-Pv-005. Ilium and pubis articulation in A) right
- 842 lateral, B) posterior, and C) right medial views. Abbreviations: ac, acetabulum; il, ilium; is, ischium; pa;
- 843 pubic apron. Scale bar: 10 cm.

844

Fig. 21. *Lajasvenator ascheriae*, MLL-Pv-007. Possible carpal/tarsal in A) dorsal, B) ventral; C) anterior,
and D) posterior views. Scale bar: 1 cm.

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Fig. 22. Simplified cladogram depicting the phylogenetic relationships of *Lajasvenator ascheriae* within
Carcharodontosauridae.

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- 852

Tooth	DHmin	СНЈМ	CHPC	FABL	AntDent	PostDent	BW	BW/FABL	AL AW		AW/AL
Pmx 1 R	?	?	?	?	?	?	?	?	9.1	7.1	0.78
Pmx 1 L	?	?	?	?	?	?	?	?	9.2	6.5	0.71
Pmx 2 L	?	?	?	?	?	?	?	?	11.4	5.7	0.50
Pmx 3 R	?	25.7	20.9	10.1	2.7	3	6.2	0.61	12	7.1	0.59
Pmx 4 R	?	10.2	?	5.8	?	?	4.7	0.81	10.3	6.1	0.59
Pmx 4 L	?	25plus	?	8.5	?	?	6.4	0.75	?	?	?
Mx 1 L	?	?	?	?	?	?	?????		10.7	4.8	0.45
Mx 2 L	?	?	?	?	?	?	?	?	13.4	6	0.45
Mx 3 R	?	?	?	?	?	?	?	?	15.6	6	0.38
Mx 3 L	?	?	?	?	?	?	?	?	16.8	6.4	0.38
Mx 4 R	?	?	?	?	?	?	?	?	13plus	?	?
Mx 4 L	?	?	?	?	?	?	?	?	17.1	7.2	0.42
Mx 5 L	?	?	?	?	?	?	?	?	20.8	8.1	0.39
Mx 6 L	?	?	?	?	?	?	? ? 18.3		18.3	7.4	0.40
Mx 7 L	?	?	?	?	?	?	?	?	10plus	?	?
D 1 R	53.2	?	?	?	?	?	?	?	?	5.1	?
D1L	53.2	?	?	?	?	?	?	?	8.1	4.3	0.40
D 2 R	53.2	13plus	?	14.2	?	?	6.4	0.45	0.45 14.5		0.49
D 2 L	53.2	?	?	?	?	?	?	?	? 11.7		?
D 3 R	53.2	?	?	?	?	?	??? 14.7		14.7	6.8	0.46
D 3 L	53.2	?	?	?	?	?	?	?	14.3	6.1	0.40
D 4 R	53.2	?	?	?	?	?	?	?	?	5.1plus	?
D 4 L	53.2	?	?	?	?	?	?	?	?	6plus	?
D 4 L	53,2	?	?	?	?	?	?	?	?	6plus	?

Table 1. Teeth and alveoli measurements of *Lajasvenator ascherieae*. Premaxillary and maxillary teeth from specimen MLL-Pv-005, Holotype; dentary teeth from specimen MLL-Pv-007. Abbreviations: ?, unknown; AL, anteroposterior length of alveolus; AW, transverse alveolus width; AntDent, number of anterior denticles per mm; BW, basal width of crown; D, dentary tooth; DHmin, minimum height of dentary; CHJM, crown height from the jaw margin, CHPC, crown height along posterior carina; FABL, fore-aft basal length; L, left; Mx, maxillary tooth; Pmx, premaxillary tooth; PostDent, number of posterior denticles per mm; R, right. All measurements in mm.

	clnas	clv	clwc	caww	cah	срw	cph	cnw	th	nsh	nmdl	wap	wapz	llppz	watp	wapp
6	82	81	102	57	64	61.5	59.8	29	?	?	?	?	83est	?	?	60.6
7	66.8	72	90	63	36	62.3	47.8	30.5	126.5	66.5	29	74	71.6	109.6	128	66
8	65	69.5	103	48	43	65	47	32.1	129	68	30	68.8	69	86.4	134	71.3
9	62	65.1	92	59	40.5	68.5	48.9	34.2	128.3	64.7	21	70	74	66	144.4	66.6
10	?	?	?	59.5	44plus	?	?	?	124pl us	69.2	17	73.7	?	?	150	59.4
15	47plus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	70.5	71	?	61.5	59est	60.6	58est	14.4	?	?	?	?	?	?	?	?
17	71.4	64.9	?	63.4	53plus	53.6	56.3	15.5	?	?	?	?	?	?	?	?
18	72.6	65.6	?	49	52.3	55	60.6	15.3	?	?	?	?	?	?	164est	?
19	?	?	?	?	?	?	86	?	?	?	?	?	?	?	160est	?
20	68	68.7	?	53plus	88.3	65.7	77.2	16plus	?	?	?	?	?	?	160est	?
21	74.2	70.1	?	70	82.3	70.5	79.4	25	?	?	?	?	?	?	156	49
22	71.3	67.5	?	75.6	80.4	66plus	83	27.1	?	?	?	?	?	?	124plu s	54.3
23	?	?	?	?	93.6	?	?	27	?	?	?	?	?	?	?	?
S2	?	59plus	?	?	?	?	?	32	?	?	?	?	?	?	?	?
S3	?	68	?	55	?	58	?	35	?	?	?	?	?	?	89	?
S4	?	35plus	?	58	?	58	?	?	?	?	?	?	?	?	60est	?
C15 ?	?	?	?	?	?	?	?	?	?	?	?	?	24.4	?	?	?
C16 ?	58plus	?	?	?	?	30.8	39.6	13	104	61	20.8	30.3	24.6	84	88est	?
C17 ?	65.5	66	?	31.6	34.7	33.6	41	14.2	99	58est	23	38	24.6	81	100	?
C18 ?	65.3	67	?	38.6	36	32.4	36	15.6	?	?	?	41	?	?	96.7	?

Table 2. *Lajasvenator ascherieae*, Holotype, specimen MLL-Pv-005. Table of vertebral measurements. Abbreviations; 6 to 23: presacral vertebrae 6<sup>th</sup> to 23<sup>rd</sup>; ?, unknown; C, caudal vertebrae; cah, centrum anterior height; caw, centrum anterior width; clnas, centrum length at neural arch suture; clv, centrum length at ventral side; clwc, centrum length with condyle; cnw, centrum narrowestr width; cph, centrum posterior height; cpw, centrum posterior width; est, estimated; lppz, length prezygapophyseis – postzygapophysis; nmdl, neural spine maximum distal

length; nsh, neural spine height above canal roof; S, sacral vertebrae; th, total height; wap, width across prezygapophyseis; wapp, width across parapophyses; wapz, width across postzygapophyses; watp, width across transverse processes. All measurements in mm.

A new genus and species of carcharodontosaurid theropod (*Lajasvenator ascheriae*) is described.

Lajasvenator is the oldest Cretaceous carcharodontosaurid record.

*Lajasvenator* represents the first Lower Cretaceous, South American carcharodontosaurid.

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### **Declaration of interests**

 $\boxtimes$  The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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