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Record of *Carcharocles megalodon* in the Eastern Guadalquivir Basin (Upper Miocene, South Spain)

Registro de Carcharocles megalodon *en el sector oriental de la Cuenca del Guadalquivir (Mioceno superior, Sur de España)*

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ABSTRACT

Tortonian diatomites of the San Felix Quarry (Porcuna), in the Eastern Guadalquivir Basin, have given isolated marine vertebrate remains that include a large shark tooth (123.96 mm from apex to the baseline of the root). The large size of the crown height (92.2 mm), the triangular shape, the broad serrated crown, the convex lingual face and flat labial face, and the robust, thick angled root determine that this specimen corresponds to *Carcharocles megalodon*. The symmetry with low slant shows it to be an upper anterior tooth. The total length estimated from the tooth crown height is calculated by means of different methods, and comparison is made with *Carcharodon carcharias*. The final inferred total length of around 11 m classifies this specimen in the upper size range of the known *C. megalodon* specimens.

The palaeogeography of the Guadalquivir Basin close to the North Betic Strait, which connected the Atlantic Ocean to the Mediterranean Sea, favoured the interaction of the cold nutrient-rich Atlantic waters with warmer Mediterranean waters. The presence of diatomites indicates potential upwelling currents in this context, as well as high productivity favouring the presence of large vertebrates such as mysticetid whales, pinnipeds and small sharks (*Isurus*). These large vertebrates recorded in the Eastern Guadalquivir Basin were potential prey of *C. megalodon*.

Keywords: *Carcharocles megalodon*; fossil tooth; Guadalquivir Basin; Tortonian.

RESUMEN

Las diatomitas tortonienses de la antigua Cantera de San Félix (Porcuna, Jaén), en el sector oriental de la Cuenca del Guadalquivir, han proporcionado restos aislados de vertebrados marinos entre los que destaca un gran diente de tiburón (123.96 mm desde el ápice hasta la línea basal de la raiz). La altura de la corona (92.2 mm), su forma triangular con bordes aserrados, la presencia de una cara lingual convexa y una labial plana, conjuntamente con la raíz angulosa y robusta, permiten determinar que este diente perteneció a un ejemplar de *Carcharocles megalodon*. La alta simetría de la pieza, su tamaño y su relación longitud/anchura de la corona permiten afrimar que se trata de un diente superior anterior. La longitud total estimada para este tiburón, es calculada a partir de diferentes métodos basados principalmente en la comparación con el tiburón blanco *Carcharodon carcharias*. La longitud total inferida finalmente para este ejemplar ronda los 11 m, lo que permite incluir este ejemplar dentro del rango de los ejemplares de *C. megalodon* de gran tamaño.

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La paleogeografía de la Cuenca del Guadalquivir próxima al Estrecho Nordbético que conectaba el Océano Atlántico con el Mar Mediterráneo, favoreció la interacción de aguas atlánticas frías y ricas en nutrientes con las aguas más cálidas del Mediterráneo. La presencia de diatomitas indica la actividad potencial de corrientes de *upwelling* en este contexto, así como la alta productividad que suele favorecer a grandes cetáceos y pinnípedos. Estos mamíferos marinos, registrados en el sector oriental d la Cuenca del Guadalquivir fueron potenciales presas de pequeños tiburones como *Isurus* el gran *C. megalodon*.

Palabras clave: *Carcharocles megalodon*; diente fósil; Cuenca del Guadalquivir; Tortoniense.

Introduction

The *Carcharocles megalodon* is the largest macropredatory shark to have ever lived. However, the fossil record of this predator is restricted to isolated teeth and vertebral centra due the cartilaginous skeleton of most of the sharks. The most complete specimen is an associated column of around 150 vertebral centra from the Miocene of the Antwerp Basin, Belgium (Leriche, 1926). The record of *C. megalodon* teeth ranges from 17 to 2 Ma (middle Miocene to Pleistocene) (Gottfried *et al*., 1996; Purdy, 1996; Pimiento *et al*., 2010).

Based on tooth size, *C. megalodon* reached a maximum inferred total length around 16 m (Randall, 1973; Gottfried *et al*., 1996), more than twice the reported maximum length of the white shark *Carcharodon carcharias* with 6.4 m (Bigelow & Schroeder, 1948; Randall, 1973; Compagno, 1984). The largest tooth of *C. megalodon* measures 168 mm (specimen PF 1168, Field Museum of Natural History of Chicago).

Data on *C. megalodon* from the Iberian Peninsula are relatively scarce, sometimes reported only as news in the daily press, without scientific revision. Descriptions of remains of *C. megalodon* from the Iberian Peninsula are those of Areitio (1877) and Meseguer Pardo (1924) from Messinian diatomites of the Lorca Basin (Southeastern Spain); Balbino (1995) from uppermost Miocene of the Alvalade Basin (Portugal); and García *et al*. (2009) from the Arenas Fm (Huelva, Spain) in the western Guadalquivir Basin.

In this work a complete tooth of *C. megalodon* from the Eastern Guadalquivir Basin (South Spain) is reported and examined in detail, including comparisons with other shark teeth of *C. megalodon* and *C. carcharias* described in the literature.

Geological setting

The Guadalquivir Basin is the foreland basin of the Betic Cordillera and it opens directly to the Atlantic to the WSW (Gulf of Cádiz). Autochthonous units to the north and allochthonous units to the south may be differentiated in this basin (Fig. 1A). The allochthonous units are composed by olistostrome deposits and olistoliths, located at the frontal part of the Subbetic nappes, which are mixed with Miocene clays and marls.

The shark tooth was collected in diatomaceous marl blocks obtained from the old quarry of San Félix, located 2 km south of Porcuna (coord. 37° 51′21.4″N; 4° 11′21.6″W) (Fig. 1B). The diatomaceous marls are white to yellowish, sometimes laminated, and they alternate locally with greyish marls without visible stratification. These deposits belong to the highest part of the Valenzuela Formation (Aquitanian-Torttonian in age, Tjalsma, 1971), whose stratotype was established in the San Félix Quarry. The marls contain abundant diatoms and subordinately sponge spicules, silicoflagellates and radiolarians. The sediments of the type section (San Felix Quarry area) have a planktic foraminiferal assemblage with *Globorotalia menardii*, *Globigerina globorotaloidea*, *Globigerina nepenthes* and *Globigerinoides obliquus*, among others (Tjalsma, 1971). This foraminiferal assemblage belong to the zone N16 of planktic foraminifera (Tortonian) equivalent with most of the middle part of the stratotype of the Tortonian. The main diatom assemblages consist mostly of planktic (*Thalassionema*, *Thalassiotrix*, *Thalassiosira*) and scarce benthic (*Delphineis*) forms typical of cold oceanic upwelling waters (Molina *et al*., 1987; López-García & Bustillo, 1994). The outcrops belong to the third and last episode of diatomitic sedimentation defined in this area by Bustillo & López-García (1997) of the *Thalassiosira yabei* Zone (Middle Tortonian).

In this area of the North Betic Strait, which connected the Atlantic Ocean to the palaeo-Mediterranean sea, high concentrations of diatomaceous deposits were produced because it was more oceanographically dynamic than the Atlantic. The Guadalquivir Basin was an Atlantic basin connecting with the palaeo-Mediterranean through small basins (e.g. Granada Basin and Guadix Basin) to the south by straits.

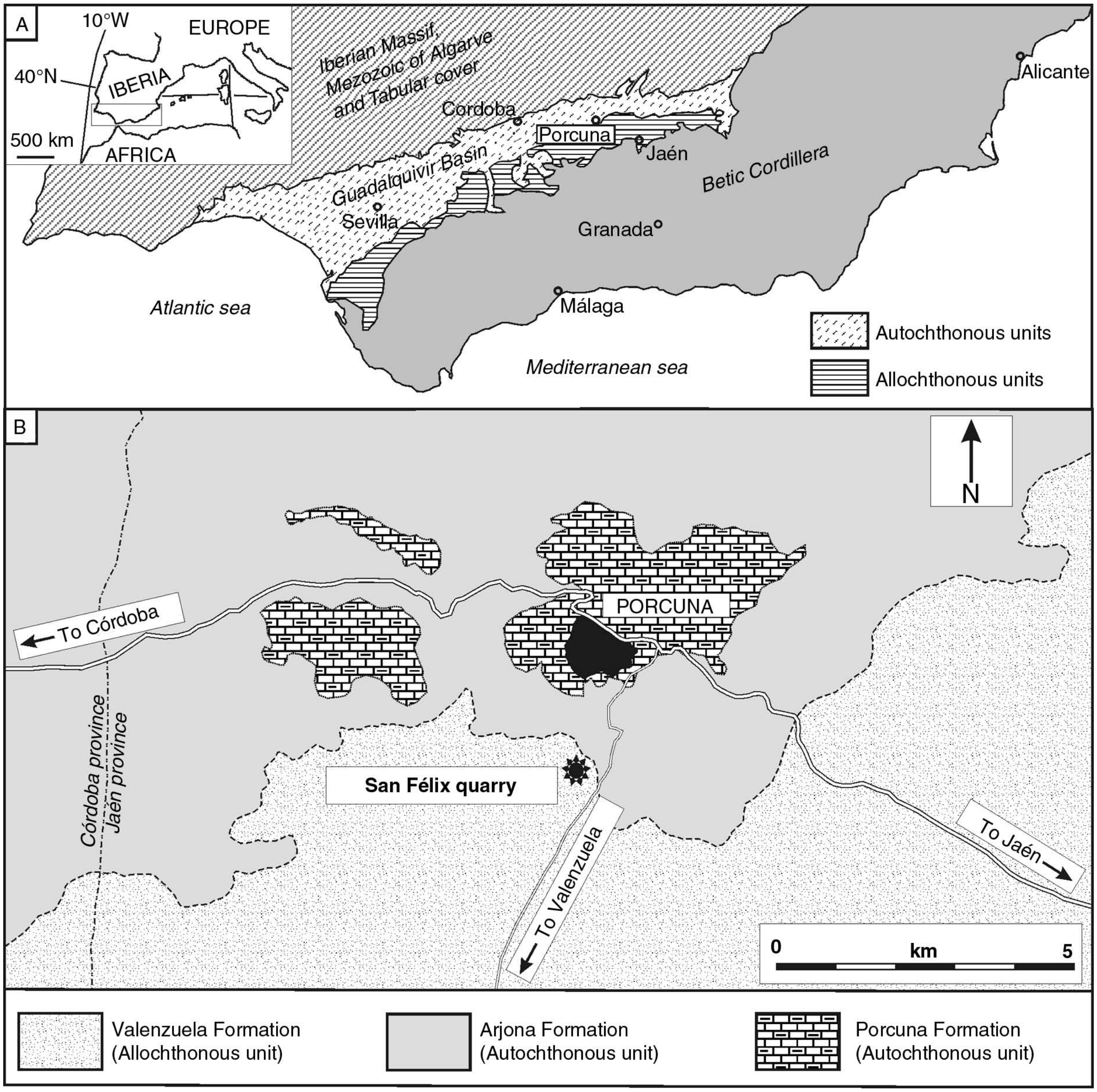

Fig. 1.—Geological setting. A. Location of the Guadalquivir Basin with the autochthonous and allochthonous units. B. Geological sketch of the Porcuna area with the location of the San Félix Quarry.

Flood-tidal currents as well as temperature and salinity gradients favoured movement of sea-water (e.g. Reolid *et al*., 2012; García-García *et al*., 2014; Martín *et al*., 2014). The interaction of the cold nutrient-rich Atlantic waters with the gulfs, bays, small basins and bottom topography of the North Betic Strait caused upwelling, and high productivity of biogenic silica (Molina *et al*., 1987). The narrowing of the strait from the Langhian to the Tortonian could have caused the progressive upwelling deduced from the study of the diatomites. This narrowing could also explain the evolution of the upwelling from open sea conditions to near shore conditions (Bustillo & López-García, 1997).

The youngest part of the Valenzuela Fm, in which the area of the San Felix Quarry is included, has to be considered parautochthonous of the syn-olistostromic sequence of the middle-late Tortonian times (Riaza & Martínez del Olmo, 1996), while the older parts of the Valenzuela Fm belong no doubt to the allochthonous basin filling that have travelled longer distances.

Methods

The tooth analysed, coming from diatomites of the Eastern Guadalquivir Basin, is now displayed in the Museo Obulco (Porcuna, Jaén province). This tooth is described following traditional measurements used by previous authors working on *C. megalodon* and *C. carcharias* (e.g. Applegate & Espinosa-Arrubarrena, 1996; Hubbell, 1996; Mollet *et al*., 1996).

The main measurements for describing the tooth and estimating the total length of the shark are the crown height and the crown width (Fig. 2). According to Gottfried *et al*. (1996) and Hubbell (1996), the crown height or tooth height is the vertical distance between a straight line touching the lower extensions of the enamel adjacent to the root at the base of the crown and a parallel line touching the tip of the enamel. For these authors, the crown width is the widest part of the enamel at the base of the crown (Fig. 2).

The Recent white shark *Carcharodon carcharias* is the closest living relative of *C. megalodon*, and therefore several authors have used skeletal material of *C. carcharias* as the primary basis for comparison with *C. megalodon* and to infer lifestyle (Uyeno *et al*., 1989; Applegate, 1991; Gottfried *et al*., 1992, 1996; Applegate & Espinosa-Arrubarrena, 1996; Adnet *et al*., 2010; Pimiento *et al*., 2010). In order to better approximate the total length of the specimen of *C. megalodon* from Porcuna, we considered data on crown height and crown width of upper anterior teeth from 102 specimens of *C. carcharias* (85 specimens) and *C. megalodon* (17 specimens) available in the literature (Table 1).

Results

This tooth presents the diagnostic characters of *C. megalodon* such as large size, triangular shape, fine serration on the cutting edges, a convex lingual

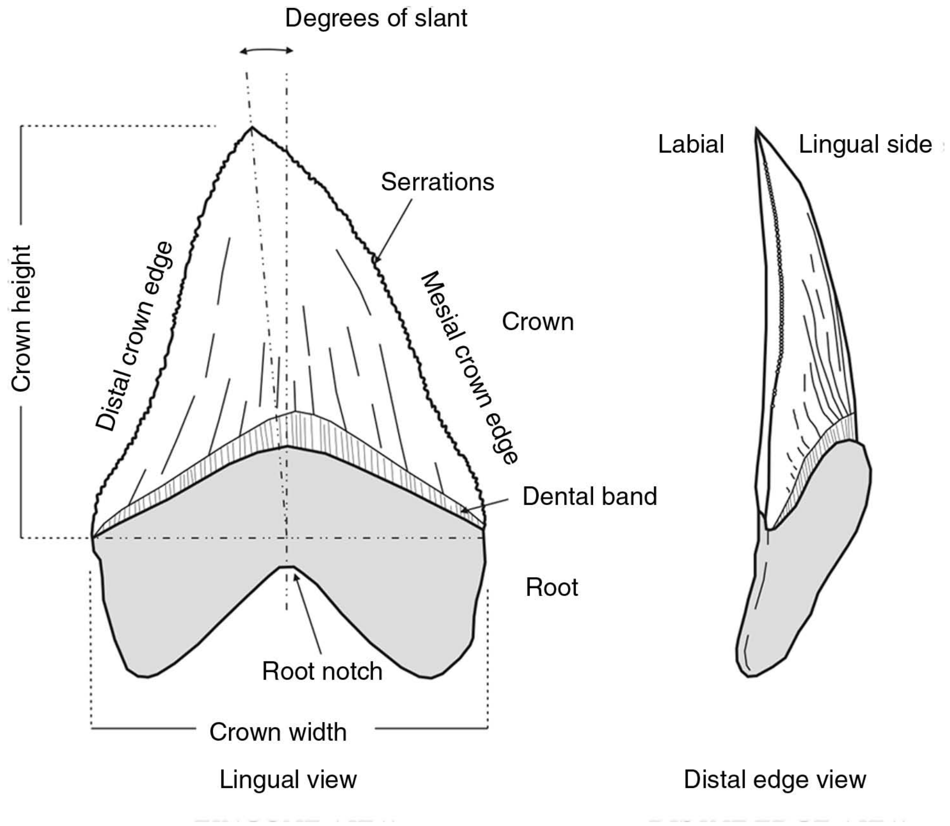

Fig. 2.—Tooth measurements employed in the description of the tooth of *Carcharocles megalodon*.

Table 1.—**Total length, crown height and crown width from *Carcharodon carcharias* and *Carcharocles megalodon* from the upper tooth A2 (locally A3). Note that total length from *C. megalodon* is calculated according to regression equation proposed by Shimada (2002)**

Specimen ID	Total length (m)	Crown height (mm) UA 2	Crown width (mm)	Genus	Reference
	2.42	21.0		*C. carcharias*	Siccardi *et al*. (1981)
	2.56	25.5		*C. carcharias*	Randall (1973)
	2.67	24.5		*C. carcharias*	Randall (1973)
	2.71	22.5		*C. carcharias*	Randall (1973)
	2.80	25.2		*C. carcharias*	Randall (1973)
DAE-871111-01	2.83	23.6		*C. carcharias*	Mollet *et al*. (1996)
DAE-871111-02	2.93	28.1		*C. carcharias*	Mollet *et al*. (1996)
NSB-BRI-873	3.02	28.1		*C. carcharias*	Mollet *et al*. (1996)
	3.05	28.0		*C. carcharias*	Siccardi *et al*. (1981)
UAP 1303	3.07	27.5	21.5	*C. carcharias*	Cione *et al*. (2012)
UAP 1301	3.10	22.7	24.5	*C. carcharias*	Cione *et al*. (2012)
	3.14	26.0		*C. carcharias*	Randall (1973)
	3.31	29.9		*C. carcharias*	Randall (1973)
F61583B	3.35	28.5	21.0	*C. carcharias*	Hubbell (1996)
F6785A	3.35	30.0	23.0	*C. carcharias*	Hubbell (1996)
	3.64	38.0	36.0	*C. carcharias*	Mollet *et al*. (1996)
	3.71	31.0		*C. carcharias*	Randall (1973)
T4239	3.79	32.5	25.0	*C. carcharias*	Hubbell (1996)
	3.79	32.5	26.0	*C. carcharias*	Mollet *et al*. (1996)
SP22294	3.91	32.5	28.0	*C. carcharias*	Hubbell (1996)
F6785B	3.96	33.0	25.0	*C. carcharias*	Hubbell (1996)
F83083	3.96	33.0	30.0	*C. carcharias*	Hubbell (1996)
F2680B	3.96	35.5	31.0	*C. carcharias*	Hubbell (1996)
	4.08	35.5		*C. carcharias*	Randall (1973)
F12484B	4.11	33.5	25.0	*C. carcharias*	Hubbell (1996)
H31683	4.11	34.0	28.0	*C. carcharias*	Hubbell (1996)
H93086	4.17	38.5	35.0	*C. carcharias*	Hubbell (1996)
F81287	4.27	35.0	27.0	*C. carcharias*	Hubbell (1996)
F9886A	4.27	34.0	28.0	*C. carcharias*	Hubbell (1996)
F4683	4.27	33.0	30.0	*C. carcharias*	Hubbell (1996)
X11384C	4.27	34.5	30.0	*C. carcharias*	Hubbell (1996)
ADCJ	4.27	36.0	50.1	*C. carcharias*	Hubbell (1996)
F122793	4.27	35.0		*C. carcharias*	Hubbell (1996)
H32089	4.42	40.5	33.0	*C. carcharias*	Hubbell (1996)
F51089	4.57	35.0	28.0	*C. carcharias*	Hubbell (1996)
H72689	4.57	37.0	34.0	*C. carcharias*	Hubbell (1996)
F9682	4.57	42.0	34.0	*C. carcharias*	Hubbell (1996)
	4.67	34.0		*C. carcharias*	Royce (1963)
	4.70	37.0		*C. carcharias*	Mollet *et al*. (1996)
SW41285	4.71	39.5	39.0	*C. carcharias*	Hubbell (1996)
S41285	4.71	40.0		*C. carcharias*	Mollet *et al*. (1996)
G121382	4.72	38.5	33.0	*C. carcharias*	Hubbell (1996)
SP1394	4.74	43.5	40.0	*C. carcharias*	Hubbell (1996)
	4.82	43.9		*C. carcharias*	Randall (1973)
F10882	4.88	39.5	34.0	*C. carcharias*	Hubbell (1996)

Table 1.—**(continued)**

Specimen ID	Total length (m)	Crown height (mm) UA 2	Crown width (mm)	Genus	Reference
F111882	4.88	38.0	35.0	*C. carcharias*	Hubbell (1996)
H2888	4.88	39.5	36.0	*C. carcharias*	Hubbell (1996)
F92982	4.88	42.5	37.0	*C. carcharias*	Hubbell (1996)
	4.88	45.0		*C. carcharias*	Randall (1973)
LACM 42894	4.94	34.6	33.0	*C. carcharias*	Mollet *et al*. (1996)
	4.96	44.2	43.1	*C. carcharias*	Kenyon (1959)
H10886	5.03	43.5	35.0	*C. carcharias*	Hubbell (1996)
	5.10	46.0		*C. carcharias*	Follet (1966)
	5.11	44.7		*C. carcharias*	Randall (1973)
X10892	5.16	44.5	38.0	*C. carcharias*	Hubbell (1996)
F7687	5.18	48.5	35.0	*C. carcharias*	Hubbell (1996)
H8993	5.18	40.5	37.0	*C. carcharias*	Hubbell (1996)
H3884	5.18	40.0	39.0	*C. carcharias*	Hubbell (1996)
F82817	5.18	44.5	39.0	*C. carcharias*	Hubbell (1996)
F22490	5.18	46.0	39.0	*C. carcharias*	Hubbell (1996)
N11693	5.23	45.0	43.0	*C. carcharias*	Hubbell (1996)
	5.30	48.3		*C. carcharias*	Mollet *et al*. (1996)
R92185	5.36	47.5	42.0	*C. carcharias*	Hubbell (1996)
LACM CCS85-9	5.37	47.0	39.9	*C. carcharias*	Mollet *et al*. (1996)
	5.37	49.3		*C. carcharias*	Randall (1973)
F52683	5.38	39.5	38.0	*C. carcharias*	Hubbell (1996)
X11384B	5.47	45.0	37.0	*C. carcharias*	Hubbell (1996)
X11384B	5.47	45.0		*C. carcharias*	Mollet *et al*. (1996)
	5.52	40.0	37.0	*C. carcharias*	Mollet *et al*. (1996)
X1138C	5.53	40.0		*C. carcharias*	Mollet *et al*. (1996)
H10991	5.54	43.0	36.0	*C. carcharias*	Hubbell (1996)
X11384A	5.54	41.0	37.0	*C. carcharias*	Hubbell (1996)
F82380	5.54	49.0	41.0	*C. carcharias*	Hubbell (1996)
L11685	5.63	48.0	43.0	*C. carcharias*	Hubbell (1996)
L11985	5.63	49.0		*C. carcharias*	Mollet *et al*. (1996)
F42787	5.64	48.0	36.0	*C. carcharias*	Hubbell (1996)
SW31287	5.64	52.0	46.0	*C. carcharias*	Hubbell (1996)
M91683	5.76	45.5	42.0	*C. carcharias*	Hubbell (1996)
H5384	5.94	49.0	36.0	*C. carcharias*	Hubbell (1996)
F7282	5.94	44.5	39.0	*C. carcharias*	Hubbell (1996)
H112690	5.94	45.0	40.0	*C. carcharias*	Hubbell (1996)
LJVC-870303	6.00	48.6	50.0	*C. carcharias*	Mollet *et al*. (1996)
CV. CGP	6.70	56.0	53.0	*C. carcharias*	Adnet *et al*. (2009)
	7.01	46.9	38.4	*C. carcharias*	Mollet *et al*. (1996)
	7.01	51.6		*C. carcharias*	Cappo (1988)

face, a slightly convex to flat labial face, and a large v-shaped neck (Fig. 3). Two root lobes are well-differentiated and rounded on the basal root edge. The crown height is 92.2 mm and the crown width is 81.3 mm. The total height of the tooth measured perpendicular from the apex of the tooth to the baseline of the root is 123.96 mm.

The tooth is symmetrical and nearly perpendicular, only slightly slanted (2.1°). For this reason, the mesial crown edge length is 102.0 mm while the distal

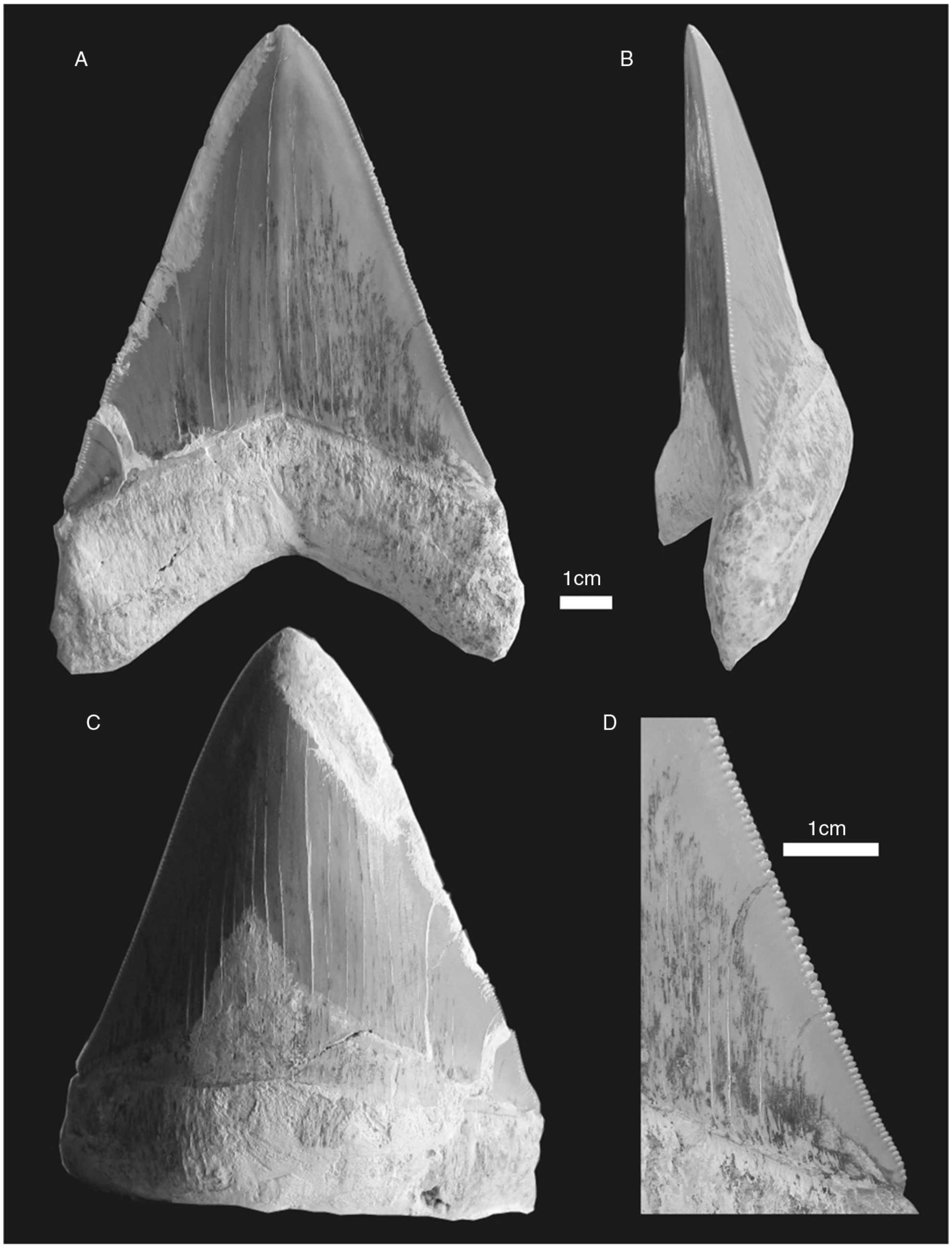

Fig. 3.—Tooth recorded in the Tortonian diatomites from Porcuna (Eastern Guadalquivir Basin). A. Labial view. B. Messial edge view. C. Lingual view. D. Detail of serration in the mesial edge.

crown edge length is 94.8 mm. The size of the teeth varies within the jaw, anterior teeth being large and symmetrical, whereas the large posterior teeth are asymmetrical and feature slanted crowns (Applegate & Espinosa-Arrubarrena, 1996; Hubbell, 1996; Pimiento *et al*., 2010). Taking into account the symmetry and the size, this tooth probably corresponds to the upper anterior (A2 or A3 *s*. Hubbell, 1996; or I or III s. Applegate & Espinosa-Arrubarrena, 1996) or the second upper lateral position.

The cutting edge presents 135 serrations in the mesial crown edge and 126 serrations in the distal crown edge (Fig. 3D). There are approximately 13 serrations per cm, and they are smaller and denser close to the root and the apex. The points of basal serrations are oriented 90° with respect to the cutting edge.

Discussion

Due to the fact that the cartilaginous skeleton of chondrichthyans is only preserved in rare instances (e.g. Uyeno *et al*., 1990; Shimada, 1997; Ehret *et al*., 2009a; Kriwet *et al*., 2014), the lack of more complete fossil specimens has led to conflicting interpretations about taxonomy. The taxonomic assignment of this species has long been debated and there are two main interpretations:

A) The *megalodon* shark is placed in the genus *Carcharocles* (Family Otodontidae) (Casier, 1960; Gluckman, 1964; Capetta, 1987; Ward & Bonavia, 2001; Nyberg *et al*., 2006; Ehret *et al*., 2009a, 2012; Pimiento *et al*., 2010).

B) The genus of *megalodon* shark is congeneric with the living white shark *Carcharodon carcharias* (Family Lamnidae) (Uyeno *et al*., 1989, Applegate, 1991; Applegate & Espinosa-Arrubarrena, 1996; Gottfried *et al*., 1992, 1996; Purdy, 1996).

We follow the first hypothesis, where *C. megalodon* is separated from genus *Carcharodon* on the basis of tooth features such as large size, absence of lateral denticles, and fine serrations—as opposed to a small size, large serrations and the presence of lateral denticles in *C. carcharias*. However, *Carcharocles* and *Carcharodon* are included in the Order Lamniformes, and in the absence of living members of Otodontidae, *Carcharodon carcharias* is the most analogous species available.

Size estimation

Among the different measurements on *C. carcharias*, the crown height of the upper anterior tooth A2 presents a higher correlation with the total length of the specimen (r=0.92) than the crown width (r=0.53) (Fig. 4). In addition, the correlation is extremely good between the crown width and crown height in the case of *C. megalodon* (r=0.94), better than in *C. carcharias* (r=0.83) (Fig. 5). For these reasons, commonly, for the estimation of total length of *C. megalodon* from fossil teeth in comparison with the most analogous specie *C. carcharias*, it is used the crown height only.

The largest tooth specimen of *C. megalodon* is the first upper anterior tooth of the Field Museum of Natural History of Chicago (specimen PF 1168), measuring 168 mm in total height and 125 mm in total width, and the 2nd upper lateral tooth of the British Museum of Natural History (specimen P10725), with 154 mm total height and 134 mm total width.

Applegate & Espinosa-Arrubarrena (1996) estimated 12 m length for the individual having the first upper anterior tooth of the Field Museum (Chicago). This estimation was based on comparison with the same tooth of *C. carcharias*, of known length. *C. megalodon* dentition is apparently similar in morphology and the number of tooth rows to that of *C. carcharias* (Uyeno *et al*., 1989). However, the jaws of *C. megalodon* must be somewhat more robust, larger and thicker, having more massive muscles than those of the *C. carcharias* (Gottfried *et al*., 1996). Correspondingly to great jaws and teeth, the head would have most likely been massive as well, with a large branchial region for respiration. In turn, a large stomach and intestine would be necessary for processing large prey, meaning a morphology similar to *C. carcharias* but more robust.

Previous authors assume that the ratio of upper A2 tooth size to total length of the *C. megalodon* is similar to that in white sharks, and that tooth size increased along with the total length of the shark in both species. The upper A2 tooth in Recent white sharks ranges in size from 56–63 mm height and 40–50 mm width for adult females, with a total length of 490–600 cm (Gottfried *et al*., 1996). A simple method for obtaining a relative total length ratio of the *C. megalodon* specimen from the Guadalquivir Basin with respect to the white shark consists of determining the tooth height ratio of the *C. carcharias* and *C. megalodon* from the Guadalquivir Basin. In the case of the *C. carcharias*, Gottfried *et al*. (1996) propose an average height for the upper A2 tooth of 59.2 mm, corresponding to an average total length of 550 cm.

$$550\ \text{cm} \times 92.2\ \text{mm} / 59.2\ \text{mm} = 856.6\ \text{cm}$$

According to this method, the studied tooth belonged to a specimen around 8.5 m in length.

Using the upper A2 height measurements from 85 specimens of *C. carcharias* (Table 1; Fig. 4), a linear least-squares regression was calculated following Gottfried *et al*. (1996).

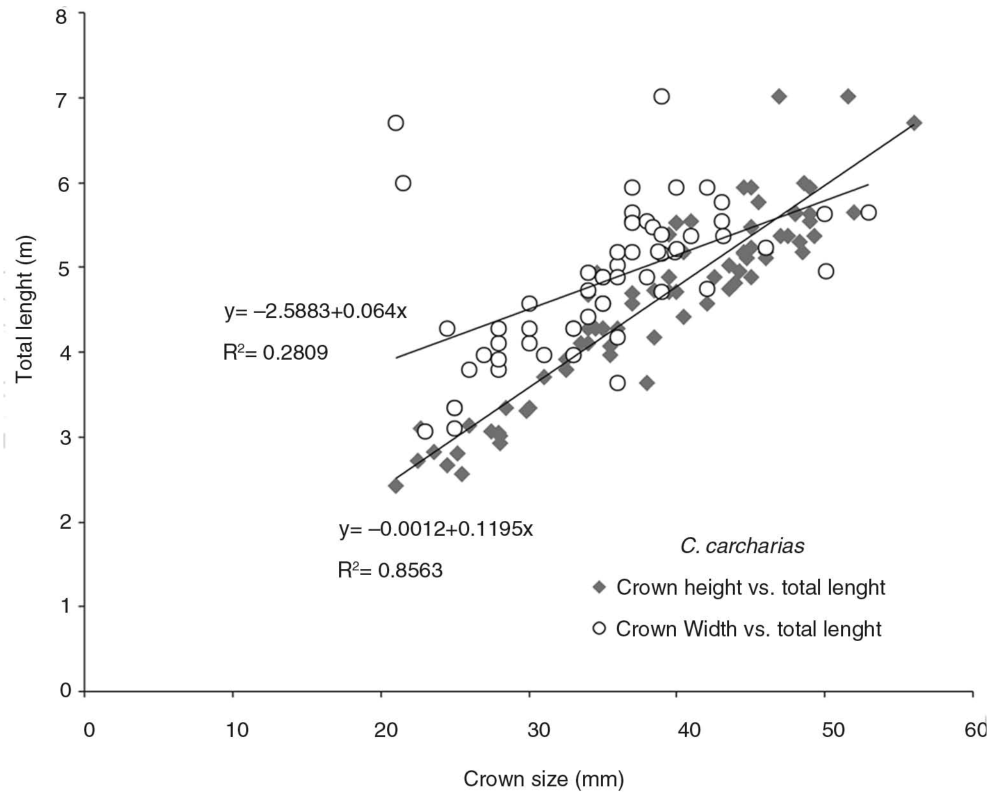

Fig. 4.—Linear relationship between the different crown measurements of the upper second anterior tooth (crown height and crown width) and the total length in *Carcharodon carcharias*.

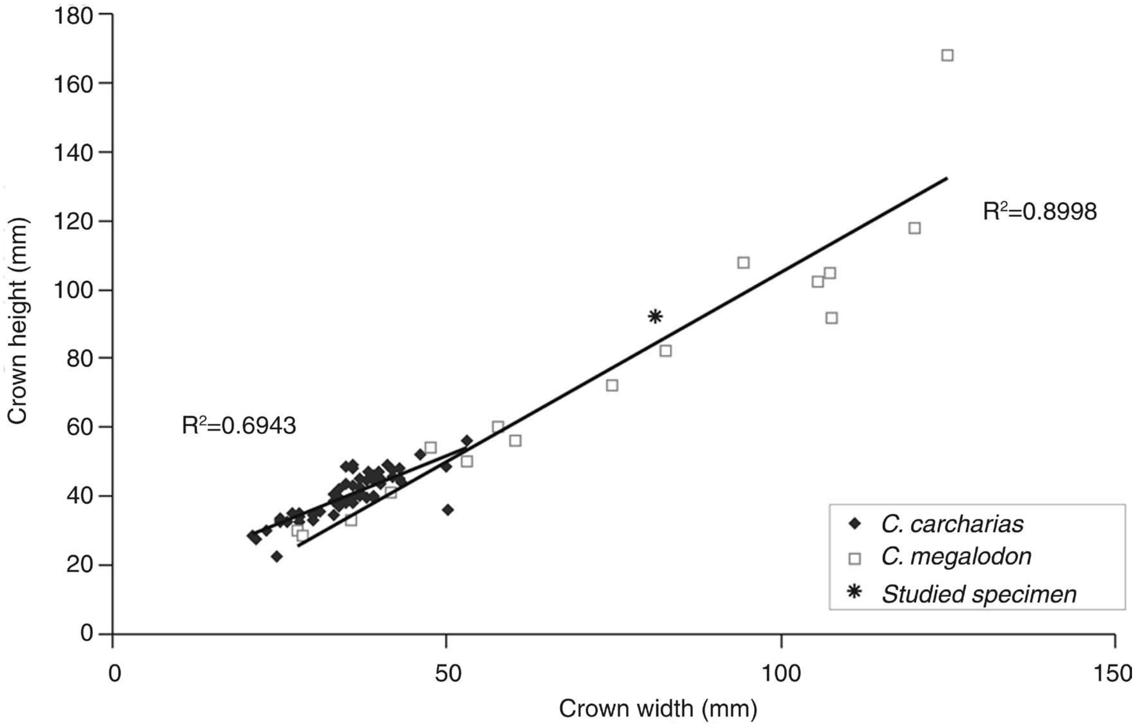

Fig. 5.—Comparison of crown width vs. crown height in *C. carcharias* and *C. megalodon*.

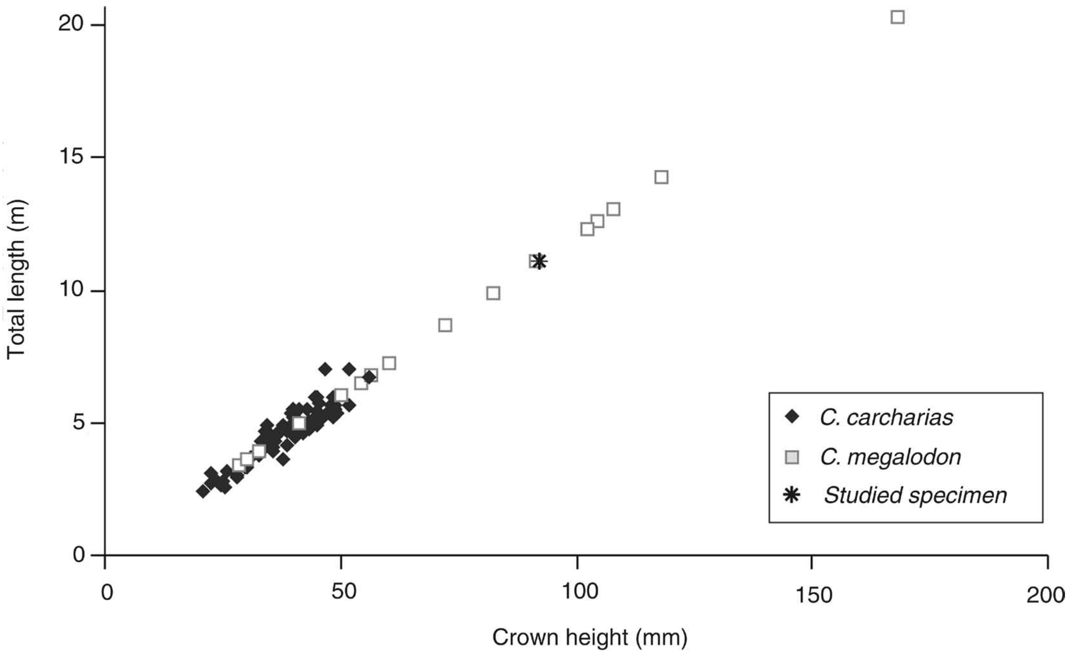

Fig. 6.—Linear relationship between the crown height of the upper second anterior tooth and the total length in *Carcharodon carcharias* and *Carcharocles megalodon*. Note total length in *C. megalodon* calculated according to regression equation of Shimada (2002).

Total Length (m) = a+b (upper A2 height (mm))

where a and b, as calculated, were −0.001 and 0.119, respectively (r^2=0.85; Fig. 4). Using 92.2 mm as the crown height for the *C. megalodon* specimen of Porcuna, we obtain −0.001+0.119 (92.2 mm) = 10.97 m.

Shimada (2002) proposes a linear least-square regression based on relationship between crown height and total length in *C. carcharias*, but taking into account all the positions of the tooth set. This relation is calculated as:

Total Length (cm) = a+b (Crown Height (mm))

with a being a constant and b being the slope of regression line. Shimada (2002) propose a and b values for predicting the total length of any tooth from *C. carcharias*.

Bearing in mind that the tooth from Porcuna (92.2 mm) is probably an upper anterior tooth A2, a=−2.160 and b=12.103 (Shimada, 2002):

Total length = −2.160+12.103 (92.2 mm) = 1113 cm

That is, the tooth of Porcuna belonged to an adult, and is in the large size range of specimens of *C. megalodon* (Fig. 6).

According to Shimada´s (2002) method, the largest tooth of *C. megalodon*, the upper anterior A2 of the Field Museum of Natural History of Chicago (specimen PF 1168), which reaches a crown height of 168 mm, would have belonged to a shark 20.31 m long (Fig. 6); and the second upper lateral tooth of the British Museum of Natural History (specimen P10725), reaching a crown height of 154 mm, belonged to a shark 20.73 m long.

Palaeoecology

Tooth structure and size indicate that *C. megalodon* began primarily as a fish feeder and evolved to feed on marine mammals (Applegate & Espinosa-Arrubarrena, 1996). The almost worldwide distribution of the *C. megalodon* in the Miocene to Pliocene seas in near-shore deposits at moderately high temperature latitudes indicates environmental requirements close to those favouring living *C. carcharias*. These environments are nutrient rich shelf areas where large marine mammals are relatively abundant. The record of bite marks of *C. megalodon* on fossil cetacean remains indicates that whales and dolphins were regular prey (Demèrè & Cerutti, 1982; Cigala-Fulgosi, 1990; Purdy, 1996; Ehret *et al.*, 2009b). In the Guadalquivir Basin, and

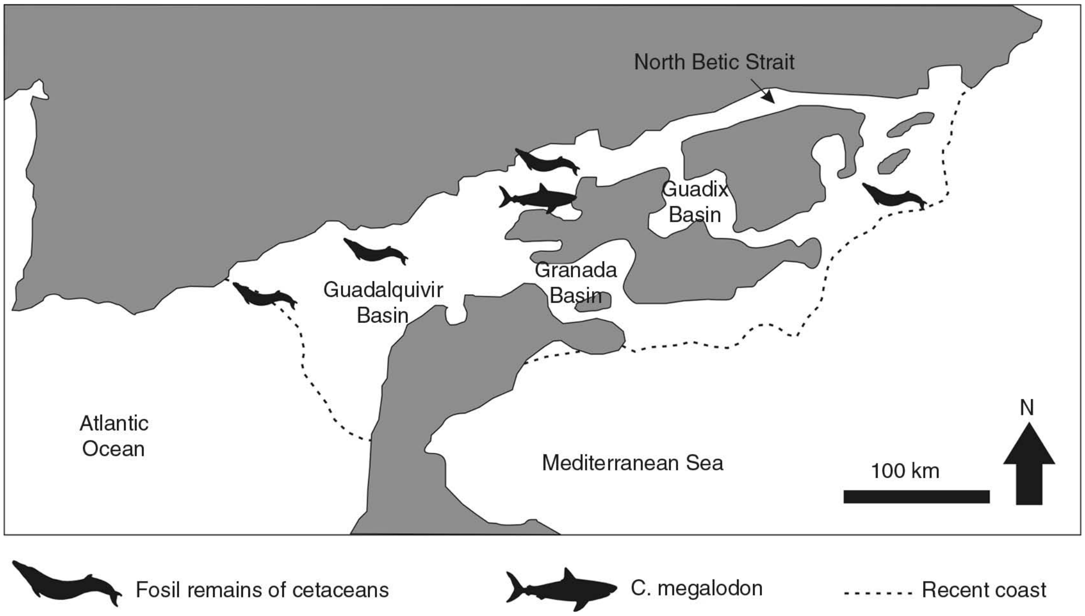

Fig. 7.—Palaeogeography of the Betic-Rifian Cordillera during the Late Tortonian modified from Martín *et al*. (2014), and location of the fossil remains of cetaceans (Sendra, 1997; Sendra & Bajo Campos, 2013; Toscano *et al*., 2013; Reolid *et al*., 2014) and the *C. megalodon* teeth studied.

concretely in the sector between Porcuna and Bailén, numerous remains from large marine vertebrates have been recorded, including *Isurus*, indeterminate pinnipeds and whales (Reolid *et al*., 2014), which could be potential prey of *C. megalodon*. The palaeogeography of this basin, as an Atlantic branch connecting with the Mediterranean Sea, probably favoured the hunting techniques of *C. megalodon*. Obviously, this is very speculative due the scarce record of marine vertebrate fossils from Upper Miocene in this basin (Fig. 7). However, the record of *C. megalodon* is congruent in a context as the North Betic Strait where high productivity is reported (Molina *et al*., 1987; Bustillo & López-García, 1997) favorable for marine mammals, also recorded in the same basin (Reolid *et al*., 2014).

Conclusions

A large shark tooth is recorded in Tortonian diatomites of the Eastern Guadalquivir Basin (Porcuna, Jaén). The large size (92.2 mm crown height), triangular shape, broad serrated crown, lingual face convex, labial face flat, large neck, and robust, thick angled root determine that this specimen corresponds to *Carcharocles megalodon*. The symmetry with a low slant indicates this is an upper anterior tooth. The total length estimated from the tooth crown height is around 11 m.

In the North Betic Strait, which connected the Atlantic Ocean to the palaeo-Mediterranean sea, the interaction of the cold nutrient-rich Atlantic waters with the palaeogeography and the bottom topography caused upwelling, and a high productivity of biogenic silica (diatomites). High nutrients and productivity favoured the presence of large vertebrates such as mysticetid whales, pinnipeds and small sharks (*Isurus*) recorded in the Upper Miocene deposits of this area. These large vertebrates constitute potential prey of *C. megalodon*. The palaeogeography of this basin, as an Atlantic branch connecting with the Mediterranean Sea, was probably well suited to the hunting techniques of *C. megalodon*.

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