



New fossil teeth of the White Shark (*Carcharodon carcharias*) from the Early Pliocene of Spain. Implication for its paleoecology in the Mediterranean

Sylvain Adnet, Montpellier, Ausenda C. Balbino, Evora, Miguel Telles Antunes, Lisboa and J. M. Marín-Ferrer, Elche

With 3 figures

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Abstract: We report here supplementary fossil evidence from Guardamar del Segura (south-eastern Spain) that the White Shark, *Carcharodon carcharias* inhabits the Mediterranean since the Early Pliocene. Moreover, new fossils reveal that the body size of this great predator probably exceeded 6.7 m in total length, a rare size in fossil record and never verified for living specimens to date as discussed in regard of material and methods. A review of fossil evidences of the largest sharks in the Western Mediterranean at the Mio-Pliocene seems to display a gradual ecological replacement of the giant fossil Megatooth shark (“*M.*” *megalodon*) by the modern *C. carcharias* beyond the dramatic marine environmental crisis that underlines the Miocene/Pliocene boundary in the Mediterranean.

Key words: *C. carcharias*, estimated size, Early Pliocene, Mediterranean.

1. Introduction

The (Great) White Shark: *Carcharodon carcharias* (LINNÉ, 1758) (Chondrichthyes, Lamnidae), is the largest living “macropredatory” shark, with a possible maximum total length beyond 6 meters (COMPAGNO 2001). Due to their spectacular appearance and reputation, *C. carcharias* and its fossil relatives have received a great deal of attention, both in the popular media and in scientific studies. Despite this notoriety, many gaps remain in our knowledge of this taxon including for instance, the systematic relationships within fossil lamnid sharks. The remarkable similarity in tooth morphology suggested since long ago that the fossil “megatooth” species [of genera such *Carcharocles* or *Megaselachus* according to most phyletic assumptions] as the famous species “*Megaselachus*”

megalodon (AGASSIZ in CHARLESWORTH 1837) were closely related to living *C. carcharias* (e.g. PURDY 1996) even if significant differences caused other palaeontologists to place them and *C. carcharias* into two separate families (e.g. GLUCKMAN 1964; CAPPETTA 1987, 2006). The recent controversy regarding fossil lamnid shark relationships based on tooth morphology (e.g. MUIZON & DEVRIES 1985; NYBERG et al. 2006) improved the debate in proposing a possible origin of modern *Carcharodon* from some Miocene isurid sharks (e.g. *Cosmopolitodus*). We follow this last assumption because we are agree with their result showing that differences of tooth morphology (tooth shape and root shape) between *Cosmopolitodus* species and *C. carcharias* are very thin except on presence of more serrated cutting edges in the living species. At the contrary, teeth of “*Mega-*

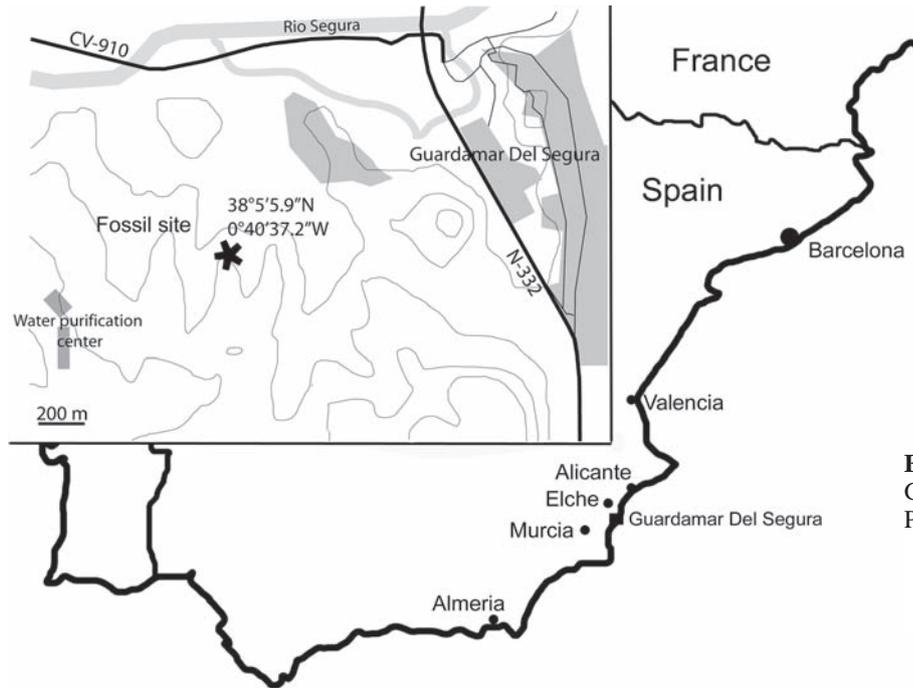


Fig. 1. Location of fossil site near Guardamar del Segura, Alicante Province, south-eastern Spain.

selachus” *megalodon* may be characterized by the presence of a large chevron-shaped “neck” (enameloid free-band at the crown-root junction) on the lingual crown face and by two root lobes which are well-differentiated and often rounded on the basal root edge. Such characters have never been observed on the teeth of living *C. carcharias* nor on fossils but they remind those of the Upper Palaeogene Otodontidae as envisaged by GLUCKMAN (1964). This explains in part our use of the old genus *Megaselachus* GLUCKMAN, 1964 renewed and adopted by CAPPETTA (2006) for the species “*M.*” *megalodon*.

The discussion of White Shark taxonomy (as genus *Megaselachus*) is beyond the scope of this paper and whatever the case, origin of the extant species *C. carcharias* probably took place either off South or Central America in the late Miocene as the fossil record recovered from the Gulf of Mexico-Caribbean sea (KRUCKOW & THIES 1990; ITURRALDE-VINENT et al. 1996; PURDY 1996) or Pacific coasts (e.g. JORDAN

1907; ESPINOSA-ARRUBARRENA & APPLIGATE 1981; MUIZON & DEVRIES 1985; LONG 1993 updated by WALSH & SUAREZ 2005) indicate. The teeth assigned to *C. carcharias* in deposits older than the late Miocene is problematic and must be taken with caution because confusion with contemporaneous taxa remains highly possible and the ages of deposits are sometimes uncertain.

Fossil teeth of *C. carcharias* are most clearly distinct and more frequently reported in Pliocene deposits world-wide (e.g. CAPPETTA 1987). Concerning the Mediterranean where the extant *C. carcharias* is currently indigenous (FERGUSON 1996), reports of fossil *C. carcharias* in Western Spain and Italy suggest that it frequented this area since at least the late Pliocene. Early Pliocene occurrences however have been reported in old literature but required confirmation. We therefore intend to present new fossil material that can be assigned to *C. carcharias* from the early Pliocene of south-western Spain.

Fig. 2. Teeth of *C. carcharias* from Early Pliocene of Guardamar del Segura, lingual view (A), labial view (B) and enlargement of the cutting edge (C). 1: Upper anterior tooth (CV.GCP 611). 2: Upper anterior tooth (CV.GCP 4005). 3: Upper antero-lateral tooth (CV.GCP 4006). 4: Upper antero-lateral tooth (CV.GCP 4007). 5: Lower antero-lateral tooth (CV.GCP 4008). 6: Upper lateral tooth (CV.GCP 4009). 7: Lower lateral tooth (CV.GCP 4010). 8: Lower anterior tooth (CV.GCP 4011). 9: Lower antero-lateral tooth (CV.GCP 4012).

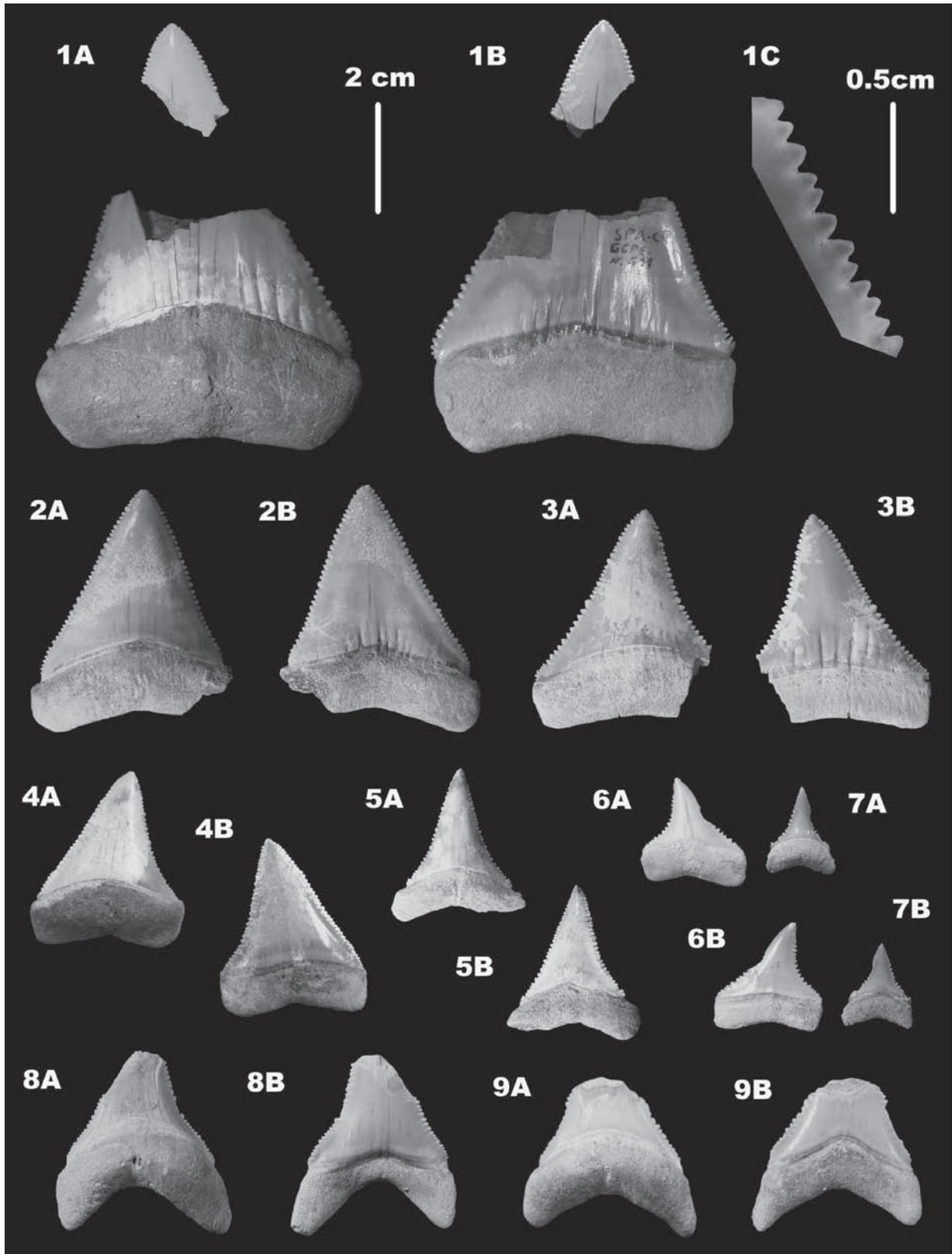


Fig. 2 (Legend see p. 8)

2. Provenance and geological setting

One of us (J. M. MARÍN-FERRER) discovered numerous fossil selachian teeth, including those of *C. carcharias* described here. All teeth which are attributable to *C. carcharias* come from Guardamar del Segura municipality (Alicante province, south-eastern Spain) at 1 km west of town (Fig. 1). The sandy shales that produced the teeth occupy a large part of locality and belong to the “Rojales Sandstone Formation” from the Bajo Segura Basin (MONTENAT 1973), at the top of the Pliocene unit I of MONTENAT (1977). The fossiliferous level corresponds to the P1/P2 system in CARACUEL et al. (2005) and SORIA et al. (2005) which is Early Pliocene in age. The selachian fauna supports this even if there is no temporal taxon restricted to the early Pliocene. However a younger age is not probable because of the co-occurrences of *Megascyliorhinus miocaenicus* (ANTUNES & JONET, 1970), *Premontreia (Oxyscyllium) dachiardi* (LAWLEY, 1876) and *Dipturus* aff. *olisiponensis* (JONET, 1968) in the same level and which have been recorded only up in the early Pliocene in the Mediterranean region (CAPPETTA & NOLF 1991; CAPPETTA & CAVALLO 2006, MARSILI 2006).

MONTENAT (1977) and SORIA et al. (2005) detailed with care the geodynamic evolution and environmental contexts of Mio-Pliocene sedimentary deposits in the Bajo Segura Basin. According to these authors, the studied fossils were deposited when the marine ingression culminated after the Messinian Crisis. This formation, mainly exposed in coastal sections of South Elche, is highly fossiliferous (e.g. echinoids, bivalves), and includes selachian assemblages previously reported by MORA MOROTE (1996) and MENDIOLA (2002). The fossil selachian fauna of Guardamar del Segura is essentially dominated by sharks whose extant counterparts inhabit primarily coastal continental and insular shelves (e.g. *Carcharias taurus*, *Squatina* and *Carcharhinus* spp.). This suggests a coastal depositional environmental in accordance with sedimentologic evidence (SORIA et al. 2005). This is compatible with the behaviour of living *C. carcharias*, which is known to occur in in-shore and offshore waters from the intertidal to the epipelagic zone and even on the upper slope. Geological mapping and further sedimentological details can be found in PIGNATELLI et al. (1972) and SORIA et al. (2005), respectively. Collections, including the specimens figured here, are housed at the MUPE-Museo Paleontológico de Elche (Spain).

3. Systematic Paleontology

Class Chondrichthyes HUXLEY, 1880

Order Lamniformes BERG, 1958

Family Lamnidae MÜLLER & HENLE, 1838

Genus *Carcharodon* SMITH in MÜLLER & HENLE, 1838

Carcharodon carcharias (LINNÉ, 1758)

Fig. 2

1833-1843 *Carcharodon sulcidens* AGASSIZ, p. 254, pl. 30a, figs. 3-7.

1876 *Carcharodon productus* LAWLEY, p. 22.

1876 *Carcharodon caifassi* LAWLEY, p. 23.

1876 *Carcharodon angustidens*, AGASSIZ. – LAWLEY, p. 23.

1881 *Carcharodon etruscus* LAWLEY, p. 17, pl.2, figs. 1-9, pl.3, figs.1-8, pl.4, fig. 2.

1895 *Carcharodon rondeleti* MÜLLER & HENLE. – DE ALESSANDRI, p. 269, pl. 1, fig. 63.

1900 *Carcharodon megalodon*. – SEGUENZA, p. 503, pl. 5, fig. 3.

1956 *Carcharodon carcharias*, LINNÉ. – GHELARDONI, p. 35, pl. 1, figs. 20-21, pl. 2, figs. 1-14.

Synonym list is restricted to the fossils from the Mediterranean area only. See MARSILLI (2006: 67 f.) for other synonym references about material from Mediterranean fossil deposits.

Referred material: 16 lower and upper teeth (Fig. 2) deposited in MUPE as CV. GCP.

Locality and age: All the teeth were collected at Guardamar del Segura, in marine deposits of the “Rojales Sandstone Formation”. Early Pliocene.

Description: Teeth of the extant species exhibit considerable variation in their morphology, both in a single specimen or between juveniles and adults, as largely exposed by HUBBELL (1996) and PURDY et al. (2001), among others.

In anterior and anterolateral upper teeth (Fig. 2.1-2.4), the broad triangular crown is nearly symmetrical, vertical, occasionally with a slight labial inclination at the apex. The labial surface is perfectly flat while the lingual surface is very slightly convex in lateral view. The enamel is entirely smooth, excepted in the basal median part of the labial surface where deep enamel folds may be marked over the crown-root junction, especially in large teeth (Fig. 2.1A). The cutting edges are continuous from base to apex, straight to slightly concave and evenly serrated. The serration is irregularly spaced. There is always a pointed tip (Fig. 2.1C). Root is as long as crown but moderate in height. The root lobes are not well individualized; the basal edge of the root is nearly straight (Fig. 2.1) to slightly concave (Fig. 2.4). The lateral root extremities are frequently rounded. The lingual surface of the root is flat or convex in its median part. The labial surface is convex; nutritive foramina or a groove are badly marked or absent. The lateral

upper teeth (Fig. 2.4) are characterized by a distally inclined rather than erect crown.

The lower anterior teeth are badly preserved (Fig. 2.8-2.9). The first anterior lower teeth can be distinguished from the upper ones by their thicker crowns, some cutting edges more concave in lingual or labial views, and better individualized root lobes. In lower anterior teeth, the root lobes may arch labially (Fig. 2.8) and the basal edge of the crown may slightly overhang medially the root-crown junction (Fig. 2.8A). In some lower lateral teeth (Fig. 2.5, 5.7), both cutting edges are basally marked by a notch which however does not define a real pair of cusplet. Absence of well-defined lateral cusplets on these teeth confirms that they belong to young adults and not to juveniles.

In some young adult teeth and lateral teeth (Fig. 2.5-2.7), the crown is less developed in comparison to the root. The cutting edges range from smooth near the apex to coarsely serrated basally (Fig. 2.7). The cutting edges of teeth ascribed to young adults are coarsely serrated, becoming finer in larger replacement teeth as a consequence of crown growth.

4. Discussion

The upper teeth are clearly distinct from those with triangular and serrated crowns belonging to the Megatooth Shark: “*Megaselachus*” *megalodon*, by a root more lightly lobed and not elongated (especially in upper teeth of adults); by the absence of a large chevron-shaped “neck” (enameloid free-band at the crown-root junction) on the lingual crown face, and by cutting edges not regularly and finely serrated (Fig. 2.1C). Fossil material belongs to genus *Carcharodon*, currently known in the fossil record by the extant species *C. carcharias* (LINNÉ, 1758). Several species were tentatively described on fossil teeth as *C. arnoldi* (JORDAN, 1907) and *C. aifassi* (LAWLEY, 1876) for instance, but none are currently considered as valid (CAPPETTA, 2006).

Among the ten available upper teeth, one is particularly large (CV.GCP 611, Fig. 2.1). As the crown is quite symmetrical, we consider this specimen as a first or second anterior upper tooth and hence among the largest ones of *C. carcharias* teeth set. Its crown is badly abraded and incomplete so that accurate measurements cannot be obtained. However, we could estimate that the greatest height is at least 70 mm (measured perpendicular from the apex of the tooth to the baseline of the root, with 56 mm for the enamel height) by extending virtually the two secant cutting edges according to the apex shape. The original tooth would have been slightly higher than indicated here by these indirect measurements. As preserved, the width across the widest portion is 53 mm.

Quantitative relationships between various measurements on soft and hard-tissue anatomy and total length (TL) or mass of body were attempted to predict *a posteriori* the growth parameters of *C. carcharias* (see RANDALL 1973, 1987; BASS et al. 1975). The “Tooth Enamel Height” (named TEH) from the two first upper teeth is one of the usual values to predict the body size (TL) of *C. carcharias*, presenting the advantage to able to be extracted from damaged body several decades after the death of the fish. These simple models are based on allometric equation performed on many measurements in comparison with the associated TL of mass of fish body. MOLLET et al. (1996) revised and tested the main measurements (TEH included) usually used to extrapolate the TL of *C. carcharias* from 63 recent specimens. The aim of their analysis was to validate or not the reported sizes of the two greatest *C. carcharias* ever captured (from Malta and Australia) and only known by indirect measurements. They concluded that such largest reports are consistent for the Australian specimen at least, even if they noted that the estimated sizes varied between 25 % and 50 % according to the confidence range, as calculated from the TEH for instance.

In order to better approximate the TL from an isolated upper anterior tooth, we reconsidered all the data TL/TEH available in literature (synthesized by RANDALL 1973; MOLLET et al. 1996; HUBBEL 1996; SHIMADA 2002) for the fresh material (questionable >7 m sharks are omitted in analysis) and thus, for the first and second upper anterior teeth mixed (Fig. 3). We secondary adjusted an allometric size-on-size equation from these values ($y = ax^b$, usually proposed as the most suitable equation for characterizing growth). New parameters of this power function were calculated using regression models available in the statistical package of R© v. 2.5.1 from mixed TL / TEH of 1st and 2nd upper teeth ($R = 0.97$, $p < 2.2 \cdot 10^{-6}$) as showed in Figure 3. Equation parameters a and b are 105.2502 (s.d. = 0.05702, $N = 132$) and 1.03177 (s.d. = 0.01632, $N = 132$), respectively.

Using this new equation parameters, values of the TEH of the largest fossil tooth from Guardamar del Segur show that CV.GCP 611 reliably is from a near 7 meters long individual (estimated TL = 6.7 m, confidence TL range = 5.9-7.5 m calculated from the standard deviation of equation parameters). TEH of CV.GCP 611 is significantly larger than in 1st or 2nd upper teeth of any living *C. carcharias* (Fig. 3) available in literature; including the two questionable 7 m long specimens (TEH of 1st upper tooth = 51.6

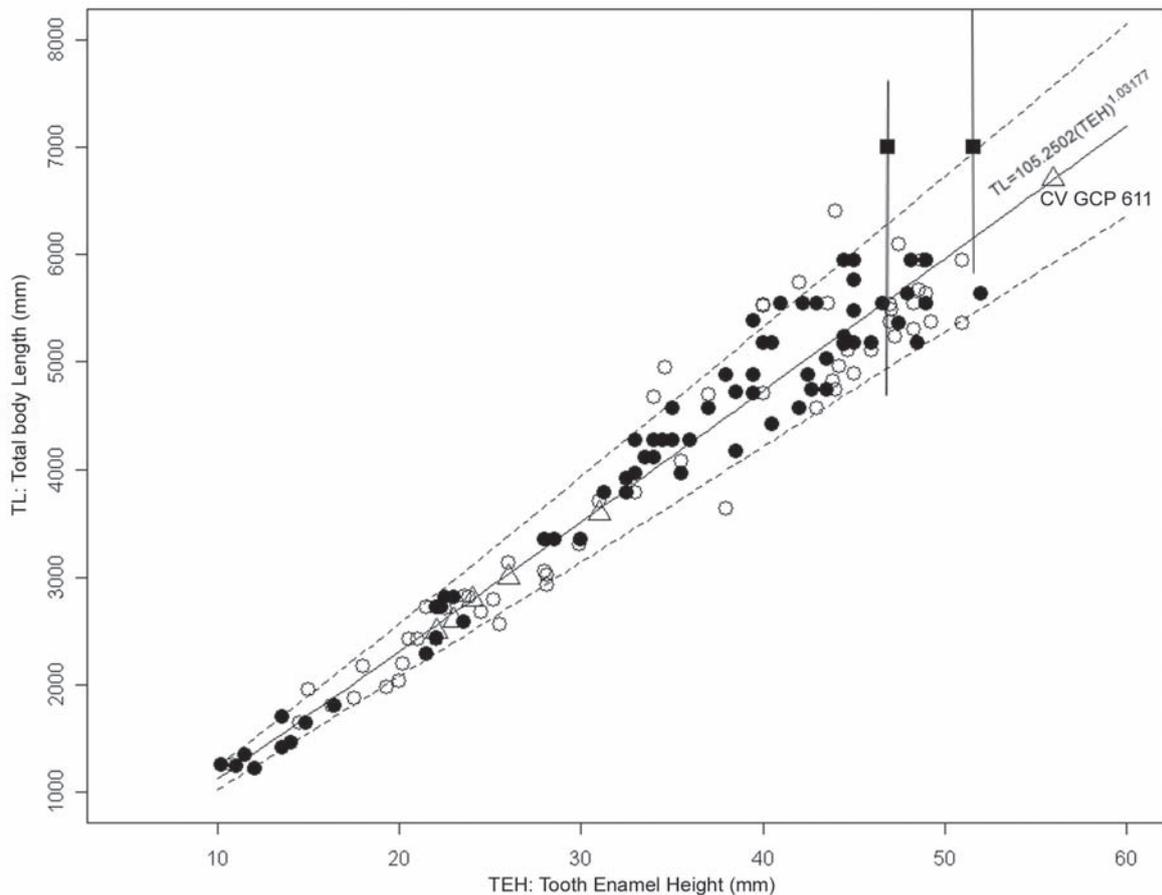


Fig. 3. Allometric relationship between Tooth Enamel Height (TEH) of the 1st-2nd upper teeth and Total body Length (TL) of 132 Recent specimens of *C. carcharias*, spanning 1.22-6.48 m TL and with TEH available from 1st (○) and 2nd (●) upper teeth, respectively. Data compiled from HUBBELL (1996), MOLLET et al. (1996) and SHIMADA (2002). ▲: Fossil teeth from Guardamar del Segur (this work) placed on the regression curve ($R= 0.97$, $p < 2.2 \cdot 10^{-6}$) calculated from previous data (Dashed lines: standard deviations). ■: Teeth from the supposed largest extant white sharks with confidence range of estimated size (vertical line, in MOLLET et al. 1996: 97).

and 46.9 mm, see Mollet et al. 1996:104) estimated about 6.1 (5.4-6.9 m) and 5.6 m (4.9-6.2 m) respectively according to our model. As MOLLET et al. (1996) concluded, we cannot reject the estimated 7 m TL for one of both specimens, even if our estimation of its size is lower than previously announced, but we correctly can argue that CV.GCP 611 was clearly larger than those. TEH of the other upper teeth from Guardamar del Segura that we considered anteriors (e.g. Fig. 2.2), indicates a maximum sizes range from the 2.5-3.6 m in TL (Fig. 3) for specimens.

SHIMADA (2002) proposed another model based on linear regression analysis performed from various upper tooth files belonging to 12 fresh-jaws ($y = 5.234 + 11.522x$ for the first upper tooth file, for instance). With such a model, TL of CV.GCP 611

could be estimated to be about 6.5 m (+/- 0.53m according we consider that tooth is a first or second tooth). However, analysis of SHIMADA was performed from relatively reduced sample sizes and is based on linear size-on-size regressions which suppose that the growth rate between tooth and total body length is isometric contrary to the observation of MOLLET et al. (1996: 97).

The maximal size of living White Shark remains actually unknown. The largest White Sharks reported in the literature are stated as measuring more than 6 m in length, but the length has often been deduced from photographic evidence, oral communication or has been estimated from preserved vertebrae, teeth or body parts. This explains why the length of large individuals is notoriously difficult to validate and

remains under discussion (RANDALL 1987; MOLLET et al. 1996; DE MADDALENA et al. 2001). Reports of specimens reaching total lengths close to 6.4 m are nevertheless adopted by the scientific community (COMPAGNO 2001) even if they have rarely been confirmed by visual measurement. It appears that Early Pliocene evidence under study from the Southwestern Mediterranean represents one of the largest sizes for fossil *C. carcharias* ever estimated through tooth measurements. Rare *C. carcharias* teeth from the Sacacco Formation (Peru), Bahia Inglesa Formation (Chili) that have been dated as Late Miocene and Early Pliocene are quite similar in size (pers. observ.). They are close to those from the Yorktown Formation (USA) dated as Early Pliocene (PURDY et al. 2001), those from Cooper River in South Carolina (USA, pers. observ.), Italy (LANDINI 1977) and South Africa and Angola deposits (DAVIES 1964; ANTUNES 1978). The presence of several distinct and very far occurrences of very large teeth indicate that large *C. carcharias* close to 7 m long or larger were not scarce in the Early Pliocene, as suggested by LONG (1995). The apparent decrease in size until present day must be tempered because the strong Human fishing pressure on the marine life since the two last centuries might explain the rapid decline of large marine predators at least in parts (MYERS & WORM 2003).

If the White Shark is cosmopolitan since Pliocene times (CAPPETTA 1987), its fossils are scarce along the Mediterranean coasts. If we remove the misidentified reports in ante-Pliocene deposits (PASQUALE 1903; BAUZÁ 1949, pl. 30, figs. 12-15) as observed and as discussed in MARSILI (2006: 37), fossils of *C. carcharias* are actually limited to the Plio-Pleistocene elsewhere in south and eastern Spain (BAUZÁ & IMPERATORI 1956; VICENS & GRACIA 1999; MENDIOLA 2001) and in Italy (MANGANELLI & SPADINI 2003; MARSILI 2006). Another cosmopolite large predator, the giant "*M.*" *megalodon*, is also reported until the Early Pliocene of the Mediterranean (BAUZÁ & IMPERATORI 1956; GONZÁLEZ & PORTA 1977; COSTA 1865; MARSILI 2006). This suggests they partially cohabited and may have been in competition at the top of marine food web during the Early Pliocene as it has been assumed for Angola (ANTUNES 1978). Early Pliocene evidence of *M. megalodon* in the Mediterranean is however much more scarce than in upper Miocene sediments and was sometimes erroneously reported, as in Guardamar del Segura by MORA MOROTE (1996, in MENDIOLA & MARTÍNEZ 2003). We highly suspect that the Early Pliocene occurrences of

M. megalodon resulted from a secondary invasion from the Portuguese coasts where this species is known during the Messinian (latest Miocene) and Early Pliocene (BALBINO 1996; ANTUNES et al. 1999). Reason of such assumption is that we expect that a top predator as *M. megalodon* may have been dramatically sensitive to the change in the marine ecosystems following the Messinian salinity crisis and the partial or global dessication of the Mediterranean basins (see KRIJGSMAN et al. 1999; ROUCHY & CARUSO 2006). Even if the timing and amplitude of the fish turnover remains debated and discussed (CARNEVALE et al. 2006), the marine food chain may have been deeply affected especially for the higher consumers. Further data, especially related to the Mio-Pliocene boundary in the Mediterranean, are needed to confirm this.

The paleobiogeographic story of the modern White Shark in the Mediterranean is simpler according to the fossil record. The extant species has probably taken advantage of the rapid restoration of the normal marine conditions at the beginning of the Pliocene to newly invade the place and to gradually occupy the empty niche of high marine predators in the Mediterranean (BIANUCCI et al. 2000), especially after the total disappearance of *M. megalodon* at the end of the Early Pliocene (MARSILI 2006).

C. carcharias globally tends to replace *M. megalodon* in the Pliocene but these two taxa overlapped in their stratigraphical and geographical ranges during the Early Pliocene at least. PURDY (1996) suggested that these two cosmopolite taxa did not have exactly the same areas of life in order to explain the co-occurrences of two largest predators. However teeth of *M. megalodon* and *C. carcharias* have sometimes been recorded together in the same deposit (FRANKEL 1972; ANTUNES 1978; ESPINOSA-ARRUBARRENA & APPLIGATE 1981; FERNANDES DOS REIS 2005) suggesting that both species were strictly contemporaneous and have really coexisted. In the Mediterranean, evidences that these two large predators frequented exactly the same places at the Early Pliocene remain still uncertain (BAUZÁ & IMPERATORI 1956; MORA MOROTE 1996) or unverified (see MARSILI 2006). However, it appears that they clearly occurred together in the Mediterranean and probably hunted the same prey in Early Pliocene times. Contrary to the expected scenario, the marine environmental crisis that marked the end of the Miocene in the Mediterranean does not seem to have encouraged an ecological exclusion or a replacement of a large marine predator by another.

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Addresses of the authors:

SYLVAIN ADNÉT, Université Montpellier 2, cc 064. Place Eugène Bataillon. 34095 Montpellier Cedex 5, France; e-mail: sylvain.adnet@univ-montp2.fr

AUSENDA, C. BALBINO, Departamento de Geociências, Universidade de Évora, Largo dos Colegiais, Portugal & Centro de Investigação em Ciência e em Engenharia Geológica UNL, Quinta da Torre, 2829-516 Caparica, Portugal; e-mail: acaceres@uevora.pt

MIGUEL TELLES ANTUNES, Centro de Investigação em Ciência e em Engenharia Geológica UNL, Quinta da Torre, 2829-516 Caparica, Portugal & Academia das Ciências de Lisboa, Rua da Academia das Ciências, nº 19, Lisboa; e-mail: ip241333@ip.pt

J. M. MARÍN-FERRER, Museo Paleontológico de Elche, Spain; e-mail: info@cidarismpe.org