

Analysing trophic competition in †*Otodus megalodon* and *Carcharodon carcharias* through 2D-SEM dental microwear

Analizando la competencia trófica en †*Otodus megalodon* y *Carcharodon carcharias* mediante microdesgaste dental en 2D-SEM

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Abstract: The extinction of the massive apex predator †*Otodus megalodon* during the Pliocene is a subject of debate, with climate change and emergence of competitors as potential factors, such as *Carcharodon carcharias*. We explore trophic interactions of †*O. megalodon* and the *C. carcharias* by the analysis of dental microwear. For this purpose, high-resolution casts were made from ten megalodon teeth and six white shark teeth. Then, replicas were produced for examination using a Scanning Electron Microscope. Following a previous work on non-occlusal teeth of bony fishes, density and scratch length as well as mean vector were taken into account for the analysis. Our findings revealed that †*O. megalodon* shows a slight preference for less abrasive diets compared to *C. carcharias*. However, no significant differences were found in the dental microwear patterns of both species. These results provide additional evidence of a similar trophic spectrum between *C. carcharias* and †*O. megalodon* in the Mediterranean Sea basin, contrasting with previous data obtained through texture analysis. However, due to the inability to estimate sizes, we cannot rule out possible ontogenetic dietary differences. Therefore, future studies estimating sizes and incorporating data from other basins could provide more information.

Resumen: La extinción del gran depredador †*Otodus megalodon* durante el Plioceno es motivo de debate, con el cambio climático y la aparición de competidores como *Carcharodon carcharias* como potenciales factores. Exploramos las interacciones tróficas de †*O. megalodon* y *C. carcharias* mediante el análisis del microdesgaste dental. Para ello, se realizaron moldes de alta resolución a partir de diez dientes de megalodón y seis dientes de tiburón blanco. Tras ello, se realizaron réplicas para su examen mediante un microscopio electrónico de barrido. En base a un trabajo previo en dientes no oclusales de peces óseos, se tuvo en cuenta la densidad y longitud de las marcas, así como el vector medio para el análisis. Nuestros resultados revelaron que †*O. megalodon* muestra una ligera preferencia por dietas menos abrasivas que *C. carcharias*. Sin embargo, no se encontraron diferencias significativas en el patrón de microdesgaste dental de ambas especies. Estos resultados aportan evidencia adicional de un espectro trófico similar entre *C. carcharias* y †*O. megalodon* en la cuenca del mar Mediterráneo, contrastando con datos previos obtenidos mediante análisis de texturas. Sin embargo, dada la imposibilidad de estimar tamaños no podemos descartar posibles diferencias dietéticas a nivel ontogenético. Es por lo que, estudios futuros estimando tamaños e incorporando datos de otras cuencas, podrían aportar más información.

Received: 14 February 2024

Accepted: 24 May 2024

Published: 28 May 2024

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Keywords:

Dental microwear

Megalodon

Dietary proclivities

Great white shark

Palabras-clave:

Microdesgaste dental

Megalodón

Tendencias dietéticas

Tiburón blanco

INTRODUCTION

†*Otodus megalodon* (Elasmobranchii, Lamniformes, Otodontidae) is considered one of the largest apex predators of the oceans, with consistent reports of maximum length estimations ranging between 15 and 20 m (Pimiento & Balk, 2015; Perez *et al.*, 2021; Shimada, 2019; Shimada *et al.*, 2021, 2023), inhabiting the seas from the Miocene to the Pliocene (23–2.6 My) (Gottfried *et al.*, 1996; Pimiento & Clements, 2014; Pimiento & Balk, 2015; Pimiento *et al.*, 2016;

Boessenecker *et al.*, 2019). Considering the significant role that modern sharks play in regulating prey communities and ecosystem structure (Ferretti *et al.*, 2010), its extinction likely had a profound impact on the functioning of the ecosystem and the dynamics of the trophic web within ancient marine communities (see Pimiento & Clements, 2014; Cooper *et al.*, 2022).

Conventionally, it has been hypothesised that †*O. megalodon* was constrained to warm temperatures,

linking its extinction and climate change (Gottfried *et al.*, 1996). The peak global abundance of †*O. megalodon* during the Middle Miocene coincided with the Mid–Miocene Climate Optimum (MMCO), while its continuous decline correlated with the oscillation of warm and cold temperatures during the Pliocene (Pimiento *et al.*, 2016). In addition, Gottfried *et al.* (1996) also proposed that shifts in the distribution of marine mammals, like cetaceans and pinnipeds, to higher latitudes might have contributed to the †*O. megalodon* extinction. This suggested that megalodon would be an ectothermic fish incapable of following the migrations of marine mammals to latitudes far from the tropics. Contrasting with previously held hypotheses regarding its distribution, additional fossil findings across the globe (see table S1 of Pimiento *et al.*, 2016) show that †*O. megalodon* exhibited a cosmopolitan distribution, and during the Pliocene cooling events, no evident population concentration in warmer waters was observed (Pimiento *et al.*, 2016). These findings are in line with the evidence of a regional endothermy in this apex predator as it occurs in the extant members of Lamnidae (Ferrón, 2017; Ferrón *et al.*, 2018; Griffiths *et al.*, 2023), which gives them the capacity to inhabit colder waters (Goldman, 1997). Moreover, 3D modelling of megalodon strongly implied that it was able to migrate across oceans, and thus naturally inhabit a wider range of temperatures (Cooper *et al.*, 2022). This hypothesis has recently also been supported by fossil evidence of an *in situ* megalodon tooth found far out in the Pacific Ocean (Pollerspöck *et al.*, 2023). Under these considerations, it is more plausible that temperature changes were not the main factor affecting their survival, although other abiotic factors related to climate change, such as sea-level changes, could have been of more importance (see Pimiento *et al.*, 2017). Regardless, biotic factors, such as prey availability and competition with other predators, may have played a more fundamental role in the extinction of megalodon. The presence of marine mammal remains within the same faunal assemblages where †*O. megalodon* remains have been recovered, along with signs of predation by this shark (see Purdy, 1996; Godfrey & Altman, 2005; Aguilera *et al.*, 2008; Kallal *et al.*, 2012; Antunes *et al.*, 2015; Carrillo-Briceño *et al.*, 2016; Collareta *et al.*, 2017a; Godfrey *et al.*, 2018, 2021; Godfrey & Beatty, 2022), has led to the inference that this group of mammals may have constituted an important part of its diet. Consequently, the decreasing diversity of marine mammals towards the late Miocene (see Allmon, 2001; Marx & Uhen, 2010), likely resulted in a reduction of trophic resources for megalodon populations. Additionally, the emergence and diversification of novel competitors during the Middle Miocene, such as macrophagous sperm whales (see Lambert *et al.*, 2010), or first killer whales (*Orcinus*) (Lindberg & Pyenson, 2006) and white shark (*Carcharodon carcharias*) in the Pliocene (Ehret *et al.*, 2012), could have contributed to the extinction

of †*O. megalodon*. *C. carcharias* is the largest extant macrophagous lamniform and the only extant lamniform with serrated teeth (Shimada, 2002, 2019). Its dental morphology (see Cappetta, 2012), the studies based on stomach contents (e.g., Bruce, 1992; Hussey *et al.*, 2012; Grainger *et al.*, 2020), *in situ* observations of predation (e.g., Taylor *et al.*, 2013) and scavenging events (e.g., Fallows *et al.*, 2013), evidence *C. carcharias* feed on marine mammals. In addition to feeding interactions between Pliocene representatives of the genus *Carcharodon* and cetaceans have been found in the fossil record (Ehret *et al.*, 2009). These features led to considering the white shark as the closest extant ecological analogue of †*O. megalodon* and, therefore, one of its main possible competitors. The calcium and nitrogen isotopic analyses revealed that †*O. megalodon* occupied a higher trophic level than *C. carcharias*, implying differences in the trophic proclivities of both species (Martin *et al.*, 2015; Kast *et al.*, 2022). One suggested explanation is a potential ontogenetic dietary shift, as observed in other extant shark species (e.g., Tricas & McCosker, 1984; Lowe *et al.*, 1996; Ebert, 2002; Newman *et al.*, 2012). Consequently, competition may arise between adult individuals of *C. carcharias* and juvenile populations of †*O. megalodon* (Boessenecker *et al.*, 2019). In this regard, the zinc isotope values reported in McCormack *et al.* (2022), which includes some juvenile teeth of †*O. megalodon* (see supplementary data of McCormack *et al.* 2022), found similar values for the trophic position of both sharks. Regardless of discrepancies in isotopic analyses, both *C. carcharias* and †*O. megalodon* would be apex predators within marine communities and are expected to exhibit some degree of dietary overlap. Dental microwear analyses refers to micro-meter scale wear indentations, that result from dietary abrasiveness and feeding events (Romero & De Juan, 2012). Therefore, the quantification of microwear signatures allows the inference about the type of food ingested and aspects of masticatory biomechanics (see Gordon, 1988). The earliest studies in dental microwear analysis, beginning in the 1950s, utilized a qualitative approach based on optical light microscopy (Butler, 1952; Mills, 1955; Baker *et al.*, 1959). By the late 1970s, the preferred method shifted to Scanning Electron Microscopy (SEM) (2D approach), which allowed for quantitative analysis of enamel surface features by SEM micrographs. This advancement enabled researchers to investigate the relationship between diet and microwear patterns, especially in early hominins (Grine, 1977, 1986; Rensberger, 1978; Walker *et al.*, 1978). Since the early 2000s, particularly following the works of Grine *et al.* (2002) and Semprebon *et al.* (2004), dental microwear texture analysis techniques (DMTA) (3D approach) began to be employed (Scott *et al.*, 2005, 2006; Ungar *et al.*, 2003). Unlike analysis using SEM micrographs, DMTA employs a scanning white light confocal microscope and scale-sensitive fractal analysis. Although the

preferred technique currently is DMTA, a comparison between 2D tooth microwear and DMTA revealed the effectiveness of both methods for dietary discrimination in other groups of aquatic vertebrates (Purnell *et al.*, 2012). In fact, both techniques have demonstrated to be useful tools for inferring dietary proclivities in extant and extinct vertebrates: mammals (e.g., Teaford & Robinson, 1989; Merceron *et al.*, 2004; Adams *et al.*, 2020; Rivals *et al.*, 2022); dinosaurs (e.g., Barrett, 2001; Williams *et al.*, 2009; Ósi *et al.*, 2022); reptiles (e.g., Bestwick *et al.*, 2019; Winkler *et al.*, 2019; Gere *et al.*, 2021); and bony fishes (e.g., Purnell *et al.*, 2006, 2007, 2012, 2013; Purnell & Darras, 2015). More recently, DMTA has been applied both on extinct (McLennan, 2018) and current sharks (McLennan & Purnell, 2021), showing the potential of dental microwear analysed as a tool for understanding dietary proclivities in elasmobranchs. More specifically, McLennan (2018) found non significant differences between dental microwear texture analyses of †*O. megalodon* and *C. carcharias*, suggesting similar dietary trends and a possible direct competition between both species. However, these results are based on data from the Gulf of Mexico and Central Western Atlantic and there could be differences in other basins. Therefore, incorporating information from other geographical locations would be of interest.

With the aim of providing information on the dietary proclivities of *C. carcharias* and †*O. megalodon*, we use the 2D-SEM approach to analyse the dental microwear of *C. carcharias* from the Pliocene of Guardamar del Segura (Alicante, Spain) and †*O. megalodon* teeth from the Miocene of Ferriol (Alicante, Spain) and Vallongas (Alicante, Spain).

MATERIAL AND METHODS

For the possibility of conducting the microwear feature counting, we have examined previously the following samples: (1) Six teeth of *C. carcharias* from the Early Pliocene (5.33–3.60 My) fossil locality near Guardamar del Segura (Alicante, Spain) (Soria *et al.*, 2005; Adnet *et al.*, 2010); (2) Eight teeth of †*O. megalodon* from the Late Miocene (5.33–11.63 My) fossil locality close to Ferriol (Alicante, Spain) (García-Sanz *et al.*, 2023); and (3) two teeth of †*O. megalodon* from the Miocene (5.33–23.03 My) fossil locality Vallongas (Alicante, Spain). Finally, the total sample is comprised by six *C. carcharias* teeth and ten †*O. megalodon* teeth (see Tab. 1) since they had retained a well-preserved pattern. The specimens are housed in the Museo Paleontológico de Elche (MUPE) (Alicante, Spain). High-resolution casts of the whole crowns were made using President microsystem Affinis® Regular body (Coltène-Whaledent®) polyvinylsiloxane. Replicas were then produced from moulds using two-base component epoxy resin EPO 150 (CTS®, Spain) and following established procedures (Galbany *et al.*, 2005). Epoxy casts were examined by SEM Hitachi

S-4800 at 5 kV in Secondary Electron (SE) emission mode. All micrographs were taken at standardised magnification of 1000× following previous protocols (Purnell *et al.*, 2006). SEM micrographs were taken from the first third of crown of each tooth in their labial face. Individual scratches, (*i.e.*, a linear structure four times longer than its width) were counted and measured (μm), as well as registered their slope in the micrographs. Dental microwear analysis (Purnell *et al.*, 2006) on non-occlusal teeth of bony fishes indicated that scratch density (mean number of features per mm^2), scratch length (μm), and mean vector length ($= R$) were the most significative variables to detect proclivity dietaries. Therefore, these three microwear variables were considered: 1) Mean Length of Scratches (MLS); 2) Mean Density of Scratches (MDS); and 3) Mean vector length (R), that provides a measure of angular dispersion (Zar, 1999). Microwear metrics were counted and measured using SigmaScan ProV (SPSS™ v.15) by a single observer (MVP-A) to mitigate interobserver effects (Galbany *et al.*, 2005; Purnell *et al.*, 2006).

Data were first explored using the Kolmogorov-Smirnov test ($p > 0.05$), which showed that tooth microwear variables were normally distributed. On the base of this data, a Principal Component Analysis (PCA) was carried out in R. 4.3.0. Using R 4.3.0 a t-test was performed to assess if the variables differed significantly between *C. carcharodon* and †*O. megalodon*. The significance level was set at $\alpha = 0.05$.

Remarks on the method

Taphonomic processes, as well as cleaning, preparation and moulding of fossil specimens (*i.e.*, *post-mortem* processes) may produce alterations of dental microwear patterns. Experimental studies (e.g., Gordon, 1983, 1984; Puech *et al.*, 1985; Teaford, 1988; Maas, 1994; King *et al.*, 1999; Martínez & Pérez-Pérez, 2004; Romero & De Juan, 2012; Böhm *et al.*, 2019; Uzunidis *et al.*, 2021; Weber *et al.*, 2021, 2022) evidence that *post-mortem* alterations are visually distinguishable from *ante-mortem* ingestion-related wear features. Moreover, *post-mortem* processes rarely can overlap dental microwear pattern (King *et al.*, 1999; Böhm *et al.*, 2019; Weber *et al.*, 2021). Nevertheless, it is important to consider the possible *post-mortem* alteration that they may have undergone. Consequently, we made a first examination under the SEM to discard from the analyses those teeth with a high number of *post-mortem* features identified. This procedure has been followed by comparing with previous experimental studies (e.g., Gordon, 1983, 1984; Puech *et al.*, 1985; Teaford, 1988; Maas, 1994; King *et al.*, 1999; Martínez & Pérez-Pérez, 2004; Romero & De Juan, 2012; Böhm *et al.*, 2019; Uzunidis *et al.*, 2021; Weber *et al.*, 2021, 2022). Finally, only well-preserved dental microwear patterns have been considered for the analyses.

RESULTS

The t-test showed that there are not significant differences between the variables defined for the analysis of dental microwear pattern of †*O. megalodon* and *C. carcharias* (see Fig. 1A). Descriptive statistics for the groups are provided in Table 2. Individual microwear values are provided in Table 3.

On the PCA diagram (Fig. 1B), the area, formed by connection of marginal points for *C. carcharodon*, overlaps partially with the area formed by †*O. megalodon*. The two first components (PC1-2) with eigenvalues greater than one account for 81.80% of total variance. The PC1 (54.12%) was mainly correlated with the mean length of scratches and the mean vector length with a positive loading for both variables. Therefore, †*O. megalodon* appear to show longer scratches than *C. carcharias*. Instead, the PC2 (27.67%) captured mainly the density of scratches with a positive load. In this regard, the morphospace made by *C. carcharias* spread more extensively than †*O. megalodon*.

DISCUSSION

The extant great white shark not only preys on marine mammals but also incorporates other food items into its diet, such as fish and marine reptiles, birds, other elasmobranchs and even some invertebrates (e.g., Compagno, 1984; Cortés, 1999; Fergusson *et al.*, 2000; Johnson *et al.*, 2006; Clark *et al.*, 2023). Assuming a similar behaviour for its Pliocene representatives, the absence of significant differences in the dental microwear pattern between this species and †*Otodus megalodon* (Fig. 1A) suggests a similar wide spectrum of prey items, and analogous trophic ecologies. This hypothesis supports previously suggested ideas that the extinct megatooth shark would be a generalist, feeding on marine mammals, other elasmobranchs, bony fish, and marine reptiles (Carillo-Briceño *et al.*, 2016; Landini *et al.*, 2017). Typical of the extant *C. carcharias* (Hussey *et al.*, 2012) and other large predatory fish (Scharf *et al.*, 2000; Bornatowski *et al.*, 2014; Ferreira *et al.*, 2017), †*O. megalodon* could have developed an asymmetric feeding behaviour. For instance, the diet of smaller great white sharks is mainly composed of teleosts and other elasmobranchs, but as they grow, marine mammals gradually assume greater importance in their diet, while the consumption of the aforementioned prey items remains (Cliff *et al.*, 1989; Lowe *et al.*, 2012; Werry *et al.*, 2012; Curtis *et al.*, 2014). Among adult members of the species, smaller-sized individuals are observed actively and frequently preying on pinnipeds and small cetaceans, whereas larger individuals show preferences toward scavenging events on huge, fat-rich mysticete carcasses (Arnold, 1972; Long & Jones, 1996; Hussey *et al.*, 2012). Additionally, carrion has also been recorded as an important food source for other large macrophagous

shark species (Smith & Baco, 2003; Smith *et al.*, 2015; Aguzzi *et al.*, 2018; Lea *et al.*, 2018; Tucker *et al.*, 2019; Silva *et al.*, 2021). Considering this, along with the estimated size for †*O. megalodon* (15–20 m) (Pimiento & Balk, 2015; Pérez *et al.*, 2021; Shimada, 2019; Shimada *et al.*, 2021, 2023), larger individuals are likely to scavenge carcasses more frequently than smaller ones (Collareta *et al.*, 2017a). Unlike extant populations of *C. carcharias*, it seems unlikely that large mysticetes served as the primary source of carrion for Miocene megatooth sharks, as the maximum increase in body size of these marine mammals did not occur until the late Pliocene and Pleistocene (Bisconti *et al.*, 2023). Based on fossil evidence of bite marks and physeteroid distribution during the Miocene, it has been suggested that †*O. megalodon* and other sharks actively exploited the carcasses of these marine mammals as a source of fat (Benites-Palomino *et al.*, 2022). However, carrion is an unpredictable trophic resource as it is only sporadically available in marine ecosystems (Nowlin *et al.*, 2008), so relying on scavenging as the primary food source to sustain the high energy requirements suggested for megalodon (Cooper *et al.*, 2022) seems unlikely. Therefore, †*O. megalodon* would have to actively prey on marine mammals.

Although previous studies have described putative nursery areas for †*O. megalodon* in Miocene deposits from Spain (Herraiz *et al.*, 2020), to date, no additional nursery areas have been described for †*O. megalodon* in the deposits to which the studied teeth belong (see Tab. 1). In addition, with only ten individual teeth of †*O. megalodon* and six teeth of *C. carcharias*, a population size study is not reliable and goes beyond the objectives of the present study. We lack a sufficient sample size to make inferences in an accurate way and undertake robust statistical analyses, despite previous studies using similar or even smaller sample sizes. Hence, no population size-based study groups have could be

Table 1. Final sample selected for Dental Microwear Analyses.

Serie	Age	Fossil locality	Specie	Specimen number
Pliocene	early Pliocene	Guardamar del Segura (Alicante, Spain)	<i>Carcharodon carcharias</i>	CV-4010
				CV-4011
				CV-4236
				CV-4506
				CV-6604
				CV-6626
				CV-5944
				CV-5945
				CV-6186
				CV-6214
Miocene	Tortonian	Ferriol (Alicante, Spain)	<i>Otodus megalodon</i>	CV-6615
				CV-6622
				CV-6624
				CV-6625
				CV-5671
-		Vallongas (Alicante, Spain)	<i>Otodus megalodon</i>	CV-5672

established in this work. However, the greater variance found for the scratch length in *O. megalodon* (Tab. 2; Fig. 1) raises the need for future studies, increasing the sample size and inferring the size of individuals. Since we cannot rule out that this is a consequence of intra-specific variability among individuals of similar sizes, or it is due to differences in individual sizes. Although no significant difference has been found in the dental microwear pattern of both species (Tab. 2), a slight trend towards a higher density of shorter marks in the great white shark is observed. It is likely

due to a tendency towards a slightly more abrasive diet, where the hard items produce greater density of scratches than softer preys (e.g., Purnell *et al.*, 2006; Fahlke *et al.*, 2013). Including a higher proportion of marine reptiles (e.g., turtles) or elasmobranchs, whose dermal denticles are hypermineralised, could result in increased abrasiveness on the dental surface of *C. carcharias*. The interaction of the teeth with the mineralized endoskeleton tissues of marine mammal, could also lead to a higher density of microwear features. Nevertheless, it appears unlikely that *C. carcharias*

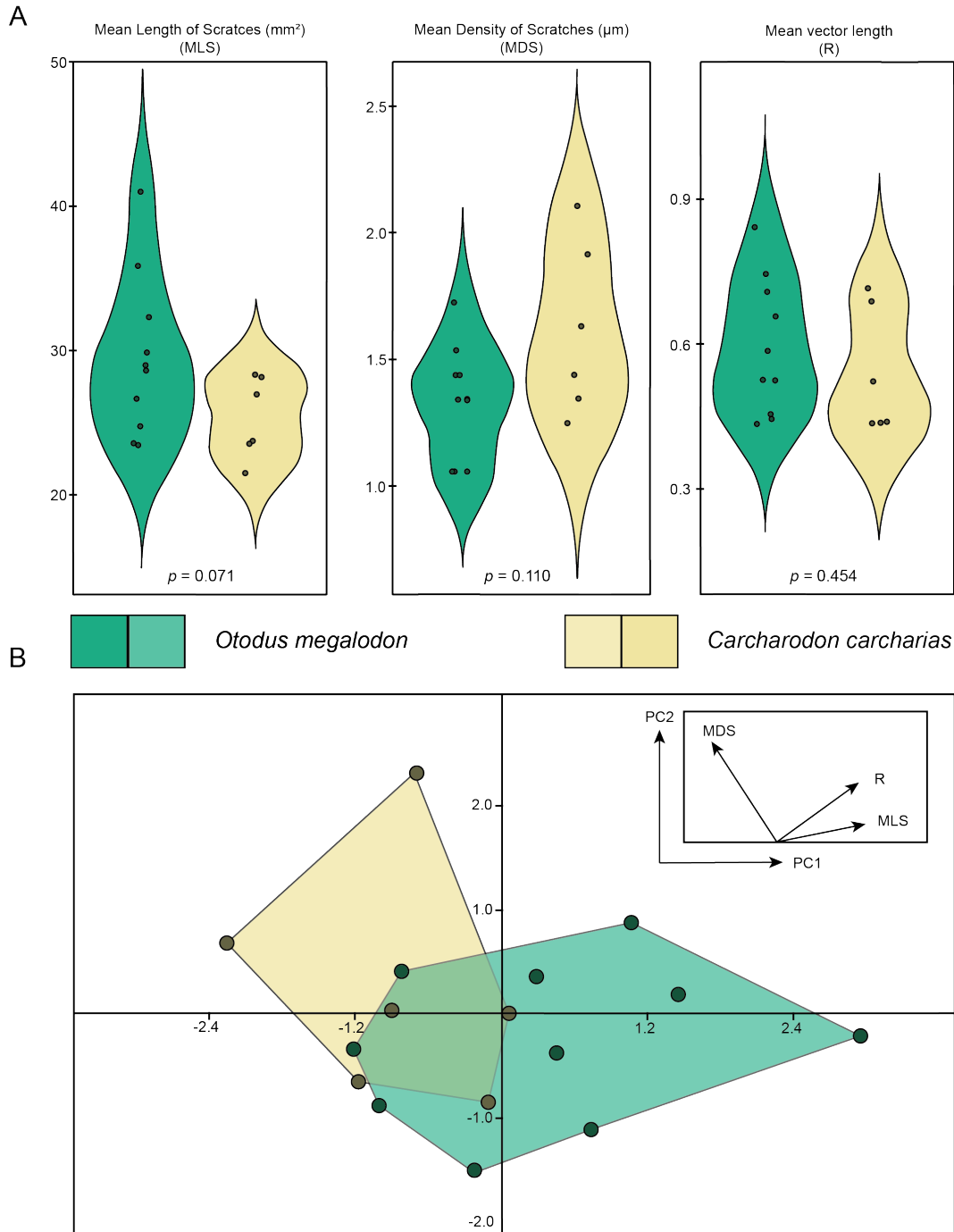


Figure 1. A, Violin plot for the variables analysed in the dental microwear of *Otodus megalodon* y *Carcharodon carcharias*. The *p-value* is indicated for each variable; **B**, Principal Component Analysis based on the employed variables. Value for PC1 and PC2 is 54.12% and 27.67%, respectively. The arrows show the loading scores for each dental microwear variable on the PCA.

would demonstrate a stronger inclination towards these items compared to *†O. megalodon*, as isotopic analyses of calcium and nitrogen indicate a slightly higher trophic position for *†O. megalodon* (Martin *et al.*, 2015; Kast *et al.*, 2022). Furthermore, marine mammals contribute less than other elasmobranchs to the diet of extant populations of *C. carcharias* (Cortés, 1999). This suggests that *†O. megalodon* could have had a greater interaction with marine mammal populations, as reflected in the increase in the size of baleen whales following its extinction (Pimiento & Clements, 2014; Cooper *et al.*, 2022). Conversely, *C. carcharias* may have had a greater interaction with populations of other elasmobranchs. Nevertheless, the lack of comparison with extant representatives does not allow us to discern which items from the suggested dietary range could be causing this slight increase in abrasiveness in the great white shark.

A potential biotic factor in the extinction of *†O. megalodon* is the competition with other marine raptorial macropredatory taxa, with large odontocetes being classically considered competitors (Pimiento *et al.*, 2016, and references therein). Also of special importance is the emergence of morphologically recognisable modern *Carcharodon* dental remains on the Mio-Pliocene fossil record (Ehret *et al.*, 2009, 2012; Pimiento *et al.*, 2016; Collareta *et al.*, 2023a). Both *C. carcharias* and *†O. megalodon* are species

considered analogous from an ecological perspective (see Introduction, Pimiento & Balk, 2015; Pimiento *et al.*, 2010, 2017; Herraiz *et al.*, 2020; Cooper *et al.*, 2020, 2022) and are apex predators occupying higher trophic levels (Martin *et al.*, 2015; Kast *et al.*, 2022; McCormack *et al.*, 2022). These facts, combined with evidence from the fossil record (Purdy, 1996; Godfrey & Altman, 2005; Aguilera *et al.*, 2008; Kallal *et al.*, 2012; Antunes *et al.*, 2015; Carrillo-Briceño *et al.*, 2016; Collareta *et al.*, 2017a; Godfrey *et al.*, 2018, 2021; Godfrey & Beatty, 2022), have led to propose that both species could compete for the same trophic resources. The absence of significant differences in the dental microwear pattern between *†O. megalodon* and *C. carcharias* suggests a similar dietary trend (see Fig. 1; Tab. 2). Similar results have found for the *†O. megalodon* and *C. carcharias* from the Gulf of Mexico and Central Western Atlantic (see McLennan, 2018). Although these findings could support previous hypotheses of potential trophic competition between *†O. megalodon* and *C. carcharias* (Pimiento *et al.*, 2016, and references therein), it is important to consider that dietary trends may vary as consequence of ontogeny, which may not be detectable in this study. In addition, further studies with additional samples and a higher number of individuals from the same fossil sites are required.

Nonetheless, competition only occurs if the resource shared by coexisting species is limited (Hutchinson, 1957; MacArthur, 1958), and areas where multiple shark species with comparable habits and morphology coexist show some niche partitioning and different use of space by subordinate competitors (Weideli *et al.*, 2023). Therefore, during the period of coexistence of both shark predators, a decrease in the availability of one or several dietary resources must have occurred. During the late Miocene and throughout the Pliocene, there was a decline in the diversity of marine mammal groups (Marx & Fordyce, 2015; Pimiento *et al.*, 2017), particularly small to medium-sized whales (2.5–7 m) (Lambert *et al.*, 2010). Probably, a decrease in the abundance of these marine mammals could have led to *C. carcharias* competing with *†O. megalodon*. However, it has been suggested that *†O. megalodon* preyed on larger marine mammals (see McLennan, 2018; Cooper *et al.*, 2022). Although our results do not allow us to infer the size of the prey, it seems likely that the larger size of *†O. megalodon* could have enabled it to actively prey on marine mammals not accessible to *C. carcharias*. While it is true that this could have minimized competition with *C. carcharias*, the possibility that it competed with other large macropredatory sharks, such as *†Carcharodon hastalis* or *†Parotodus benedenii* (Noriega *et al.*, 2007; Collareta *et al.*, 2017b, 2023b; McLennan, 2018), with which it coexisted, cannot be ruled out. During this time, a reduction in the diversity of marine mammals is noted, and previous studies have demonstrated a high trophic level of elasmobranchs for this period (Kast *et al.*, 2022; McCormack *et al.*, 2022).

Table 2. Summary descriptive for groups studied.

Group		MLS	MDS	R
<i>Otodus megalodon</i>	Mean	29.454	1.339	0.596
	Standard Deviation	5.706	0.225	0.138
<i>Carcharodon carcharias</i>	Mean	25.25	1.621	0.543
	Standard Deviation	2.852	0.341	0.128

Table 3. Individual microwear values for the specimens analysed.

Specie	Museum number	Mean Length of Scratches (MLS)	Mean Density of Scratches (MDS)	R
<i>Otodus megalodon</i>	CV-5671	32.322	1.348	0.530
<i>Otodus megalodon</i>	CV-5672	35.860	1.348	0.840
<i>Otodus megalodon</i>	CV-5944	29.816	1.733	0.713
<i>Otodus megalodon</i>	CV-5945	23.275	1.348	0.459
<i>Otodus megalodon</i>	CV-6186	26.561	1.445	0.459
<i>Otodus megalodon</i>	CV-6214	28.656	1.445	0.585
<i>Otodus megalodon</i>	CV-6615	24.650	1.541	0.534
<i>Otodus megalodon</i>	CV-6624	23.439	1.059	0.436
<i>Otodus megalodon</i>	CV-6625	28.907	1.059	0.658
<i>Otodus megalodon</i>	CV-6622	41.148	1.059	0.442
<i>Carcharodon carcharias</i>	CV-4010	26.875	1.252	0.525
<i>Carcharodon carcharias</i>	CV-4011	28.050	2.119	0.689
<i>Carcharodon carcharias</i>	CV-4236	28.228	1.637	0.862
<i>Carcharodon carcharias</i>	CV-4506	23.404	1.348	0.715
<i>Carcharodon carcharias</i>	CV-6604	26.622	1.445	0.444
<i>Carcharodon carcharias</i>	CV-6626	21.344	1.926	0.442

CONCLUSIONS

The similarity in dental microwear patterns between the Pliocene *Carcharodon carcharias* and Miocene *Otodus megalodon* suggests a comparable trophic spectrum that would include marine mammals, fish, marine reptiles, invertebrates, and other elasmobranchs. This supports the notion that megalodon was a generalist that could compete with the white shark for trophic resources.

Although no significant difference is found in the dental microwear pattern of both species, a slight trend towards a higher density of shorter scratches in the great white shark is noted. This could be attributed to a slightly more abrasive diet, possibly including a higher proportion of marine reptiles or elasmobranchs in its diet. Consequently, we propose further studies including analyses of dental microwear pattern on extant elasmobranchs with well-known diets.

In summary, the Miocene *O. megalodon* and the Pliocene *C. carcharias* exhibited a similar dietary trend in the Mediterranean Sea. However, we cannot rule out ontogenetic dietary trends, as well as the possible pre-existing trophic competition with other large sharks such as *C. hastalis* or *Parotodus benedenii*. Additional research is required to delve deeper into these dynamics and explore potential factors contributing to the extinction of *O. megalodon*.

Supplementary information. This article has no additional data.

Author contributions. MVP-A and JLH conceptualised the study. MVP-A carried out the methodology and statistical analyses. JLH and MVP-A prepared the figures. The manuscript was written by MVP-A and JLH. All authors reviewed the manuscript.

Competing interest. The authors declare no competing interests.

Funding. This study has been funded by “Ayudas a la Investigación de la Sociedad Española de Paleontología” AJISEP 2022 to MVP-A, and AYUDAS ATRACCIÓN TALENT UV.

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Acknowledgements. We would like to express our gratitude to the entire team at the MUPE museum, especially Dr Ainara Aberasturi. We also appreciate the reviewers and the editorial team at the SJP. The study of fossil collections was conducted under the authorization of the Conselleria de Cultura i Esport de la Generalitat Valenciana (file: A-2023-0716).

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