

# A non-furileusaurian caudal vertebra from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian) and morphological variation in the tail of Abelisauridae

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Recibido: 18 de julio 2022 - Aceptado: 15 de octubre 2022 - Publicado: 16 de diciembre 2022

**Para citar este artículo:** Federico Gianechini, Leonardo Filippi, Ariel Méndez, & Alberto Garrido (2022). A non-furileusaurian caudal vertebra from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian) and morphological variation in the tail of Abelisauridae. *Publicación Electrónica de la Asociación Paleontológica Argentina* 22 (2): 58–70.

**Link a este artículo:** <http://dx.doi.org/10.5710/PEAPA.15.10.2022.438>

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ISSN 2469-0228

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# A NON-FURILEUSAURIAN CAUDAL VERTEBRA FROM THE BAJO DE LA CARPA FORMATION (UPPER CRETACEOUS, SANTONIAN) AND MORPHOLOGICAL VARIATION IN THE TAIL OF ABELISAURIDAE

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**Abstract.** The Cerro Overo-La Invernada area in north Patagonia has provided a rich record of Cretaceous continental tetrapods in the last two decades, mainly from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian). The dinosaur fauna from this area is diverse, including several new taxa, with abelisaurid theropods particularly abundant. Recently, a new isolated caudal vertebra (MAU-Pv-CO-598) was here recovered. Although fragmentary, it shows features that differentiate it from other abelisaurid remains previously found in this area. It is considered a mid-caudal vertebra and is mainly characterized by a longitudinal groove on the ventral surface of the centrum; a scarcely elevated transverse process with an anteroposteriorly expanded and laterally concave distal end; a longitudinal dorsal crest anteriorly extended from the anterior border of the neural spine; and small tubercles extended from the ends of the zygapophyses, which are considered as accessory interlocking structures between vertebrae. Some characters, such as the dorsal longitudinal crest and the accessory tubercles of the zygapophyses, are present also in the non-brachyrostran abelisaurid *Majungasaurus*. However, the transverse process is similar to that of caudal vertebrae of non-furileusaur brachyrostrans, such as *Ilokelesia*, *Ekrixinatosaurus*, and *Skorpiovenator*. A phylogenetic analysis here conducted clusters MAU-Pv-Co-598 with the latter three taxa. MAU-Pv-CO-598 comes from lower levels of the Bajo de la Carpa Formation than the furileusaur *Viavenator* and *Llukalkan*. The presence of a specimen with non-furileusaurian affinities in this formation indicates that a possible replacement from non-furileusaur to furileusaur brachyrostrans occurred during the Santonian, after the proposed Turonian faunal turnover.

**Key words.** Abelisauridae. Caudal vertebra. Upper Cretaceous. Patagonia. Cerro Overo-La Invernada fossil area.

**Resumen.** UNA VÉRTEBRA CAUDAL NO FURILEUSAURIANA DE LA FORMACIÓN BAJO DE LA CARPA (CRETÁCICO SUPERIOR, SANTONIANO) Y VARIACIÓN MORFOLÓGICA EN LA COLA DE LOS ABELISAURIDAE. El área Cerro Overo-La Invernada (Patagonia norte) ha provisto un rico registro de tetrápodos continentales cretácicos en las últimas dos décadas, principalmente de la Formación Bajo de la Carpa (Cretácico Superior, Santoniano). La fauna de dinosaurios de esta área es diversa, incluyendo nuevos taxones, siendo los terópodos abelisáuridos particularmente abundantes. Recientemente, una vértebra caudal aislada (MAU-Pv-CO-598) fue recuperada aquí. Aunque fragmentaria, muestra características que la diferencian de otros restos de abelisáuridos previamente hallados en esta área. Es considerada una vértebra caudal media y está caracterizada por un surco longitudinal ventral en el centro; un proceso transversal escasamente elevado con un extremo distal anteroposteriormente expandido y lateralmente cóncavo; una cresta longitudinal anteriormente extendida desde el borde anterior de la espina neural; y tubérculos pequeños extendidos desde los extremos de las zigapófisis, considerados como estructuras accesorias entrelazadas entre las vértebras. Algunos caracteres, como la cresta dorsal longitudinal y los tubérculos accesorios de las zigapófisis, están presentes en el abelisáurido no braquirostro *Majungasaurus*. Sin embargo, el proceso transversal es similar al de las vértebras caudales de braquirostros no furileusaurios, como *Ilokelesia*, *Ekrixinatosaurus* y *Skorpiovenator*. Un análisis filogenético agrupa a MAU-Pv-CO-598 con los últimos tres taxones. MAU-Pv-CO-598 proviene de niveles más bajos de la Formación Bajo de la Carpa que los furileusaurios *Viavenator* y *Llukalkan*. La presencia de un espécimen con afinidades no furileusaurianas en esta formación indica un posible reemplazo de braquirostros no furileusaurios ocurrido durante el Santoniano, luego del propuesto recambio faunístico del Turoniano.

**Palabras clave.** Abelisauridae. Vértebra caudal. Cretácico Superior. Patagonia. Área fosilífera Cerro Overo-La Invernada.

THE PATAGONIAN record of abelisauroid theropods from the Upper Cretaceous is so far the most abundant and diverse within the regions that comprised the ancient continent of Gondwana (e.g., Bonaparte & Powell, 1980; Bonaparte, 1991a; Baiano *et al.*, 2020). In particular, the stratigraphic record of abelisaurids encompasses all Patagonian Upper Cretaceous basins in which continental rocks are preserved (e.g., Neuquén Basin, Somuncura-Cañadón Asfalto Basin, Golfo San Jorge Basin, and Austral Basin). The knowledge of this family of theropods concerning their anatomy, evolutionary history, and phylogenetic relationships has increased notably in recent decades, with the Patagonian records providing the most novel information due to the abundance and diversity of the group to date (e.g., Bonaparte, 1985; Bonaparte & Novas, 1985; Bonaparte *et al.*, 1990; Coria & Salgado, 1998; Coria *et al.*, 2002; Calvo *et al.*, 2004; Canale *et al.*, 2009; Novas *et al.*, 2013; Gianechini *et al.*, 2015,

2021; Filippi *et al.*, 2016, 2018b; Méndez *et al.*, 2018, 2022; Cerroni & Paulina-Carabajal, 2019; Cerroni *et al.*, 2020; Aranciaga-Rolando *et al.*, 2021; Baiano *et al.*, 2021, 2022).

In the north of Argentine Patagonia, the locality of Cerro Overo is contiguous with the locality of La Invernada (Fig. 1.1). The separation between these adjacent zones is actually artificial because they are geographically and stratigraphically continuous. In this way, they correspond together to a unique fossiliferous area, which has proved to be a site of a great abundance of continental tetrapod fossils (Coria *et al.*, 2013; Filippi *et al.*, 2018a; Cruzado-Caballero *et al.*, 2019, 2022; Barrios & Filippi, 2021). The Bajo de la Carpa Formation (Upper Cretaceous, Santonian) is one of the Cretaceous lithostratigraphic units that outcrops in this area. Several abelisauroid remains have been recorded in other parts of the Neuquén Basin where this formation outcrops (Bonaparte, 1991b; Ezcurra & Méndez, 2009; Brissón Egli *et al.*, 2016).

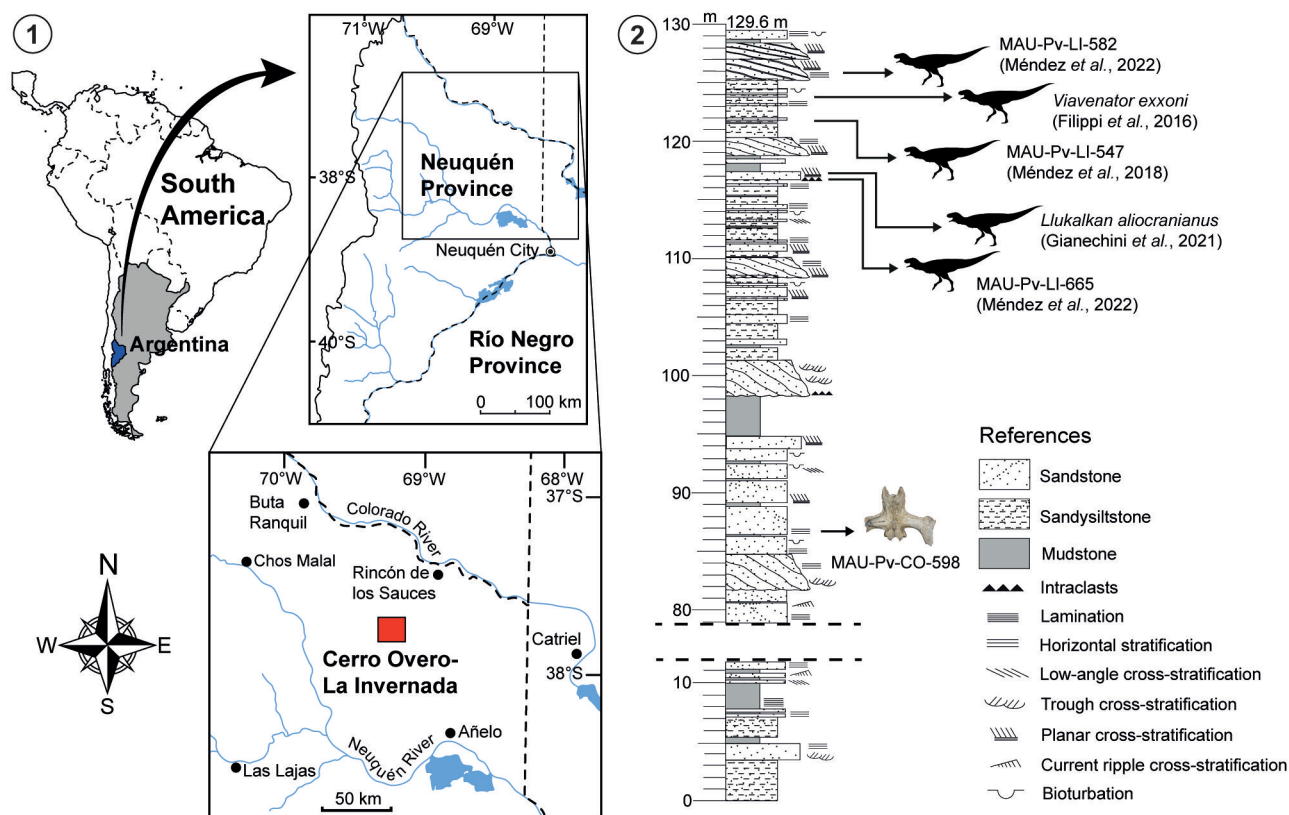


Figure 1. 1, Geographic location of the Cerro Overo-La Invernada fossil area where MAU-Pv-CO-598 was recovered; 2, stratigraphic column of the Bajo de la Carpa Formation showing the levels from which MAU-Pv-CO-598 and other abelisaurids have been recovered in Cerro Overo-La Invernada area. A section of the inferior half of the column was removed for better accommodation. Abelisaurid silhouettes by Jack Mayer Wood, under Creative Commons license (<https://creativecommons.org/licenses/by-sa/3.0/>).

Specifically, at the La Invernada locality, abelosaurids are strikingly abundant (Fig. 1.2, specimens with the acronym MAU-Pv-LI). To date, two species have been recognized, *Viavenator exxoni* (Filippi *et al.*, 2016) and *Llukalkan aliocranianus* (Gianechini *et al.*, 2021), as well as isolated brachyrostran and furileusaurian remains (Méndez *et al.*, 2018, 2022). Here we present new brachyrostran abelosaurid remains from the Bajo de la Carpa Formation at Cerro Overo, which, together with the previous records, support this group of theropods as the dominant predator component in this part of Patagonia during the Santonian.

**Institutional abbreviations.** **FMNH PR**, Field Museum of Natural History, Paleo Reptile, Chicago, Illinois, USA; **MACN-CH**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Chubut, Ciudad Autónoma de Buenos Aires, Argentina; **MACN-PV-RN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Paleontología de Vertebrados, Colección Río Negro, Ciudad Autónoma de Buenos Aires, Argentina; **MAU-Pv-LI**, Museo Municipal “Argentino Urquiza”, Paleontología de Vertebrados, Colección La Invernada, Rincón de los Sauces, Neuquén Province, Argentina; **MAU-Pv-CO**, Museo Municipal “Argentino Urquiza”, Paleontología de Vertebrados, Colección Cerro Overo, Rincón de los Sauces, Neuquén Province, Argentina; **MCF-PVPH**, Museo “Carmen Funes”, Paleontología de Vertebrados Plaza Huinul, Plaza Huinul, Neuquén Province, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Paleontología de Vertebrados, Neuquén, Neuquén Province, Argentina; **UNPSJB-PV**, Universidad Nacional de la Patagonia “San Juan Bosco”, Paleontología de Vertebrados, Comodoro Rivadavia, Chubut Province, Argentina.

**Anatomical abbreviations.** **ACH**, height of the anterior articular surface of the centrum; **ACW**, width of the anterior articular surface of the centrum; **as**, articular surface of the zygapophysis; **ce**, centrum; **CL**, maximum length of the centrum; **CL/PCH**, ratio between the length of the centrum and the height of the posterior articular surface of the centrum; **dc**, dorsal crest anterior to the neural spine; **latl**, lateral lamina; **ls**, lateral scar; **nc**, neural canal; **ns**, neural spine; **PCH**, height of the posterior articular surface of the centrum; **PCW**, width of the posterior articular surface of the centrum; **pos**, postzygapophysis; **pre**, prezygapophysis; **tp**,

transverse process; **TPL**, length of the transverse process; **TPL/CL**, ratio between the length of the transverse process and the total length of the centrum; **tub**, accessory tubercle of the zygapophysis; **vs**, ventral sulcus.

## SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

CERATOSAURIA Marsh, 1884

ABELISAURIDAE Bonaparte & Novas, 1985

BRACHYROSTRA Canale *et al.*, 2009

BRACHYROSTRA indet.

Figure 2.1–2.6

**Material.** MAU-Pv-CO-598. Incomplete middle caudal vertebra.

**Geographic occurrence.** Cerro Overo, a locality 50 km southwest of Rincón de los Sauces city, Neuquén Province, Patagonia, Argentina.

**Stratigraphic occurrence.** Bajo de la Carpa Formation (Upper Cretaceous, Santonian), Río Colorado Subgroup, Neuquén Group of the Neuquén Basin.

**Description.** The caudal vertebra (MAU-Pv-CO-598) reported here is well preserved and is nearly complete, only lacking the distal end of the left transverse process, and showing partial damage on the ventral margin of both articular surfaces of the centrum (Fig. 2). The centrum is anteroposteriorly elongate, with amphiplatyan articular surfaces that are slightly oval in outline (Tab. 1). The lateral and ventral surfaces are anteroposteriorly concave and pneumatic characters (*i.e.*, foramina or fossae) are not present. The dorsal margin of the posterior articular surface has a notch, as in preserved anterior, middle, and posterior caudals of *Viavenator*, which corresponds to the neural canal, whereas the anterior surface also has a dorsal notch although less marked. The ventral surface of the centrum has a longitudinal shallow groove.

The neural arch presents a set of very particular characteristics. The transverse process exhibits an elevation of approximately 10° with respect to the horizontal plane. The process is projected posterolaterally in dorsal view and has

an expanded distal end with anteriorly and posteriorly directed projections. The posterior projection is more developed, although the anterior one is incomplete. The distal margin of the transverse process is concave in dorsal and ventral view. The neural spine is low, transversely narrow, vertically directed, and located over the posterior half of the neural arch. The dorsal margin of the neural spine is convex

with the posterior end located higher than the anterior one. Longitudinal thickenings are present on the lateral surface of the distal end of the neural spine, likely corresponding to attachment scars of interspinous ligaments (Fig. 3.1). A dorsal crest develops in front of the neural spine, almost reaching the anterior end of the neural arch (Figs. 2.3–2.4, 3.1–3.2). A marked lamina extends anteroposteriorly from

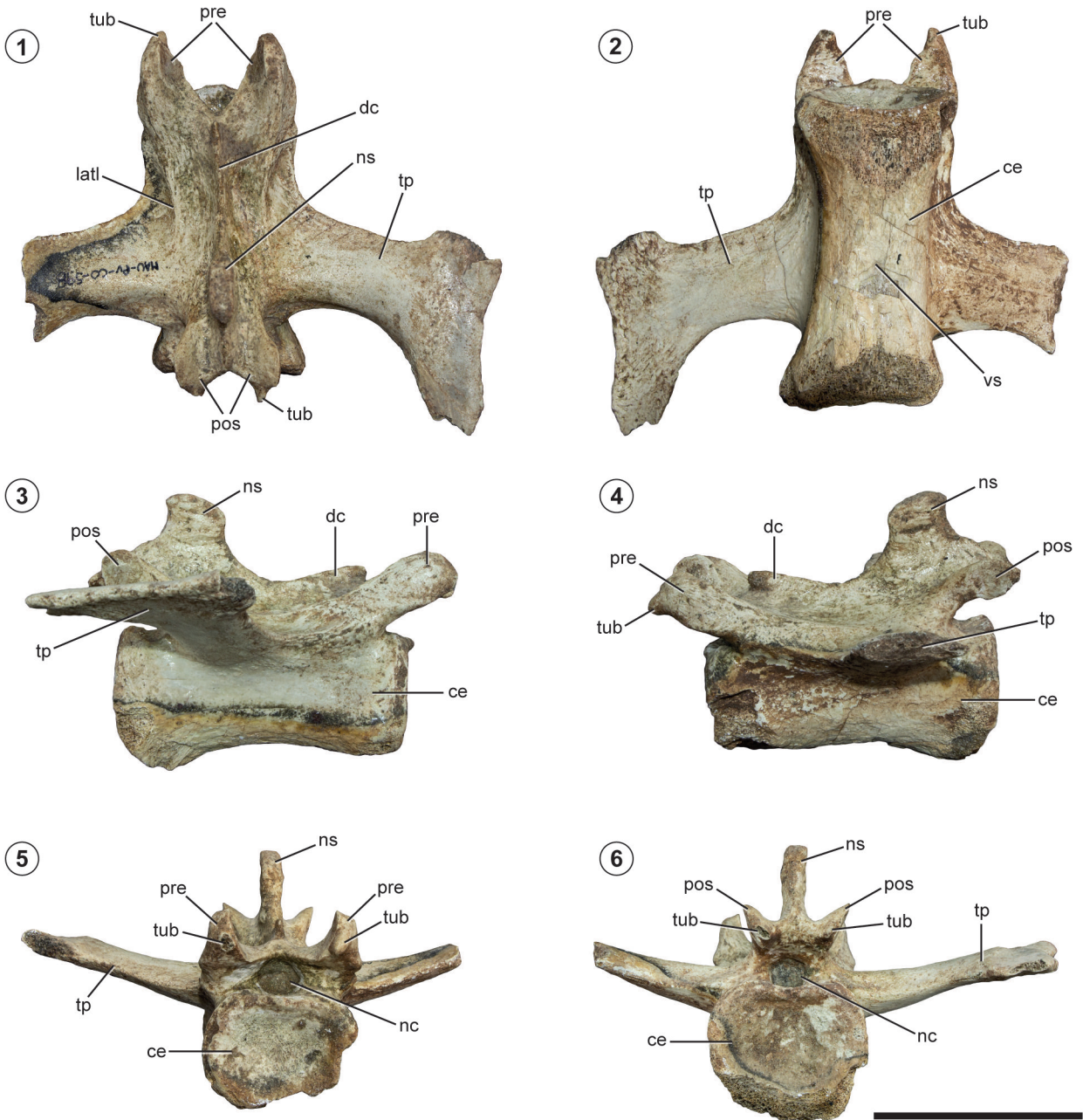


Figure 2. MAU-Pv-CO-598. 1, dorsal view; 2, ventral view; 3, right lateral view; 4, left lateral view; 5, anterior view; 6, posterior view. Scale bar= 5 cm.

the dorsal border of the prezygapophyseal process until it disappears over the middle part of the base of the transverse process (Fig. 3.2). The articular surface of the prezygapophysis has an oval contour anterodorsally-posterodorsally inclined. In anterior view, this surface is slightly concave and is mainly laterally and slightly dorsally faced. The prezygapophyseal process extends beyond the anterior border of the vertebral centrum. A striking feature is the presence of a small tubercle located anterior to the articular surface of the prezygapophysis (Fig. 3.3). This tubercle has a rough conical form with the tip directed anterodorsally. The dorsal border of this structure is continuous with the dorsal border of the prezygapophyseal process, although its ventral border is separated from the ventral bor-

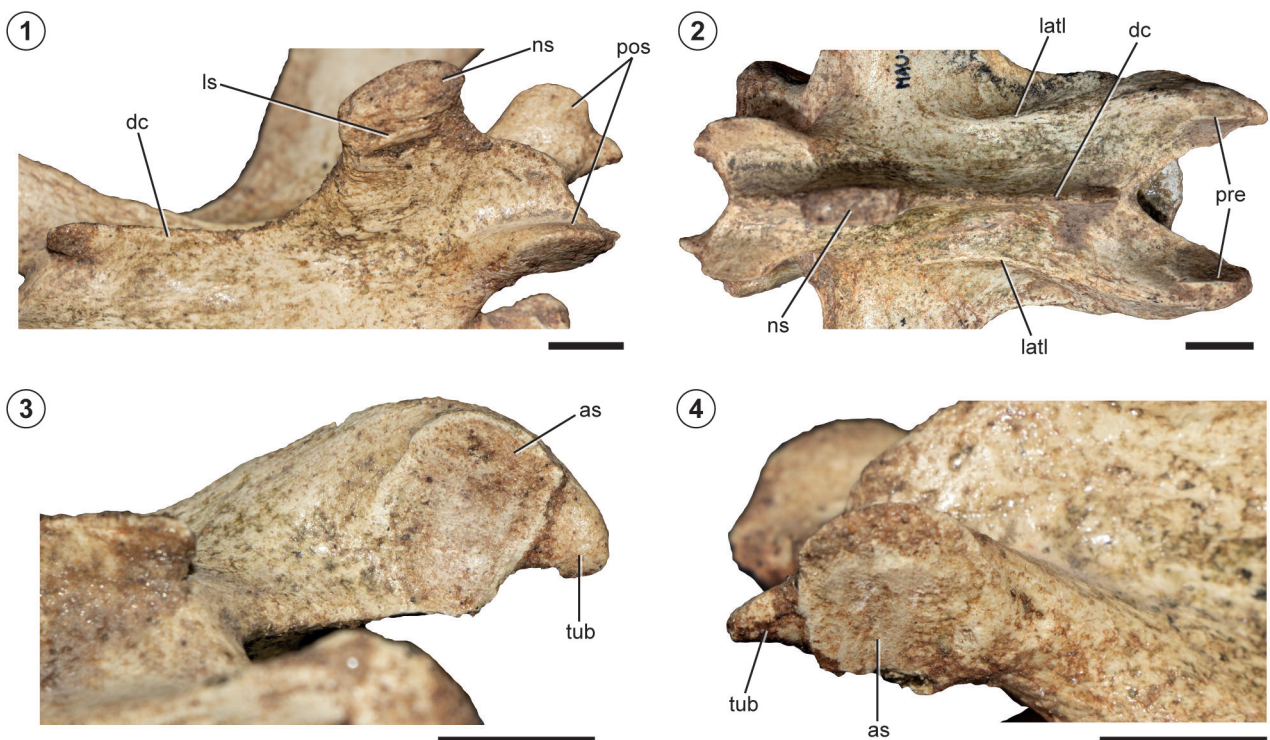
der of the prezygapophyseal process by a notch. The articular surface of the postzygapophysis is subcircular in outline, almost vertical, and located just above the posterior end of the centrum. Immediately posterior to the articular facet of the postzygapophysis, a small, conical tubercle projects posteriorly (Fig. 3.4). The dorsal and ventral borders of this tubercle are separated from the respective borders of the postzygapophyseal process by a notch.

**PHYLOGENETIC ANALYSIS**

A phylogenetic analysis was conducted to evaluate the position of this specimen within Abelisauridae. The character matrix of Gianechini *et al.* (2021) was used for context, which in turn is a modified version of previous datasets

**TABLE 1 – Measurements of MAU-Pv-CO-598 (in mm)**

CL	ACW	ACH	PCW	PCH	TPL	TPL/CL	CL/PCH
70	32	29	34	33	60	0.86	2.12



**Figure 3.** Anatomical details of MAU-Pv-CO-598. 1, middle and posterior parts of the neural arch in left dorsolateral view; 2, neural arch in dorsal view; 3, left prezygapophysis in medial view; 4, right postzygapophysis in lateral view. Scale bars= 1 cm.

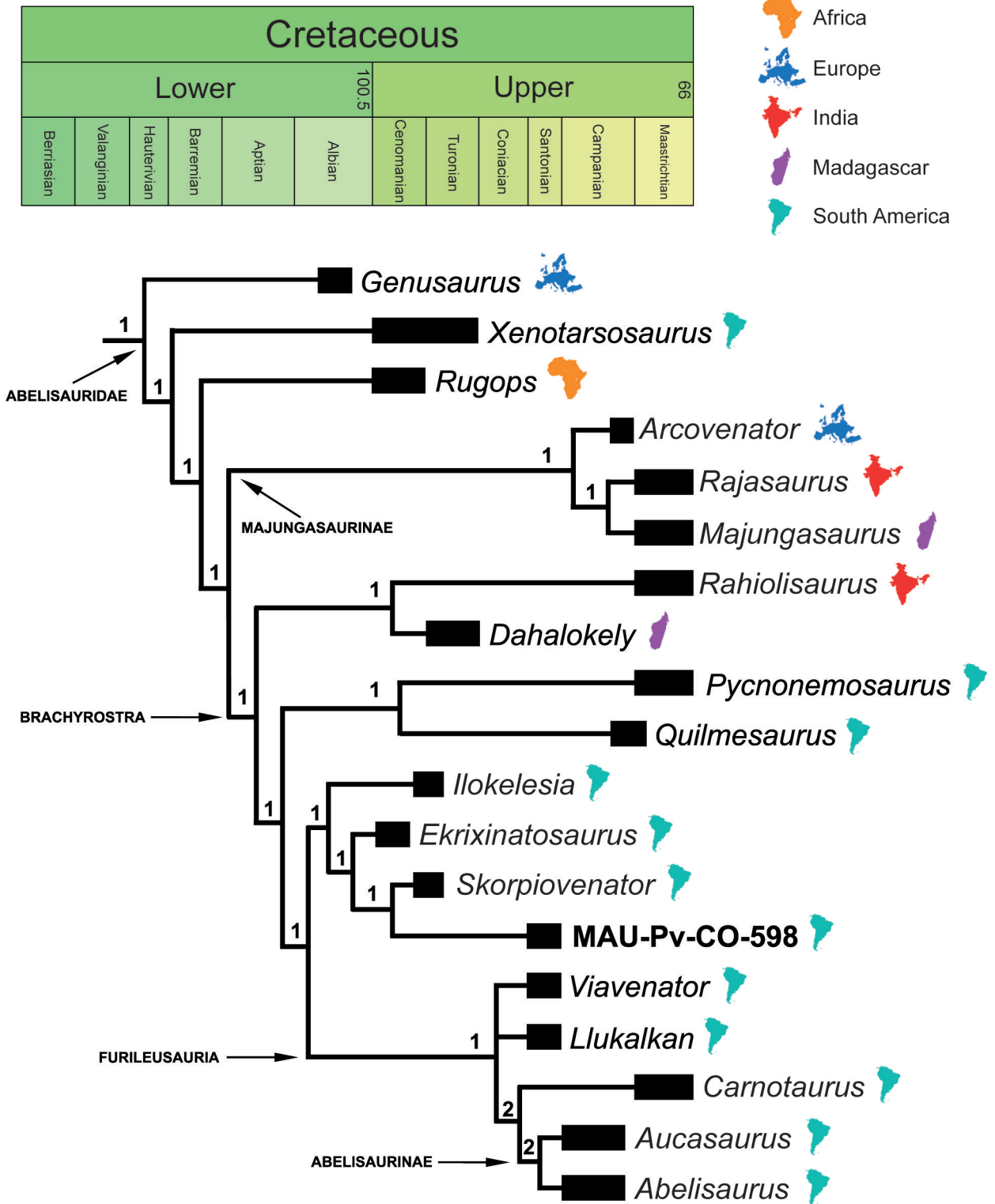


Figure 4. Time-calibrated simplified strict consensus tree of abelisaurid theropods, showing the phylogenetic relationships of MAU-Pv-CO-598. The numbers in the nodes correspond to the values of the Bremer support.

(Tortosa *et al.*, 2014; Filippi *et al.*, 2016). However, new changes were made, including the exclusion of character 274 and the addition of five new characters focused on the morphology of caudal vertebrae. Character 274 was excluded due to its ambiguous definition, which can lead to misinterpretations and consequently to wrong codifications. Additionally, original characters 270, 286, 289, 290, and 291 were modified in their states with the consequent changes in codifications in the different taxa, whereas the codifications of the remaining characters for caudal vertebrae were revised. The detailed modifications to the characters list and codifications are indicated in Supplementary Online Information I. Thus, the resulting matrix has a total of 422 characters and 35 operational taxonomic units (Supplementary Online Information II). All binary characters were equally weighted, with some multistate characters (Supplementary Online Information I) treated as additive. Several operational taxonomic units (OTUs) were excluded *a priori* from the analysis due to being highly fragmentary or with questionable ceratosaurian affinities, such as the Porcieux specimen (Buffetaut *et al.*, 1988), the La Bouchard taxon (Allain & Pereda-Suberbiola, 2003), *Indosaurus* (Huene & Matley, 1933), *Kryptops* maxilla and postcranium (Serenó & Brusatte, 2008; Carrano *et al.*, 2012; Farke & Sertich, 2013; Novas *et al.*, 2013), *Tarascosaurus* (Le Loeuff & Buffetaut, 1991), MCF-PVPH-237 (Coria *et al.*, 2006), *Camarillasaurus* (Sánchez-Hernández & Benton, 2014; Samathi *et al.*, 2021), and *Laevisuchus* (Rauhut & Carrano, 2016).

The analysis was performed with TNT v1.5 (Goloboff & Catalano, 2016) using the tree bisection and reconnection algorithm with 1000 replications and saving 10 trees per replication. The analysis resulted in six most parsimonious trees with the best score of 893 steps (CI=0.596; RI=0.724). The strict consensus shows well-resolved abelisauroid relationships (Fig. 4), although there is variation in the positions of some OTUs with respect to previous results (e.g., Filippi *et al.*, 2016; Gianechini *et al.*, 2021). Concerning Abelisauridae, three taxa branch early consecutively (*i.e.*, *Genusaurus*, *Xenotarsosaurus*, and *Rugops*). *Rugops* is the sister taxon of a clade that clusters Majungasaurinae and Brachyrostra. Within Brachyrostra, *Rahiolisaurus* and *Dahalokely* branch early, whereas *Quilmesaurus* and *Pycnonemosaurus* cluster together outside of Furileusauria

in a sister-group relationship of the clade including the Patagonian brachyrostrans. MAU-Pv-CO-598 nests deep inside the clade including *Ilokelesia*, *Ekrixinatosaurus*, and *Skorpiovenator*, and is positioned as a sister to the latter taxon.

The Bremer support (Bremer, 1988, 1994) was calculated for the different branches in TNT, retaining trees sub-optimal by ten steps and using absolute supports. The values obtained are generally low (Bremer support=1) regarding most of the branches composing Abelisauridae, demonstrating scarce support for the proposed relationships. Only two clades present a Bremer support of 2, *i.e.*, the clade comprising *Carnotaurus* plus *Aucasaurus* and *Abelisaurus*, and the clade comprising *Aucasaurus* and *Abelisaurus* (Fig. 4).

## DISCUSSION

### Comparisons with other abelisauroids

The precise position of this vertebra within the caudal series is difficult to determine. This is mainly due to the absence of relatively complete and well-preserved caudal series in abelisauroids, except for *Majungasaurus*. Skeletons of *Aucasaurus*, *Skorpiovenator*, and the abelisauroid UNPSJB-PV-1003 (Lamanna *et al.*, 2012) include much of the anterior and middle caudal series but, in the last two cases, they are relatively poorly preserved, hindering detailed comparisons. If we take into account the ratio CL/PCH (see Tab. 1) this is approximately 2.1 in MAU-Pv-CO-598, a similar value to that observed in the caudal 27 of *Majungasaurus* (O'Connor, 2007). In contrast, the caudal 12 of *Aucasaurus*, which is the last of the series with a well-preserved transverse process, has a ratio of 1.48. On the other hand, if we consider only the development and length of the prezygapophyseal process, it would coincide with the caudal vertebra 11 of *Majungasaurus*. The prezygapophyses of caudal vertebra 12 and 13 of *Aucasaurus* are more elongate than in the preceding caudals (Baiano, 2021), although they are shorter than in MAU-Pv-CO-598. Finally, if we observe the ratio TPL/CL (see Tab. 1), in MAU-Pv-CO-598 this is 0.86, while in the caudal 12 of *Aucasaurus* it is 1.28, and in the caudal 11 and 13 of *Majungasaurus* is 0.91 and 0.77, respectively. Using measurements of the transverse process and the pre and postzygapophyseal processes as parameters, MAU-Pv-



CO-598 resembles the caudals 10 to 12 of *Majungasaurus*, although if we consider the measurements of *Aucasaurus*, it could correspond to a caudal vertebra between the 15th to 20th position. Based on the general morphology and the observed parameters, we consider this caudal vertebra to be part of the middle section of the tail, possibly close to the 15th position.

The transverse process of MAU-Pv-CO-598 has a set of features similar to that observed in the middle caudal vertebrae of the basal brachyrostrans *Ekrixinosaurus*, *Skorpiovenator*, and *Ilokelesia* (Coria & Salgado, 1998; Calvo *et al.*, 2004; Canale *et al.*, 2009). One of these features is the low or no elevation of the processes with respect to the horizontal plane. Instead, the mid-caudals of more derived brachyrostran abelisaurids (*i.e.*, furileusaurids), such as *Carnotaurus* (Bonaparte *et al.*, 1990), *Aucasaurus* (Coria *et al.*, 2002), and *Viavenator* (Filippi *et al.*, 2018b), have more elevated transverse processes (25° or more with respect the horizontal plane). A second shared trait with basal brachyrostrans is the expanded distal end of the processes. In MAU-Pv-CO-598, it is clear the presence of an anterior and a posterior projection, despite the anterior one being incomplete. It is difficult to estimate the total length of the anterior projection, although the similar morphology with the mentioned basal brachyrostrans suggests it had a

similar development to the posterior projection. The basal abelisaurid *Spectrovenator* also presents transverse processes of the anterior and middle caudals with an anteroposteriorly expanded distal end (Zaher *et al.*, 2020). In contrast, in the anterior and middle caudals of *Carnotaurus*, *Aucasaurus*, and *Viavenator*, the anterior projection is much more developed or only an anterior projection is observed (Fig. 5). This is observed also in *Pycnonemosaurus* (Delcourt, 2017) and *Kurupi* (Vidoli *et al.*, 2021), although in the former this morphology is present in isolated transverse processes of indeterminate position and in the latter it is present in an anterior caudal (the 7th). Moreover, MAU-Pv-CO-598 shares with the mid-caudals of *Ekrixinosaurus*, *Skorpiovenator*, and *Ilokelesia* the presence of a concave shape of the external margin of the transverse process, which is convex in furileusaurids.

A longitudinal sulcus on the ventral surface of the centrum is also observed in the caudal vertebrae of *Ilokelesia*, *Majungasaurus*, *Aucasaurus*, *Viavenator*, and an isolated caudal from Brazil (Delcourt & Langer, 2022). The presence of a longitudinal ridge extending anteriorly from the neural spine is also present in caudal vertebrae 7 through 10 of *Majungasaurus*. In other abelisaurids, such as *Ilokelesia*, *Ekrixinosaurus*, and *Aucasaurus*, there is a faint ridge in this zone, one that is less developed than in MAU-Pv-CO-598



Figure 5. Abelisaurid transverse processes of mid-caudal vertebrae in dorsal view; 1, MAU-Pv-CO-598; 2, *Ekrixinosaurus* (MUCPv-294); 3, *Ilokelesia* (MCF-PVPH-35; inverted image); 4, *Majungasaurus* (FMNH PR 2100); 5, *Viavenator* (MAU-Pv-LI-530); 6, *Aucasaurus* (MCF-PVPH-236); 7, *Carnotaurus* (MACN-CH 894); 8, MACN-PV-RN-1012. Elements not to scale.

and *Majungasaurus*. However, a prominent ridge is also observed in other theropods, such as *Allosaurus* (Madsen, 1976), carcharodontosaurids such as *Mapusaurus* and *Acrocantnosaurus* (Harris, 1998; Currie & Carpenter, 2000; Rauhut, 2003; Coria & Currie, 2006), spinosaurids such as *Riparovenator* and *Suchomimus* (Sereni *et al.*, 1998; Barker *et al.*, 2021; Samathi *et al.*, 2021), and even basal coelurosaurs such as *Sinosauroptryx* (Currie & Chen, 2001). Concerning the dorsolateral lamina extending posteriorly from the prezygapophyses, these are most similar to those in *Majungasaurus*. Also, in *Masiakasaurus*, these laminae appear to be present, although dimly defined (Carrano *et al.*, 2002).

### Movement-limiting accessory structures in the caudal vertebrae of abelisaurids

The presence of accessory tubercles extending beyond the articular facets of the zygapophyses is rare among abelisauroids. Tubercles projected from the anterior margin of the prezygapophyses are observed in mid-caudals of *Majungasaurus* (O'Connor, 2007), *Elaphrosaurus* (Rauhut & Carrano, 2016), and the noasaurid *Masiakasaurus* (Carrano *et al.*, 2002). However, in *Majungasaurus* such structures of the prezygapophyses are particularly elongated, especially in the more posterior mid-caudal and distal caudal vertebrae. In this taxon, the prezygapophyses extend beyond the articular facet as prolongations with the same dorsoventral height as the remaining parts of the prezygapophyses. In contrast, in MAU-Pv-CO-598 the projected tubercles are shorter, have a triangular form, and are separated from the anterior margin of the facets by a shallow notch. In *Elaphrosaurus*, a similar condition to that in *Majungasaurus* is present, whereas the mid-caudals of *Masiakasaurus* exhibit small projections from the anterior end of the articular facets, thereby resembling the morphology of MAU-Pv-CO-598. In the case of *Ilokelesia*, *Aucasaurus*, and *Ekrixinatosaurus*, no tubercles or projections are located anterior to the articular facet of the prezygapophysis, although the poor preservation of *Ekrixinatosaurus* precludes a detailed consideration of this trait. Also, the zygapophyses of the caudal vertebrae of *Skorpiovenator* are poorly preserved. Concerning projections on the postzygapophyses, similar structures are observed from the 13th caudal vertebra of

*Majungasaurus* (P. O'Connor, pers. comm.) and in the mid-caudals of *Masiakasaurus* (Carrano *et al.*, 2002), in both cases be considered as epiphyses (Carrano *et al.*, 2002; O'Connor, 2007). In other abelisaurids, such as *Arcovenator*, *Viavenator*, *Aucasaurus*, and *Carnotaurus*, the zygapophyses of the caudal vertebrae do not present any accessory structure extended beyond the articular facets, although these facets are difficult to differentiate because of poor preservation in some taxa (*e.g.*, *Viavenator*).

The tubercles projected from the zygapophyses possibly correspond to accessory elements that may have restricted movement between vertebrae. Diverse types of accessory structures are common in caudal vertebrae of abelisaurids, although they are also observed along the entire vertebral column of these theropods, a feature that led to an increase in structural rigidity of the axial skeleton (Coria *et al.*, 2002; O'Connor, 2007; Méndez, 2014a, 2014b; Filippi *et al.*, 2016). However, although movement restriction is typical of abelisaurid caudal vertebrae, the type of structure involved in this trait and the degree of increase in intervertebral joints are variable between taxa. For example, non-brachyrostran taxa such as *Majungasaurus* only present tubercles projected from the zygapophyses as possible additional structures. Other taxa, such as the basal brachyrostrans *Ekrixinatosaurus* and *Skorpiovenator* have accessory hyposphene-hypantrum articulations. In the case of *Skorpiovenator*, whose tail was found articulated, the distal expansions of the transverse processes of the caudal vertebrae are in contact with each other, *i.e.*, the anterior expansion of one vertebra contacts the posterior one of the anteriorly located vertebra (Canale *et al.*, 2009; A. Méndez, pers. obs.). Thus, this type of contact possibly represented an accessory articulation between caudal vertebrae. Also, a similar articulation seems to be present in *Tralkasaurus* (Cerroni *et al.*, 2020), although in this taxon the preservation is poor and the overlap of the processes could have been exaggerated by a taphonomic artifact. Moreover, it is possible that in *Ekrixinatosaurus* and other abelisaurids with distal anterior and posterior projections of the caudal transverse processes this type of accessory articulation has existed. More derived abelisaurids, such as *Furileusaurus*, have caudal vertebrae with hyposphene-hypantrum joints and also interlocking distal expansions of transverse

processes, as in *Carnotaurus*, *Aucasaurus*, and *Viavenator* (Bonaparte *et al.*, 1990; Coria *et al.*, 2002; Filippi *et al.*, 2016, 2018b; Baiano, 2021). However, in these taxa, the anterior projection of the transverse processes is more developed and it may have contacted the central part of the distal end of the transverse process of the preceding vertebra (Coria *et al.*, 2002). Therefore, and differently from more basal brachyrostrans, the anterior projection was not restricted only to contact with the tip of the posterior projection. This trait possibly increased the articulation surface between transverse processes with a consequent increase in movement limitation. MAU-Pv-CO-598 presents distal projections of the transverse processes and the protuberances on the zygapophyses as additional structures, which, strikingly, are not present in brachyrostran taxa, including furileusaurids. However, hyposphene-hypantrum articulations are present in the anterior caudals of *Carnotaurus*, *Aucasaurus*, *Viavenator*, and *Pycnonemosaurus* (Kellner & Campos, 2002; Delcourt, 2017), whereas mid caudals of *Viavenator* lack this type of articulation. Moreover, *Carnotaurus* does not preserve mid-caudals and *Aucasaurus* preserved a caudal series from the first vertebra to anterior mid-caudals (12th and 13th). Thus, more anterior vertebrae of the same caudal series of MAU-Pv-CO-598 could have had hyposphene-hypantrum articulations. The transverse processes of MAU-Pv-CO-598 are similar to those observed in *Skorpiovenator*, *Ekrixinatosaurus*, and *Ilokelesia*, and thus the new specimen possibly presented a similar accessory articulation with the remaining vertebrae than that of the mentioned taxa. The different modes of interlocking structures between caudals in abelisaurids may correspond to different types of movement restriction, although an evolutionary trend to increase the articular surface between transverse processes of caudal vertebrae is observed in abelisaurids, a state that reaches its maximum manifestation in furileusaurian abelisaurids.

### Phylogenetic and biostratigraphic implications

Results of the phylogenetic analysis show that MAU-Pv-CO-598 clusters with *Ilokelesia*, *Ekrixinatosaurus*, and *Skorpiovenator*. However, we are cautious in our interpretations, as this specimen is fragmentary and this factor may generate a bias in the result because the characters present

in the vertebra are not enough to accomplish a more comprehensive morphological comparison with other taxa. Some characters of MAU-Pv-CO-598 are shared with the non-brachyrostran taxon *Majungasaurus*, such as the presence of a dorsal ridge anterior to the neural spine and the tubercles projected beyond the articular facets of the pre and postzygapophyses. However, some of these characters are convergent, such as the dorsal ridge, because it is present in MAU-Pv-CO-598, *Rajasaurus*, *Majungasaurus*, *Ilokelesia*, *Ekrixinatosaurus*, and *Aucasaurus* among abelisaurids, and in *Allosaurus*, other tetanurans, and some coelurosaurs, as was noted above. Taking into account this and that MAU-Pv-CO-598 shares morphological features and provenance with brachyrostran abelisaurids, it is more likely that the affinities of the new specimen agree with the result of the phylogenetic analysis.

The presence of MAU-Pv-CO-598 in the same formation where *Viavenator* and *Llukalkan* were found (Bajo de la Carpa Formation) is interesting from a biostratigraphic and evolutionary point of view. MAU-Pv-CO-598 comes from lower levels of that geologic unit (Fig. 1.2) and has a different morphology than *Viavenator* (*Llukalkan* does not preserve caudal vertebrae). Despite the new specimen coming from the same geologic unit as *Llukalkan*, we consider that the stratigraphic span separating both of them is significantly broad so as not to refer MAU-Pv-CO-598 to *Llukalkan*. By contrast, MAU-Pv-CO-598 is more similar to caudal vertebrae of stratigraphically older non-furileusaur brachyrostrans, *i.e.*, *Ilokelesia*, *Ekrixinatosaurus*, and *Skorpiovenator* from the Candeleros and Huincul formations (Cenomanian, Cenomanian–Turonian, respectively). Mid-caudal vertebrae with minimally inclined transverse processes and with anteroposteriorly expanded and laterally concave distal ends may be considered a characteristic morphotype of the early Late Cretaceous brachyrostran abelisaurids. However, the discovery of MAU-Pv-CO-598 in the Bajo de la Carpa Formation provides evidence that this morphotype persisted after the proposed late Turonian extinction that affected some theropod groups, such as carcharodontosaurids (Lamanna *et al.*, 2001; Apesteguía, 2002; Coria & Salgado, 2005; Juárez Valieri *et al.*, 2011; Canale *et al.*, 2015; Meso *et al.*, 2021), during the Coniacian and at least until the Santonian. In the case of abelisaurids during the Santonian,

an evolutionary transition process appears to have occurred from basal brachyrostrans to more derived forms such as furileusurs. Although the new record presented here is fragmentary, the morphological difference with *Viavenator* (*i.e.*, another brachyrostran abelisaurid with preserved caudal vertebrae from the same formation) is significant. The relative stratigraphic positions of MAU-Pv-CO-598 and this taxon provides evidence of a rapid transition between morphotypes during the Santonian, with a likely co-existence at some point. This evolutionary process continued in post-Santonian times with the appearance of more derived forms, such as *Aucasaurus* and *Carnotaurus*, both of which are characterized by a high development in accessory interlocking structures in caudal vertebrae.

## CONCLUSION

An isolated abelisaurid caudal vertebra (MAU-Pv-CO-598) from the Bajo de la Carpa Formation at the Cerro Overo-La Invernada region is presented here. From the same area and formation were exhumed the remains of *Viavenator* and *Llukalkan*, although the new specimen derives from lower levels in the unit. Among the morphological features that characterize MAU-Pv-CO-598, highlight small tubercles projected beyond the articular surfaces of the pre and postzygapophyses and which likely correspond to accessory interlocking elements between vertebrae. To date, this type of structure has not been recorded in Patagonian abelisaurids. Despite this, the new specimen has affinities with stratigraphically older (Cenomanian and Turonian) non-furileusaur brachyrostran abelisaurids. The presence of this specimen in the Bajo de la Carpa Formation provides evidence for the turnover of abelisaurid forms from the late Turonian to the Santonian, when furileusurs become more abundant. This evolutionary transition may also be reflected by variation of accessory interlocking elements of the axial skeleton, for example in the caudal vertebral series, as transverse processes increased their contact surface and accessory structures in zygapophyses were not present (at least based on the available information to date) in more derived furileusurs. New and more complete materials from Bajo de la Carpa Formation will provide additional information to shed light on this proposed turnover of abelisaurid forms after the Turonian.

## ACKNOWLEDGMENTS

We thank the Municipality of Rincón de los Sauces, Neuquén, for the logistic support in the fieldwork. Thank you to Patrick O'Connor, who kindly shared photographs of *Majungasaurus*, for providing us with additional information about this taxon and for reading and making valuable comments on the draft manuscript. The revisions of Mattia Baiano and Rafael Delcourt have increased the quality of the final manuscript. Financial support was provided by CONICET (PIP 11220200101108CO01) to AHM.

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doi: 10.5710/PEAPA.15.10.2022.438



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Recibido: 18 de julio 2022

Aceptado: 15 de octubre 2022

Publicado: 16 de diciembre 2022