

Allosauroid (Theropoda, Tetanurae) remains from the Sierra Barrosa Formation (Middle Coniacian, Upper Cretaceous), Patagonia, Argentina

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ALLOSAUROID (THEROPODA, TETANURAE) REMAINS FROM THE SIERRA BARROSA FORMATION (MIDDLE CONIACIAN, UPPER CRETACEOUS), PATAGONIA, ARGENTINA

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Abstract. The Late Cretaceous theropod fauna of South America is composed of Abelisauridae, Noosauridae, Spinosauridae, Carcharodontosauridae, Megaraptora, and Coelurosauria. These groups include mostly small (Noosauridae and Coelurosauria) and medium- to large-sized taxa (Carcharodontosauridae, Abelisauridae, and Megaraptora). Some of these lineages are predominantly Gondwanic (Abelisauridae, Noosauridae, Carcharodontosauridae, Megaraptora) and poorly represented in Laurasian landmasses. Particularly, several theropods have been reported from Patagonia, known either due to distinct anatomical features or due to their high degree of preservation, such as *Carnotaurus*, *Skorpiovenator*, *Giganotosaurus*, *Megaraptor*, *Alvarezsaurus*, and *Unenlagia*. Here we describe a new incomplete tibia (MAU-PV-CM-653) from the Sierra Barrosa Formation (middle Coniacian, Upper Cretaceous), Patagonia, Argentina. MAU-PV-CM-653 shows an anteroposteriorly reduced cnemial crest that is strongly curved laterally. Finally, the tibia lacks a proximal extension of the fibular crest. These traits are reminiscent of tetanuran morphology and, together with the stratigraphic provenance of MAU-PV-CM-653, they allow us to assign it to an allosauroid theropod, thus improving the Allosauroidea global record for the middle Late Cretaceous.

Key words. Late Cretaceous. Neuquén Group. South America. Patagonia. Dinosauria. Allosauroidea. Tibia.

Resumen. RESTOS DE ALLOSAUROIDEO (THEROPODA, TETANURAE) DE LA FORMACIÓN SIERRA BARROSA (CONIACIANO MEDIO, CRETÁCICO SUPERIOR), PATAGONIA, ARGENTINA. La fauna de terópodos del Cretácico Tardío de América del Sur está compuesta por Abelisauridae, Noosauridae, Carcharodontosauridae, Spinosauridae, Megaraptora y Coelurosauria. Estos grupos incluyen mayormente taxones de pequeño (Noosauridae y Coelurosauria) y de mediano a gran tamaño (Abelisauridae, Carcharodontosauridae y Megaraptora). Algunos de estos linajes son predominantemente gondwánicos (Abelisauridae, Noosauridae, Carcharodontosauridae, Megaraptora) y poco representados en los continentes laurásicos. Particularmente, distintos terópodos han sido reportados desde la Patagonia, conocidos o por sus distintivas características anatómicas o por su grado de preservación, tales como *Carnotaurus*, *Skorpiovenator*, *Giganotosaurus*, *Megaraptor*, *Alvarezsaurus* y *Unenlagia*. Aquí describimos una nueva tibia incompleta (MAU-PV-CM-653) proveniente de la Formación Sierra Barrosa (Coniaciano medio, Cretácico Superior), Patagonia, Argentina. MAU-PV-CM-653 muestra una cresta cnemial reducida anteroposteriormente, que está fuertemente curvada lateralmente. Finalmente, la tibia carece de una extensión proximal de la cresta fibular. Estos rasgos hacen recordar una morfología de tetanuro y, junto con la procedencia estratigráfica de MAU-PV-CM-653, nos permite asignarla a un terópodo allosauroideo, y por ende mejorar el registro global de Allosauroidea para la parte media del Cretácico Tardío.

Palabras clave. Cretácico Superior. Grupo Neuquén. América del Sur. Patagonia. Dinosauria. Allosauroidea. Tibia.

THE CRETACEOUS South American theropod record spans all major internal taxa (e.g., Ceratosauria, Allosauroidea, Coelurosauria), and is represented by small, medium, and large-sized specimens (e.g., Carrano & Sampson, 2008; Carrano *et al.*, 2012; Novas *et al.*, 2013). In particular, this region is the most abundant fossil area compared to other Gondwanan provinces, due to the strong increase in the

South American fossil record from the Cenomanian (Late Cretaceous) onward. The abundance of remains of some groups of theropods such as Abelisauridae, Megaraptora, and Maniraptora in the Argentine Patagonia is remarkable, with a large number of nominated taxa, some of which are distinguished by their high degree of conservation (e.g., Novas *et al.*, 2013).

The Neuquén Group is the principal lithostratigraphic unit regarding the theropod fossil record in northern Patagonia (e.g., Leanza *et al.*, 2004; Garrido, 2010), and it is subdivided in nine formations that mainly encompass the Upper Cretaceous (middle Cenomanian–middle Campanian) (Garrido, 2010). However, theropod remains are scarce from the Río Neuquén Subgroup (Portezuelo, Los Bastos, Sierra Barrosa and Plottier formations; middle Turonian–lower Santonian), except for the Portezuelo Formation (Novas, 1997, 1998; Novas & Puerta, 1997; Calvo *et al.*, 2004a; Novas & Pol, 2005). This paucity of theropods mainly affects the allosauroid record, since only two specimens have been recorded from the middle Late Cretaceous (Coria & Currie, 2016; Porfiri *et al.*, 2018). However, when we take into account the global allosauroid record (excepting Argentina), this paucity is even worse, since no middle Late Cretaceous (Coniacian–Santonian) specimens have been discovered anywhere else up to now. Here, we report a new tetanuran

theropod partial tibia from the Sierra Barrosa Formation (middle Coniacian, Upper Cretaceous) (Fig. 1) that we refer to Allosauroida based on several features of its morphology and, tentatively, to Megaraptora if we consider its stratigraphic provenance.

Institutional acronyms. MAU, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Argentina; MB, Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany; MCF, Museo Municipal Carmen Funes, Plaza Huincul, Argentina; MCT, Museu de Ciências da Terra do Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; MPCA, Museo Provincial Carlos Ameghino, Cipolletti, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MUC, Museo Universidad Nacional del Comahue, Neuquén, Argentina; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina; USNM, National Museum of Natural History, Smithsonian Institution, Washington, USA.

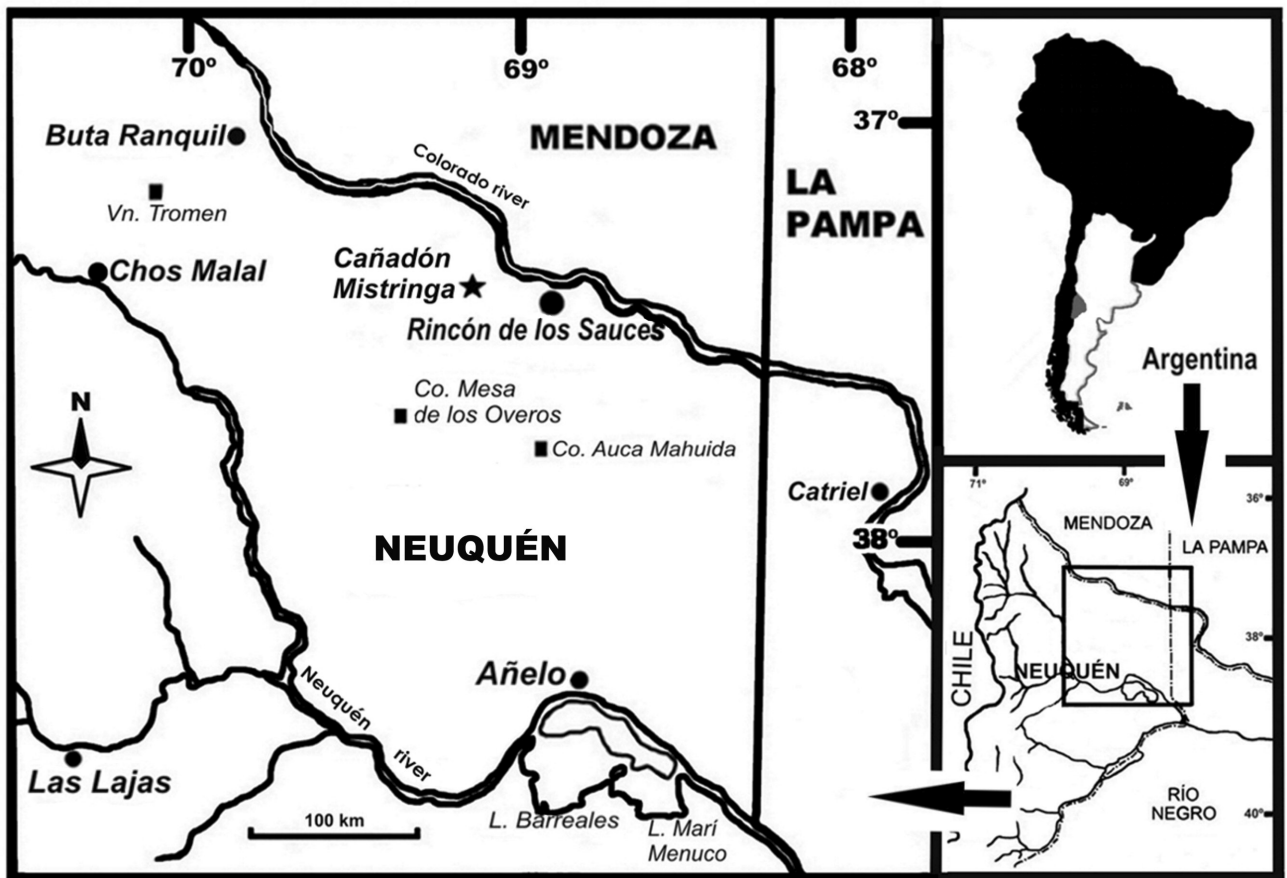


Figure 1. Locality map showing where the specimen MAU-PV-CM-653 was found, indicated by the black star.

TABLE 1 - Measurements (in cm) of the tibia MAU-PV-CM-653

Proximodistal Length	Proximodistal Length of Cnemial Crest	Anteroposterior Length of Proximal Surface	Anteroposterior Length of Cnemial Crest	Mediolateral Width of Proximal Posterior Rim
11.5*	6.6	12.7	4.3	6.8

*Asterisk indicates incomplete measurements due to missing bone.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

ALLOSAUROIDEA (Marsh, 1878)

ALLOSAUROIDEA indet.

Figures 2 and 3.1

Specimen. MAU-PV-CM-653, proximal end of the left tibia (Tab. 1).

Geographic occurrence. MAU-PV-CM-653 was found at Cañadón Mistringa locality, southwest of Rincón de los Sauces city, Pehuenches Department, Neuquén Province, Argentina (Fig. 1).

Stratigraphic occurrence. The fossil-bearing strata are attributed to the Sierra Barrosa Formation (Coniacian, Upper Cretaceous), Neuquén Group (Garrido, 2010), Neuquén Basin.

Description. MAU-PV-CM-653 corresponds to the proximal end of the left tibia, including the articular surface, the posterior condyles, and the cnemial crest. However, the specimen lacks the rest of the diaphysis, including the crista fibularis and the distal articular end. In proximal view (Fig. 2.1), the articular surface has a comma shaped outline. The proximal condyles are well defined and separated by a shallow intercondylar sulcus. The medial condyle shows a teardrop outline, whereas the lateral condyle is oval in outline, with an anteroposteriorly oriented major axis. Furthermore, the medial condyle is anteroposteriorly longer and more posteriorly projected than the lateral one. Anterior to the articular condyles there is a depression that is probably where the femoral tibial condyle articulated. The cnemial crest is anteroposteriorly reduced and is strongly curved

laterally. In fact, the anterior rim of the cnemial crest is positioned at 90 degrees with respect to the main axis of the proximal surface. The medial rim is convex due to the lateral curvature of the cnemial crest. The lateral rim is sinusoidal, since the section that corresponds to the lateral condyle is slightly convex whereas the section that corresponds to the cnemial crest is concave. The lateral condyle is separated from the cnemial crest by a deep *incisura tibialis*. However, the lateral condyle of MAU-PV-CM-653 lacks a distally directed anterolateral process. The posterior rim is w-shaped and is obliquely oriented relative to the mediolateral axis.

In medial view (Fig. 2.2), the preserved portion of the tibia is triangular in outline. The dorsal rim is almost straight, only bowing ventrally at the posterior end. In this view, the cnemial crest is horizontal and does not exceed the articular surface proximally. Near the posterodorsal corner, there is a triangular depression with a rugose surface where the muscles *flexor tibialis internus 3* (FTI3) and *flexor tibialis externus* (FTE) (Carrano & Hutchinson, 2002) were probably inserted. The surface is slightly concave near the anterior border of the cnemial crest.

In lateral view (Fig. 2.3), the medial condyle is proximally higher and posteriorly deeper than the lateral condyle, resulting in a laterodistally inclined proximal surface. The lateral condyle ends distally with a marked step. The lateral fossa of the cnemial crest is anteroposteriorly narrow with a finger-like outline and its major axis is anteroproximally-posterodistally oriented. The anterior rim of the cnemial crest is slightly convex and bears a rugose bump at the proximal end, where the muscles *ambiens* (AMB), *femorotibialis* (FMT), and *iliotibiales 1–3* (IT 1-3) would have been inserted (Carrano & Hutchinson, 2002). The fibular crest cannot be observed because of the poor preservation of the tibial

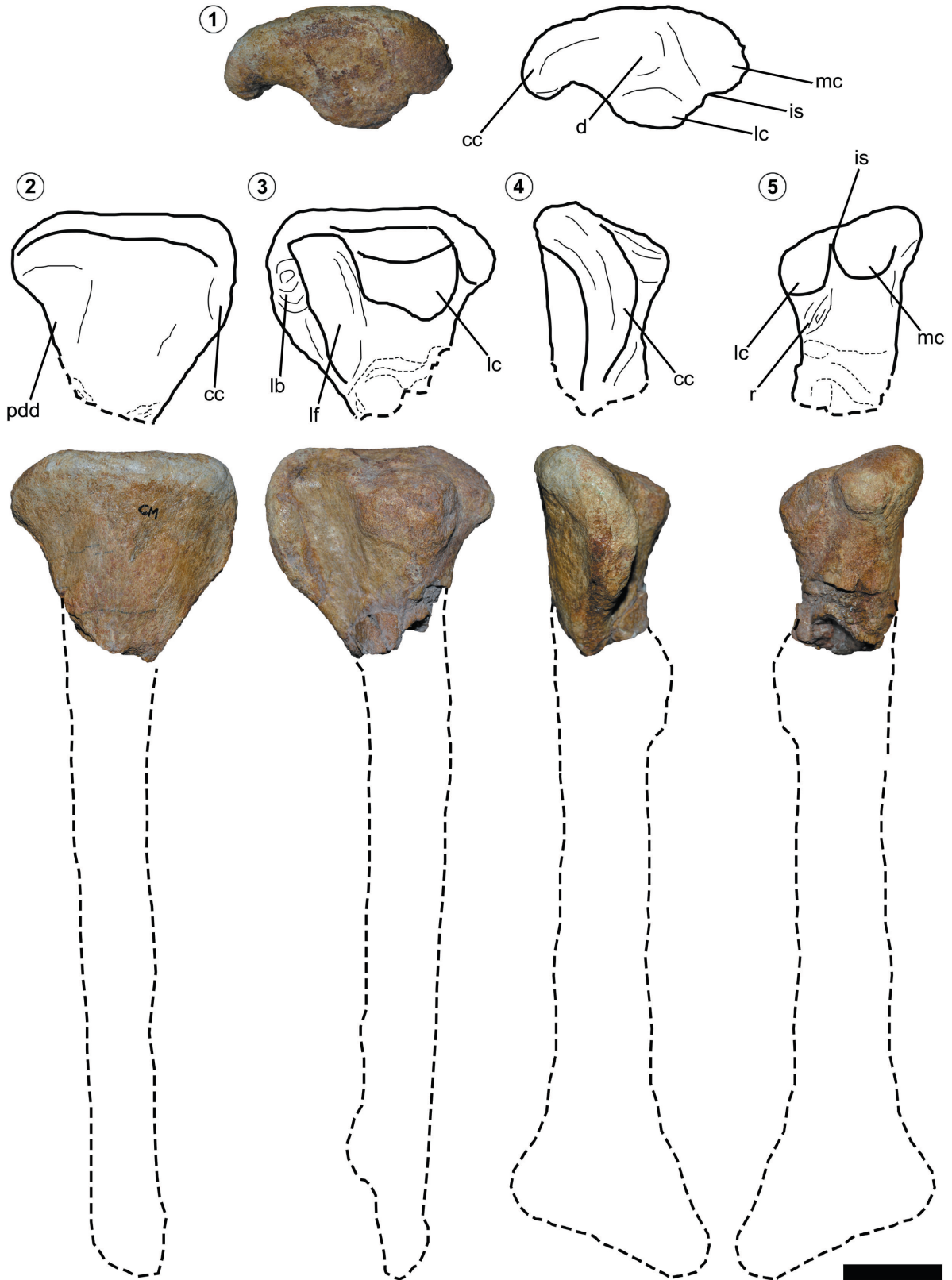


Figure 2. *Allosauroidea* indet. MAU-PV-CM-653. Tibia in 1, proximal; 2, medial; 3, lateral; 4, anterior; and 5, posterior views. Abbreviations: cc, cnemial crest; d, depression; is, intercondylar sulcus; lb, lateral bump; lc, lateral condyle; lf, lateral fossa; mc, medial condyle; pdd, posterodorsal depression; r, rugosity. Scale bar = 5 cm.

shaft. However, in the fragment of tibia presented, the fibular crest does not extend proximally or anteroproximally onto the lateral surface of the cnemial crest.

In anterior view (Fig. 2.4), the cnemial crest is laterally directed with a thick proximal end that narrows towards the distal end. On the medial part, the shallow medial depression is visible, delimited proximally and anteriorly by a stout ridge.

In posterior view (Fig. 2.5), the proximal rim is laterodistally oriented. The medial condyle is rounded and ends distally with a convex step. The lateral condyle has a rugose surface and is rectangular in shape, with the major axis mediolaterally positioned. The intercondylar sulcus is deep and distally to it there is a rugose oval area where soft tissue was probably inserted (possibly the muscle *flexor tibialis internus 1*, FT11; Carrano & Hutchinson, 2002). Although the tibial shaft has been almost completely lost, the preserved fragment shows a lateral bowing of the element.

DISCUSSION AND CONCLUSIONS

The MAU-PV-CM-653 tibia shows a posteriorly positioned medial condyle, a condition present more markedly in *Neovenator*, *Orkoraptor*, and in the indeterminate tetanuran MB.R.1763, but different from the condition present in *Australovenator*, *Fukuiraptor*, *Murusraptor*, *Phuwiangvenator*, and *Vayuraptor*, in which both proximal condyles reach roughly the same distance posteriorly (Azuma & Currie, 2000; Rauhut, 2005a; Brusatte *et al.*, 2008; Novas *et al.*, 2008; White *et al.*, 2013; Coria & Currie, 2016; Samathi *et al.*, 2019) (Fig. 3.1, 3.6, 3.8). However, the rounded posterior end of the medial condyle of MAU-PV-CM-653 differs from the triangular posterior end of *Neovenator* and of the indeterminate tetanuran MB.R.1763 (Fig. 3.1, 3.6). MAU-PV-CM-653 differs from *Allosaurus*, *Neovenator*, *Australovenator*, *Fukuiraptor*, *Murusraptor*, *Phuwiangvenator*, *Vayuraptor*, and the tetanuran MB.R.1763 since it lacks the anterolateral projection of the lateral condyle present in the other mentioned taxa (Madsen, 1976; Azuma & Currie, 2000; Rauhut, 2005a; Brusatte *et al.*, 2008; White *et al.*, 2013; Coria & Currie, 2016; Samathi *et al.*, 2019) (Fig. 3.1, 3.6, 3.8). In the same way, the absence of a ventrally oriented process of the lateral condyle observed in MAU-PV-CM-653 is shared with several tetanurans (*e.g.*, *Torvosaurus*, *Allosaurus*, *Sinraptor*,

Fukuiraptor, *Murusraptor*, *Orkoraptor*, *Vayuraptor*; Madsen, 1976; Britt, 1991; Currie & Zhao, 1993; Azuma & Currie, 2000; Novas *et al.*, 2008; Coria & Currie, 2016; Samathi *et al.*, 2019) (Fig. 3.1, 3.4, 3.7), but differs from *Neovenator*, *Australovenator*, *Tyrannosaurus*, *Phuwiangvenator*, and the indeterminate tetanuran MB.R.1763, that have a conspicuous ventrally directed process (Brochu, 2003; Rauhut, 2005a; Brusatte *et al.*, 2008; White *et al.*, 2013; Samathi *et al.*, 2019) (Fig. 3.5–6, 3.8).

The anteroposteriorly reduced and strongly laterally curved cnemial crest of the MAU-PV-CM-653 tibia is a feature that is also observed in several large (*e.g.*, *Allosaurus*, *Sinraptor*, *Murusraptor*, *Tyrannosaurus*; Madsen, 1976; Currie & Zhao, 1993; Brochu, 2003; Coria & Currie, 2016) and small-sized tetanurans (MB.R.1763; Rauhut, 2005a) (Fig. 3.1, 3.4–5), but that differs from the more open and more anteroposteriorly developed cnemial crest of the tibiae of non-averostran theropods (*e.g.*, *Dilophosaurus*; Marsh & Rowe, 2020), ceratosaurs (*e.g.*, *Ceratopsaurus*, *Eoabelisaurus*, *Velocisaurus*, *Quilmesaurus*, *Xenotarsosaurus*, *Genusaurus*, *Aucasaurus*; Gilmore, 1920; Martínez *et al.*, 1986; Accarie *et al.*, 1995; Madsen & Welles, 2000; Coria, 2001; Coria *et al.*, 2002; Pol & Rauhut, 2012; Ibricic *et al.*, 2021; MCF-PVPH-236; MPCA-PV-100; MPEF PV 3990; MUCPv-41; UNPSJB-PV 184) and basal tetanurans (*e.g.*, *Piatnitzkysaurus*; Rauhut, 2005b) (Fig. 3.1–3.3). The extension of the cnemial crest of MAU-PV-CM-653 is reduced when compared with *Aerosteon* (Aranciaga Rolando *et al.*, 2021) and *Australovenator* (White *et al.*, 2013), but similar to the development observed in *Phuwiangvenator* (Samathi *et al.*, 2019). Moreover, MAU-PV-CM-653 shows a cnemial crest almost horizontally projected in lateral view, as in the *Murusraptor* tibia but unlike the dorsally directed crest of *Aerosteon*. The lack of a proximal and an anteroproximal extension of the fibular crest onto the lateral cnemial crest and the absence of a connection between the fibular crest and the proximal rim observed in MAU-PV-CM-653 is a condition shared with tetanuran theropods (*e.g.*, *Allosaurus*, *Sinraptor*, *Murusraptor*, *Tyrannosaurus*; Madsen, 1976; Currie & Zhao, 1993; Brochu, 2003; MCF-PVPH-411) (Fig. 3.1, 3.4–5, 3.7). Whereas, coelophysoids and ceratosaurs have a fibular crest strongly developed, both proximally and anteroproximally, reaching the proximal rim (*e.g.*, *Ceratopsaurus*, *Quilmesaurus*, *Ekrixinatosaurus*,

Aucasaurus; Madsen & Welles, 2000; Rauhut, 2003; Calvo *et al.*, 2004b; MCF-PVPH-236; MPCA-PV-100; MUCPv-294) (Fig. 3.2–3.3). The bump where muscles *ambiens*, *femorotibialis*, and *iliotibiales* 1–3 would have been inserted is less developed than the one observed in several ceratosaurs (*e.g.*, *Ceratopsaurus*, *Euabelisaurus*, *Xenotarsosaurus*, *Aucasaurus*; Madsen & Welles, 2000; MCF-PVPH-236; MPEF PV 3990; UNPSJB-PV 184), some megaraptorans (*Australovenator*, *Murusraptor*; White *et al.*, 2013; Coria & Currie, 2016), and large tetanurans (*e.g.*, *Allosaurus*, *Asfaltovenator*, *Torvosaurus*, *Tyrannosaurus*; Madsen, 1976; Britt, 1991; Brochu, 2003; Rauhut & Pol, 2019). The posterior intercondylar sulcus in MAU-PV-CM-653 as well as in *Australovenator* (White *et al.*, 2013) and *Phuwiangvenator* (Samathi *et al.*, 2019), is shallower than the intercondylar sulcus of *Murusraptor* (MCF-PVPH-411). The posterior rugose area distal to the intercondylar sulcus is well marked, as in an indeterminate abelisauroid from Brazil (Abelisauroida indet. MCT 1783-R; Machado *et al.*, 2013). The posterior morphology of both condyles differs from the triangular medial condyle and the rounded lateral condyle observed in several ceratosaurs (*e.g.*, *Aucasaurus*, Abelisauroida indet. MCT 1783-R; Machado *et al.*, 2013; MCF-PVPH-236).

Taxa belonging to several theropod clades have been discovered in the cretaceous layers from Patagonia (*e.g.*, Coria, 2007; Novas, 2009; Novas *et al.*, 2013), thus yielding the most comprehensive fossil record from Gondwana (Novas *et al.*, 2013). The affinity of MAU-PV-CM-653 with Patagonian tetanurans, and the marked differences between this specimen and all known ceratosaur tibiae means it probably belonged to some tetanuran group (Megalosauroida, Allosauroida, or Coelurosauria; Rauhut *et al.*, 2016). South American megalosauroid remains are mainly from Brazil, where several spinosaurid taxa have been discovered (*e.g.*, Kellner *et al.*, 2011; Carrano *et al.*, 2012). In contrast, only a few isolated teeth have been reported from Patagonia (Canudo *et al.*, 2004; Canale *et al.*, 2017). Moreover, Megalosauroida is a clade distributed mainly in the Jurassic (Megalosauridae; Rauhut *et al.*, 2016) and throughout the Early Cretaceous up to the Cenomanian (Spinosauridae; Kellner *et al.*, 2011; Malafaia *et al.*, 2020a, 2020b). The Allosauroida fossil record from the Late Cretaceous of Patagonia is mainly composed of carcharodontosaurian taxa, although carchar-

odontosaurids disappeared globally after the Turonian (*e.g.*, Canale *et al.*, 2009; Delcourt & Grillo, 2018), with the last presence of this family documented in Asia (Brusatte *et al.*, 2009). However, a possible non-Carcharodontosauria allosauroid has been reported from the late Turonian–early Coniacian of Patagonia (Paulina Carabajal & Coria, 2015). Carcharodontosauria also includes megaraptorans (Benson *et al.*, 2010), extending the biochron of this lineage until the Maastrichtian (Novas *et al.*, 2008; Méndez *et al.*, 2012). Finally, Patagonian coelurosaurids are generally smaller sized theropods, some of them recovered as basal forms within Coelurosauria and others recovered deeply nested within Paraves (*e.g.*, Novas *et al.*, 2013; Motta *et al.*, 2020). Interestingly, an alternative scenario proposes Megaraptora as a member of Tyrannosauroida (Novas *et al.*, 2013; Porfiri *et al.*, 2014; Aranciaga Rolando *et al.*, 2019), which implies a re-evaluation of Tetanurae internal relationships.

Taking into account the morphology of MAU-PV-CM-653, plus the stratigraphic and geographic data from the records of some tetanuran clades (*e.g.*, Megalosauroida, Tyrannosauroida), we assign it to Tetanurae, possibly to a less inclusive allosauroid group such as Megaraptora. The allosauroid record is globally scarce after the Turonian age, since it only includes megaraptoran taxa and several post-Cenomanian carcharodontosaurid teeth that have been re-evaluated as belonging to Abelisauridae (see Canale *et al.*, 2009 and references therein). From Argentina proceed the Cenomanian–Turonian *Aoniraptor* and two unnamed specimens (Motta *et al.*, 2016; Lamanna *et al.*, 2020), the late Turonian–early Coniacian *Megaraptor namunhuaiquii* (Novas, 1998; Porfiri *et al.*, 2014), the middle Coniacian *Murusraptor barroensis* (Coria & Currie, 2016), and the Santonian *Tratayenia rosalesi* (Porfiri *et al.*, 2018). From the Campanian of Argentina, *Aerosteon riocoloradensis* (Sereno *et al.*, 2008), *Orkoraptor burkei* (Novas *et al.*, 2008), and several recently described unnamed megaraptorans (*e.g.*, Novas *et al.*, 2019; Ibiricu *et al.*, 2020) have been reported. In contrast, from Brazil, only an indeterminate specimen has been communicated (Martinelli *et al.*, 2013). For the Maastrichtian, the Allosauroida record is also represented uniquely by megaraptorans known from Argentina and Brazil (Méndez *et al.*, 2012; Casal *et al.*, 2019). With the exception of the Argentine and Brazilian specimens for the Coniacian-

Maastrichtian period, no other allosauroid dinosaurs are known globally. When the middle Late Cretaceous (Coniacian–Santonian) is considered, only two taxa, *i.e.*, *Murusraptor* and *Tratayenia*, and one specimen, MAU-PV-CM-653, are known.

Despite the incompleteness of MAU-PV-CM-653 and the lack of the peculiar traits that characterize the Late Cretaceous allosauroids of South America, this specimen

could represent a new theropod taxon. In this case, the finding presented here increases the theropod fauna for the Sierra Barrosa Formation that currently only includes the megaraptorid *Murusraptor barrosaensis* (Coria & Currie, 2016). The morphology of MAU-PV-CM-653 also differs from the tibia of *Aerosteon riocoloradensis* (Sereno *et al.*, 2008) that was recovered in the same geographical area but in a different stratigraphic horizon (Anacleto Formation,

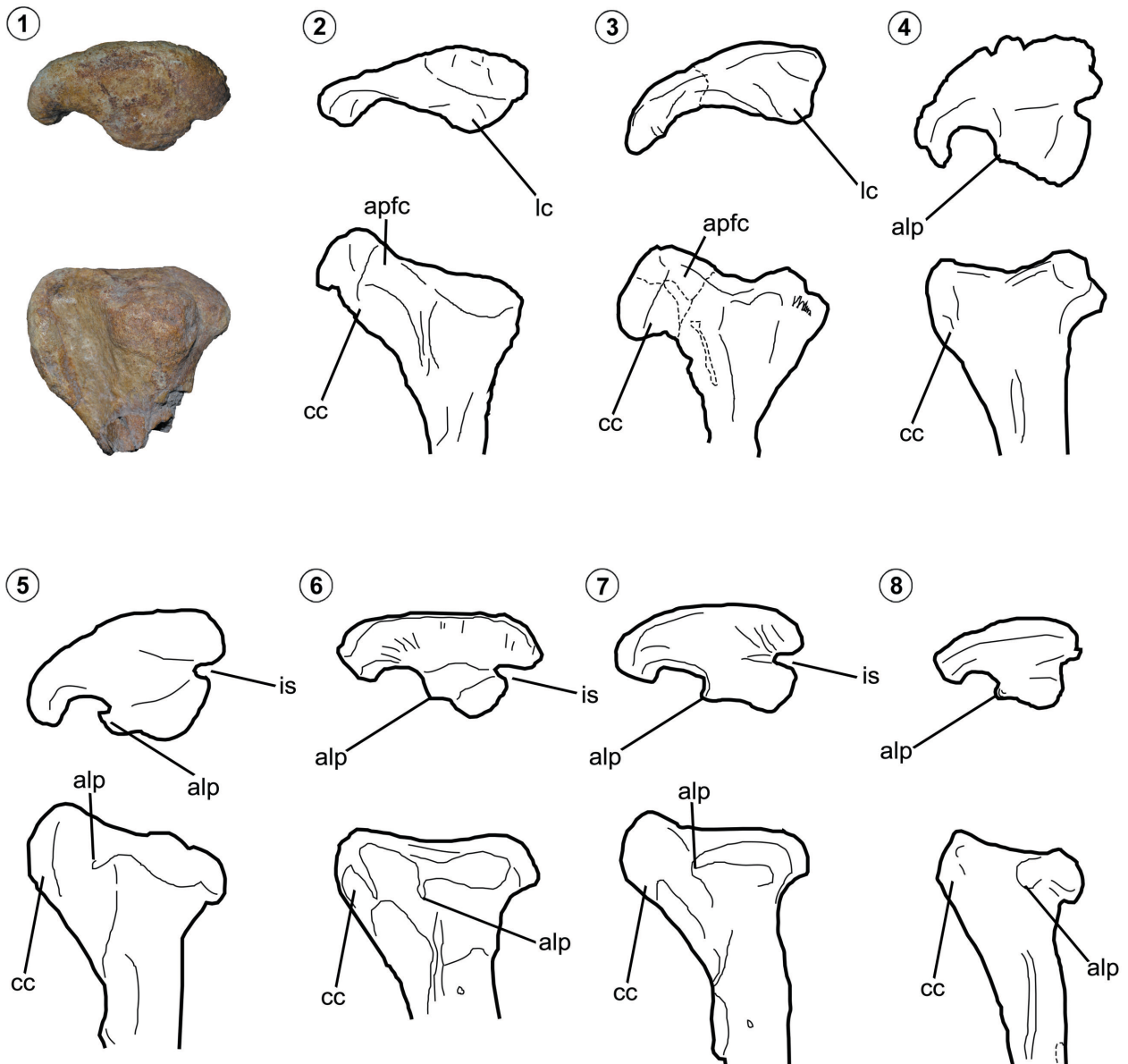


Figure 3. Comparison of theropod tibiae in proximal (top) and lateral (bottom) views. 1, *Allosauroidea* indet., MAU-PV-CM-653; 2, *Ceratosaurus nasicornis* (USNM 4735); 3, *Quilmesaurus curriei* (MPCA-PV-100; reversed); 4, *Murusraptor barrosaensis* (MCF-PVPH-411; reversed); 5, *Tyrannosaurus rex* (after Brochu, 2003); 6, *Neovenator salerii* (after Brusatte *et al.*, 2008); 7, *Allosaurus fragilis* (after Madsen, 1976); and 8, *Australovenator wintonensis* (after White *et al.*, 2013). Abbreviations: alp, anterolateral process; apfc, anteroproximal extension of the fibular crest; cc, cnemial crest; is, intercondylar sulcus; lc, lateral condyle. Image not to scale.

lower Campanian). Moreover, the allosauroid fossil record from the Coniacian to the Santonian is globally scarce, with some exceptions in South America (e.g., Coria & Currie, 2016; Porfiri *et al.*, 2018). Therefore, we consider MAU-PV-CM-653 important to fill the paucity of this clade in the middle Late Cretaceous.

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