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FIRST OCCURRENCE OF THE GIANT SHARK *CARCHAROCLES MEGALODON* (AGASSIZ, 1843) (LAMNIFORMES; OTODONTIDAE) AT BUENOS AIRES PROVINCE, ARGENTINA

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ABSTRACT – *Carcharocles megalodon* is considered a macropredatory shark that inhabited the seas around the world from middle Miocene to late Pliocene. In Argentina, it has only been formally recorded at two localities. Here, we report the first record for this taxon in the Buenos Aires Province. This occurrence is based on an isolated tooth recovered on the beach at the Punta Médanos locality, which lacks clear stratigraphic context. Based on the regional geology, the specimen probably came from Pliocene beds. Its size indicates that it probably belongs to a juvenile individual.

Keywords: *Carcharocles megalodon*, macropredatory shark, fossil teeth, Mar de Ajó.

RESUMO – *Carcharocles megalodon* é considerado um tubarão macropredador que habitou os mares ao redor do mundo desde o Mesomioceno até o Neoplioceno. Na Argentina, a espécie só foi formalmente registrada em duas localidades. Aqui, relatamos o primeiro registro desse táxon na Província de Buenos Aires. Essa ocorrência é baseada em um dente isolado recuperado na praia da localidade de Punta Médanos, que carece de contexto estratigráfico claro. Com base na geologia da região, o espécime provavelmente veio de camadas do Plioceno. Seu tamanho indica que provavelmente pertence a um indivíduo jovem.

Palavras-chave: *Carcharocles megalodon*, tubarão macropredatório, dentes fósseis, Mar de Ajó.

INTRODUCTION

Carcharocles megalodon (Agassiz, 1843) is considered a macropredatory shark that inhabited warm marine waters all around the world from the middle Miocene to late Pliocene (Applegate & Espinosa-Arrubarrena, 1996; Gottfried *et al*., 1996; Purdy, 1996; Pimiento *et al*., 2010; 2013; 2016; Cappetta, 2012; Pimiento & Clemens, 2014; Boessenecker *et al*., 2019). Because of its gigantic size and morphological distinctiveness, *C. megalodon* is one of the best-known fossil sharks (Keyes, 1972). Based on available fossils, numerous authors estimate that the size of *C. megalodon* ranged between 15 to 18 m long (Gottfried *et al*., 1996; Pimiento & Balk, 2015; Shimada, 2019; Cooper *et al*., 2020). As is the case of most Neogene sharks, its fossil record is restricted to isolated teeth and vertebral centra (Gottfried *et al*., 1996; Reolid & Molina, 2015).

Several fossiliferous deposits around the world yield teeth of *Carcharocles megalodon* and, for this reason, it is currently considered that this species had a global geographical distribution (Uyeno *et al*., 1989; Purdy *et al*., 2001; Reolid & Molina, 2015; Pimiento *et al*., 2016). However, the published reports of *C. megalodon* in Argentina are scarce and restricted to the middle Miocene Paraná Formation near to Paraná city, Entre Ríos Province (Frenguelli, 1920; Cione, 1978; Cione *et al*., 2012) and from the mid-upper Miocene beds of Puerto Madryn Formation, Chubut Province, Patagonia (Cione *et al*., 2011). The goal of this study is to document the first record of *C. megalodon* from the Buenos Aires Province, discuss the stratigraphy of the area it was found in, and calculate the total length and body mass of the shark the tooth came from.

MATERIAL AND METHODS

For descriptive purposes, we follow the nomenclature of Applegate & Espinosa-Arrubarrena (1996) (modified from Applegate, 1965). The determination of the life stage of the individual was made following the analysis of Pimiento *et al*. (2010).

The measurements (Figure 1D) were taken with a digital caliper with 0.01 mm precision. Crown height (**CH**), crown width (**CW**) and tooth height (**TH**) were taken following the criteria of previous authors (Hubbell, 1996; Shimada, 2002; Reolid & Molina, 2015; Viciano *et al*., 2018). For the determination of the position of the tooth within the jaw, we used the reconstructed dental series of Shimada (2002) and Pimiento *et al*. (2010). To estimate the total length of the individual, we applied the formula of Shimada (2002) and for body mass we followed Gottfried *et al*. (1996). Regarding the formula of Shimada (2002) (Table 1), the author has encouraged the use of upper anterior teeth to estimate the TL over other teeth when possible, but it does not mean that the estimations with non-upper teeth are wrong, they are not as accurate. Regrettably, in our case we only have one upper lateral tooth, and we did all the estimations based on this element.

Due to the limited taxonomical information of available specimens, the phylogenetic position of *Carcharocles megalodon* is disputed. Studies originally proposed that it was closely related to the great white shark (*Carcharodon carcharias*) and assigned it to the same genus within the family Lamnidae (Applegate & Espinosa-Arrubarrena, 1996; Gottfried *et al*., 1996; Purdy, 1996). However, more recent studies indicate that *C. megalodon* belongs to another lineage. A detailed study of its teeth indicates that it most probably belongs in the family Otodontidae, within the genus *Carcharocles* (Jordan & Hannibal, 1923; Casier, 1960; Gluckman, 1964; Cappetta, 1987; Ward & Bonavia, 2001; Nyberg *et al*., 2006; Ehret *et al*., 2009). Another hypothesis indicates that it should be placed among otodontids and considered as part of the genus *Otodus* (Shimada *et al*., 2017; Boessenecker *et al*., 2019; Cooper *et al*., 2020) or conforming its own subgenus as *Otodus* (*Megaselachus*) (Cappetta, 2012; Razak & Kocsis, 2018). Because of its distinctiveness and still debated phylogenetic position, we refer to it as *Carcharocles megalodon* following the proposal of Jordan & Hannibal (1923).

GEOLOGICAL SETTINGS

MMDA-101 was found on the beach at the Punta Médanos locality, close to the lighthouse (Figure 2; 36°52'46.39"S; 56°39'59.45"W), Buenos Aires Province, Argentina. The location, together with the presence of signs of marine abrasion and dark manganese stains observed on the crown surface, indicates that the specimen remained under water for some time, with some subaerial exposure on the beach.

The discovery of teeth belonging to *Carcharocles megalodon* in marine sediments around the world is common (Keyes, 1972). One of the most remarkable cases is a tooth found in 1875 during the journey of the HMS Challenger ship, while it was exploring deep waters near Tahiti (Murray & Renard, 1891). Two large teeth belonging to *C. megalodon* were recovered at 2,385 m depth. Furthermore, *C. megalodon* findings are not only common on the sea floor, but are also frequently found isolated and eroded on seashores after being transported by the sea from the fossil-bearing layers. In this

Table 1. Linear regressions applied for the possible anatomical positions (L1 to L4) of MMDA-101 taken from Shimada (2002) where **Y** is the total length of the body (**TL**) and **X** is crown height (**CH**). Average value of TL for all positions as well as the formula of Gottfried *et al*. (1996) for body mass.

Tooth position	Regression equation	TL (m)
L1	y1= 5.540 + 11.197x	5.8
L2	y2= 4.911 + 13.433x	5.48
L3	y3= 0.464 + 14.550x	5.89
L4	y4= 5.569 + 17.658x	7.2
Average value (meters)	$\frac{y1+y2+y3+y4}{4}$	6.09
Mass formula (kilograms)	$KG = 3.29\ x\ 10^{-06}\ x\ (TL^{3.174})$	2.279

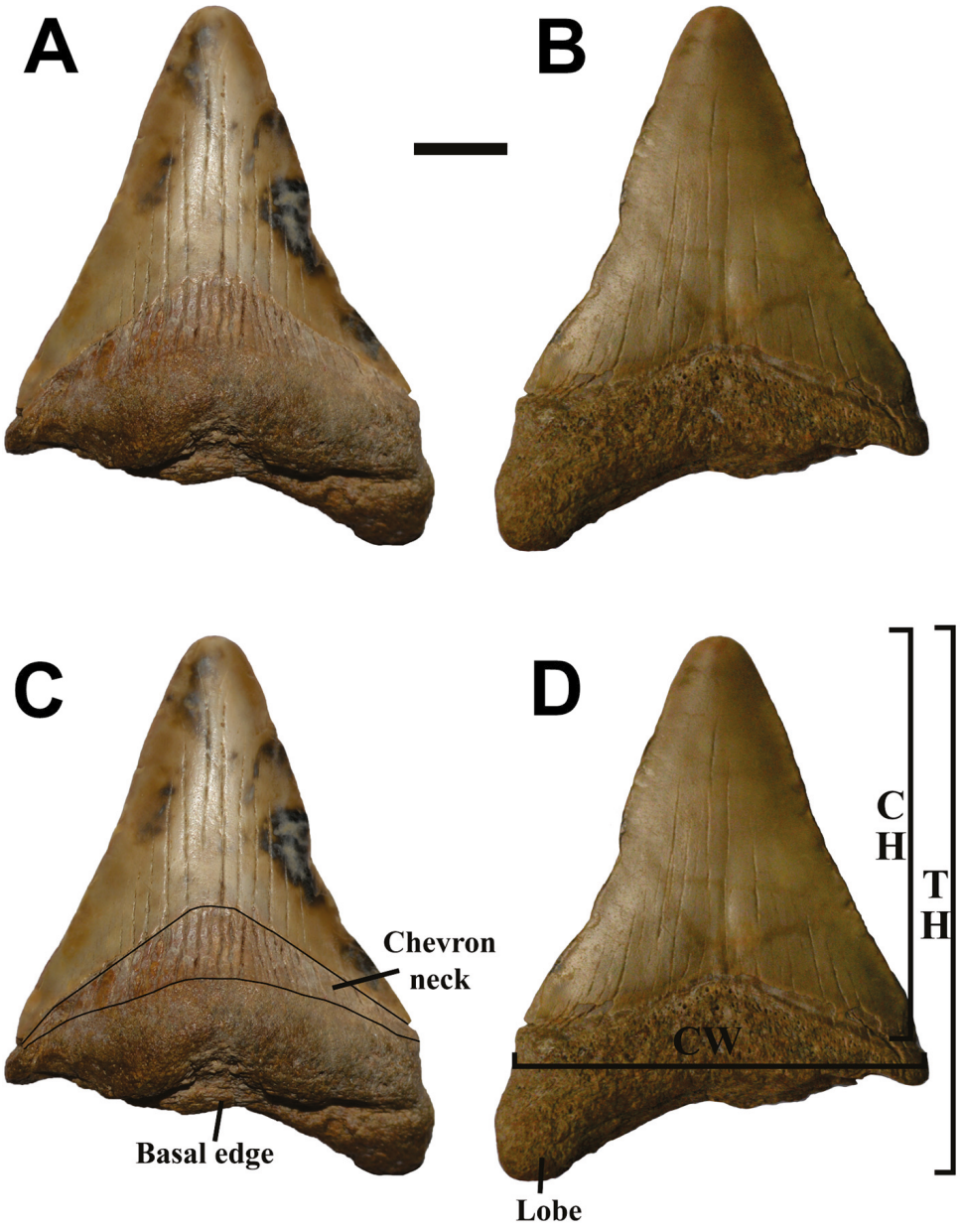

Figure 1. MMDA-101 in lingual (**A**, **C**) and labial (**B**, **D**) views. Crown height (**CH**), crown width (**CW**) and tooth height (**TH**) represent the measurements taken in the specimen. Scale bar = 1 cm.

case, we can mention the findings from Miocene–Pliocene beds from North America (Purdy *et al*., 2001; Maisch *et al*., 2020).

Fossil terrestrial megamammals (such as armored xenarthrans and giant sloths) are frequently found along the Bonaerian seashore, with most remains coming from Upper Pleistocene beds at the marine platform (Cione *et al*., 1999; Tonni & Cione, 1999). These specimens are found mixed on the same beaches with other marine vertebrates coming from more recent Holocene beds (*e.g*. Cione, 1983; Cione & Barla, 2008). However, the age of the specimens described here is uncertain because the geology of the marine platform is rather complex and includes a succession of diverse stratigraphic units. Parker *et al*. (2008) made an extensive sampling of the marine sediments along the Argentine coast. Near Punta Médanos, Parker *et al*. (2008) found five depositional sequences (**DS**): DS5 Upper Pliocene, DS4 Upper Pliocene–Lower Pleistocene, DS3-2 Pleistocene and DS1 Holocene. DS4 is the predominant marine layer exposed in the region when compared with the other sequences. Since *Carcharocles megalodon* lived from the middle Miocene through Pliocene (and some unconfirmed reports for Pleistocene sediments; Applegate & Espinosa-Arrubarrena, 1996; Gottfried *et al*., 1996; Purdy, 1996; Pimiento *et al*.,

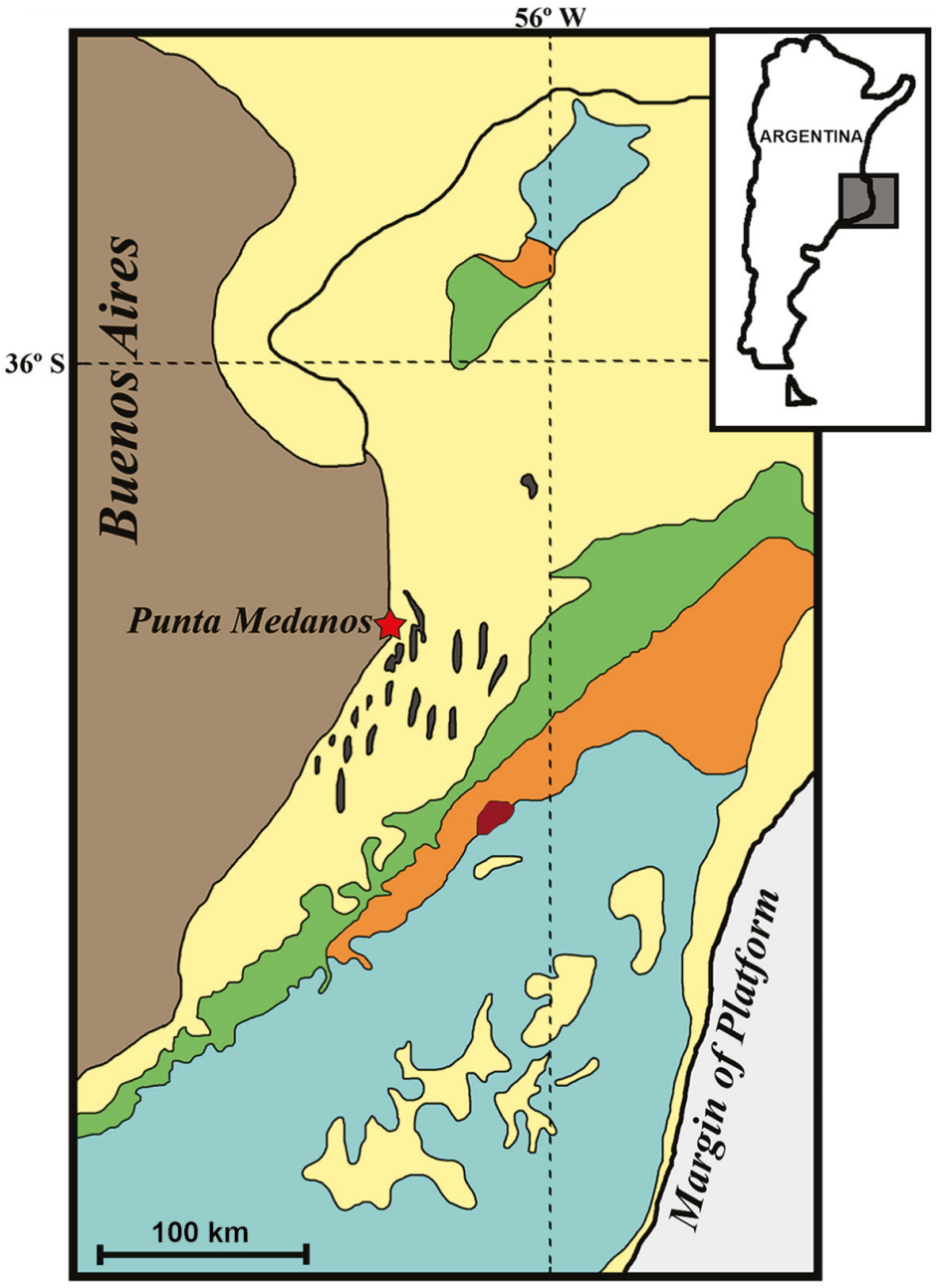

Figure 2. Geologic map based on and modified after those published by Parker *et al*. (2008). The different strata (depositional sequences or **DS**) discussed in the text are highlighted in different colors: **DS5** (purple; Upper Pliocene); **DS4** (light blue; Upper Pliocene–Lower Pleistocene); **DS3** (orange; Pleistocene); **DS2** (green; Pleistocene); Buenos Aires Formation (dark grey; Pleistocene); and **DS1** (yellow; Holocene). Red star shows the fossiliferous locality. Brown color represents the Buenos Aires Province.

2010; 2013; Pimiento & Clements, 2014; Boessenecker *et al*., 2019), it is possible that the tooth here described comes from Pliocene beds, probably DS5 or DS4 of Parker *et al*. (2008) (light blue areas in Figure 2).

Possibly some of the above-mentioned stratigraphical units, such as DS5 or DS4, may be correlated to the sandy beds informally known as the "Puelchense" (see Parker *et al*., 2008). The "Puelchense" beds are partially correlated with Miocene–Pliocene beds close to Paraná city based on its fossil record (see discussion in Cione *et al*., 2005; Cione & Barla, 2008) and belong to a subterranean aquifer that extends along a large portion of the subsoil of Buenos Aires Province, up to the Mar de Ajó locality (see also Auge *et al*., 2002). The "Puelchense" beds yielded several fossils studied by Carlos Rusconi in the 1930s during the extraction of sand destined for construction (Rusconi, 1933; 1934; Cione & Barla, 1999; Chimento, 2012). However, since the fossils were extracted with a suction tube, the specimens described

by Rusconi lacked any stratigraphical control. Interestingly, among "Puelchense" fossils, Rusconi described and illustrated several extinct sharks, such as *Carcharias acutissima*, *Carcharodon hastalis* and *Carcharhinus* spp. (Rusconi, 1948; 1949; Cione *et al*., 2005). On this basis, it is possible that the *Carcharocles megalodon* tooth described here may belong to any of the above-mentioned Miocene–Pliocene beds.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
LAMNIFORMES Berg, 1858
OTODONTIDAE Gluckman, 1964

Carcharocles Jordan & Hannibal, 1923

Carcharocles megalodon Agassiz, 1843
(Figure 1)

Referred material. MMDA-101 (Museo de Mar de Ajó, Mar de Ajó city, Buenos Aires Province, Argentina), upper lateral tooth with partially preserved root.

Description. The specimen is relatively well preserved and only lacks one of the lobes of the root (Figure 1). All the surfaces show good preservation except for the tip of the crown and some of the serrations of the mesial and distal cutting edges, which exhibit signs of marine abrasion. The tooth is relatively small when compared with other materials of *Carcharocles megalodon*. Regarding the position of this tooth in the jaw, this material differs from those of the lower jaw due to the presence of a relatively wider crown and shallower basal concavity (Pimiento *et al*., 2010; Viciano *et al*., 2018). Within the upper jaw, anterior teeth show a notably deep basal concavity, and the posterior teeth show strongly asymmetrical crown and roots (Pimiento *et al*., 2010; Viciano *et al*., 2018). Therefore, based on crown and root shape and proportions, MMDA-101 can be determined as being an upper lateral tooth (between L1–L4 positions).

The tooth crown is subtriangular in shape, nearly symmetrical in contour, with a nearly flat labial surface and a notably convex lingual one. It shows serrated mesial and distal cutting edges. In lingual view (Figures 1A, C), the crown is apicobasally tall with a CH of 40.5 mm, and CW of 44.5 mm and shows a TH of 56.1 mm. It shows apicobasally oriented linear striations. At the base of the crown, a typical chevron-shaped band is present. This band is medially thick and becomes narrower towards the mesial and distal edges of the crown. It shows numerous linear striations and is also basoapically oriented. The root is apicobasally convex and shows a rugose surface. The lingual protuberance is gently convex and is devoid of a nutrient foramina and groove. The basal concavity that separates the root lobes is shallow. The only preserved root lobe is relatively small, and it is not strongly basally projected. The root shows a mesiodistally oriented groove that runs across the tooth, which may be the result of marine abrasion. In labial view (Figures 1B, D), the apicobasal crown striations are fewer and shallower than those of the lingual surface. The root shows a nearly flat, rugose surface that is covered by small pores as a result of marine abrasion.

DISCUSSION

As indicated above, in spite of marine abrasion, the specimen MMDA-101 is confidently identified as *Carcharocles megalodon* on the basis of the following combination of characters: relatively large crowns which are subtriangular in contour, with a convex lingual surface and a nearly flat labial surface, presence of a chevron-shaped band on the lingual surface separating the root from the crown, poorly developed lingual protuberance of roots, and well-differentiated root lobes separated by a shallow basal concavity (Gottfried *et al*., 1996; Pimiento *et al*., 2010; Cappetta, 2012; Cione *et al*., 2012; Medina-Gavilán *et al*., 2015; Boessenecker, 2016; Viciano *et al*., 2018). Furthermore, the CW and CH of MMDA-101 fall within the morphological cloud of *C. megalodon* carried out by Pimiento *et al*. (2010) (Figure 3A). Therefore, the identification of MMDA-101 as *C. megalodon* is supported by quantitative and qualitative information.

MMDA-101 is smaller than adult specimens of *Carcharocles megalodon*, but it is also much bigger than the great white shark (*C. carcharias*; Gottfried *et al*., 1996; Cione *et al*., 2012). Teeth of juvenile specimens of *C. megalodon* have been documented several times, and a paleo-nursery referred to this species has been recognized from the Gatun formation in Panama (Gottfried *et al*., 1996; Pimiento *et al*., 2010). Because of its relatively small size, we included the specimen MMDA-101 in the data matrix of the analysis by Pimiento *et al*. (2010) which compares the different life stages of the species. This analysis compares the CH *vs*. CW from adult and juvenile individuals of *C. megalodon*, showing that this species changes its tooth-measurements during its life. In this sense, the size range for juvenile specimens of *C. megalodon* falls within 4–10 m long.

Based on CH, we estimated the total length of the specimen MMDA-101 following the regression analyses proposed by Shimada (2002). As noted above, the specimen could have many positions within the jaw (L1–L4). For this reason, we calculated the regression for the four possible positions and their average (Figure 3C). The resulting length estimate for the specimen is approximately 6 m (Figure 3B), which falls within the range of sizes of juvenile specimens of *Carcharocles megalodon* proposed by Pimiento *et al*. (2010). Finally, we estimated the body mass following the formula proposed by Gottfried *et al*. (1996). The resulting weight is approximately 2,279 kilograms for MMDA-101, which also fits within the juvenile category of other specimens of equivalent length of *C. megalodon* (Viciano *et al*., 2018).

The fossil record of *Carcharocles megalodon* in Argentina is limited to a few adequately published findings restricted to

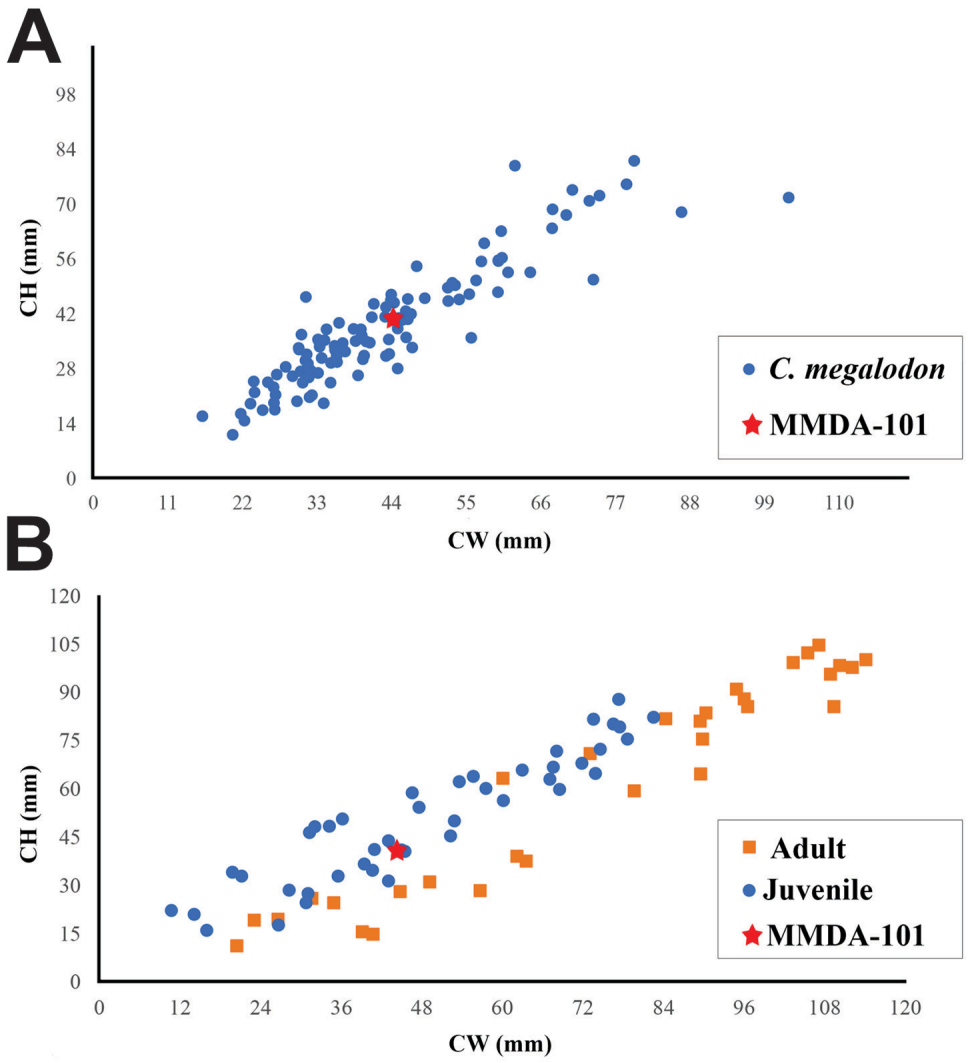

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Figure 3. Tooth comparisons in mm of *Carcharocles megalodon* and MMDA-101 using CW and CH measurements and data of previous work. **A**, scatter plot showing the anatomical data for *C. megalodon* (blue dots) published by Pimiento *et al.* (2010) and MMDA-101 (red star). **B**, scatter plot showing the anatomical data for juvenile (blue dots) and adult (orange squares) of *C. megalodon* published by Pimiento *et al.* (2010) and MMDA-101 (red star).

the Miocene of Entre Ríos Province and Patagonia (Arratia & Cione, 1996; Cione *et al.*, 2011; Pimiento *et al.*, 2016). MMDA-101 represents the first record of *C. megalodon* in the Buenos Aires Province and one of the few published findings of the species in Argentina. Furthermore, it constitutes a valuable data point that helps to fill the geographical gap of this poorly known species in the South Atlantic Ocean. It is worth noting that despite the few published records, the presence of *C. megalodon* in Argentina should not be considered as exceptional, since fossil teeth of the species are not rare in the collections of other paleontological institutions in the country. Although most of these records remain unpublished, most also lack an adequate stratigraphic control, and therefore are of limited value.

Despite the uncertain geochronology of this fossil, we believe that this specimen is of high importance to the paleontological heritage of the Buenos Aires Province and for the reconstruction of the biotic history of the entire area.

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