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The Iberian fossil record of †*Otodus megalodon* rejects Mediterranean dwarfism and supports nursery use

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†*Otodus megalodon*, the largest known macropredatory shark, was globally distributed from the Miocene to Pliocene, yet most ecological and palaeobiological inferences rely heavily on American collections. This geographical bias limits understanding of its population structure and life-history strategies elsewhere. Two explanations have been proposed for its body-size patterns: a Bergmann-type cline, with larger individuals at higher, cooler latitudes and a related hypothesis of Mediterranean dwarfism; and the influence of localized nursery areas that generate assemblages dominated by small juveniles, as documented in several American sites and the Reverté quarries in the western Mediterranean. Here, we present the first extensive dataset outside the Americas designed to test these alternatives across two adjacent basins. Body-size estimates show no significant difference between Atlantic and non-Reverté Mediterranean populations, whereas the Reverté assemblage is smaller. This pattern contradicts basin-wide Mediterranean dwarfism and does not support a Bergmann-type size–latitude relationship. Instead, it strongly indicates a localized nursery at Reverté. More broadly, the results align with an emerging view of widespread nursery habitats in †*O. megalodon*, comparable to those of extant sharks. By filling a key regional gap, the Iberian record provides tests of competing hypotheses and refines understanding of †*O. megalodon* population structure and life history.

1. Introduction

Apex predatory sharks play a central role in structuring marine ecosystems [1–4], yet their evolutionary dynamics, and extinction and diversification drivers remain poorly constrained in the fossil record despite the relative abundance of fossil teeth [5–7]. †*Otodus megalodon*, the largest macropredatory shark in Earth's history, reached estimated lengths exceeding 15 m [8–11]. Despite its iconic status, debate persists over its maximum body size, ecological role and the strategies that underpinned its evolutionary success before its extinction by the end of the Pliocene [12,13]. One possible explanation for this success is the use of nursery habitats—geographically discrete, shallow and productive areas that host high relative abundances of juveniles, which repeatedly return to these sites for food and protection—widely regarded as essential for maintaining shark population sustainability [14–16]. Such habitats are widespread among modern sharks [14,17–20] and have been hypothesized for †*O. megalodon* at several fossil sites [21,22]. However, more recently, Shimada *et al.* [23] have questioned whether assemblages dominated by small individuals represent nurseries or instead reflect body-size variation explained by Bergmann's rule. According to this ecogeographical rule, body size in widely distributed species or clades correlates with temperature and latitude, with larger sizes typically occurring in cooler environments [24–28]. Resolving this debate is essential for understanding †*O. megalodon*'s life history and its ecological strategies as a global apex predator.

Although †*O. megalodon* was globally distributed across warm seas during the Miocene and Pliocene [29,30], ecological and palaeobiological studies have relied disproportionately on abundant American collections. Classic assemblages from the Calvert and Temblor formations (USA), the Pisco Formation (Perú), the Gatún and Chucunaque formations (Panamá), the Bahía Inglesa Formation (Chile) and the Yorktown and Bone Valley formations (USA) underpin most current hypotheses [21,23]. This geographical bias obscures patterns in other regions and limits our ability to test global models of population structure, nursery use and body-size evolution. A notable exception beyond the Americas is the recently described Mediterranean assemblage from the Middle Miocene Reverté quarries, a set of Langhian outgroup localities in northeastern Spain. Analysis of the teeth reveals a bimodal body size distribution, with a dominant peak of small juveniles and a minor peak of large adults. Kernel probability density estimates further support this pattern, consistent with interpreting the Reverté quarries as a nursery locality [21]. However, Shimada *et al.* [23] proposed an alternative interpretation, suggesting that Mediterranean populations may represent instances of insular dwarfism. In this view, the relative isolation of the Mediterranean and Paratethys basins imposed long-term ecological constraints, with smaller body sizes reflecting these pressures rather than localized nursery behaviour.

The Iberian Peninsula is a key region for evaluating these competing ideas due to its strategic position between the Atlantic and Mediterranean basins, coupled with the Mediterranean's complex palaeogeographic history—including the Messinian Salinity Crisis and subsequent Zanclean flooding—which created fluctuating connections with the Atlantic and the potential to shape distinct †*O. megalodon* population dynamics [31–34]. If the dwarfism hypothesis [23] is correct, no significant body-size differences should exist among Mediterranean localities—including Reverté—but clear contrasts should emerge with Atlantic occurrences. In contrast, if the nursery hypothesis is correct, Reverté should differ from both Atlantic and other Mediterranean assemblages, while the latter two should be indistinguishable from one another [11,35].

Recent isolated finds in Spain and Portugal highlight the region's importance and its potential to contribute to this debate [36–42], but no comprehensive dataset has yet been assembled to test these expectations. Here we present the first large-scale dataset of †*O. megalodon* teeth outside the Americas: 335 specimens recovered from outcrops with either Mediterranean or Atlantic affinities. This record enables us to directly test the predictions of the dwarfism *versus* nursery hypotheses, to evaluate body-size variation across Atlantic and Mediterranean populations and to clarify the ecological significance of the Reverté assemblage. By filling a critical geographical gap, our study rebalances the heavily American-centred view of †*O. megalodon* and establishes the Iberian fossil record as an essential resource for reconstructing the population structure, life history, and ecology of this iconic apex predator.

2. Material and methods

A total of 335 †*O. megalodon* teeth were examined to compile the database, primarily through direct or photographic study of specimens housed in multiple Iberian institutions, supplemented by bibliographic review [43,44], to identify additional material for potential inclusion (electronic supplementary material, figure S1 and datas S1, S2). Although the exact localities of some specimens were unknown, all teeth could be assigned to sedimentary basins with known Mediterranean or Atlantic affinities, providing sufficient resolution for the purposes of this study. Portuguese collections included the Lisbon Academy of Sciences Museum, Laboratório Nacional de Energia e Geologia, Lourinhã Museum, Museu de História Natural de Lisboa and Observatório Vulcanológico e Geotérmico dos Açores. Spanish collections included the Museu del Cau del Tauró de l'Arboç, Museu de Ciències Naturals de Barcelona, Museu de Geologia del Seminari de Barcelona, Centre de Geologia de Menorca, Museu de Ciències Naturals de Mallorca, Universidad de Huelva (RNM293 Group), Museo de Ciencias Naturales de Madrid, El Paleontològic-Museo de Colecciones Naturales, Museo de Historia Natural de la Universitat de València, Museo Paleontológico de Elche, Museo Obulco de Porcuna, Museo de La Carolina, Universidad de Jaén and Universidad de Las Palmas de Gran Canaria (figure 1).

(a) Measurements and body-size estimation

Each tooth was assessed for preservation and assigned to one of five categories: (1) complete or nearly complete; (2) minor apical or root damage; (3) major but interpretable damage; (4) heavily damaged with significant portions missing; or (5) small fragments unsuitable for analysis (electronic supplementary material, figure S1). Only specimens in categories 1–3 were considered for metric analyses to ensure measurement reliability. Teeth were morphologically compared with published reference material to assign tentative jaw positions [9,22,45,46]. Again, to avoid overestimation biases associated with lateral and posterior teeth [10], only upper and lower anterior teeth were used in size analyses. Crown height was measured and converted into estimated total body length using regression equations developed for *Carcharodon carcharias* (table 1) by Shimada [47], following the protocol of Pimiento *et al.* [22]. When possible multiple tooth positions were assigned to a specimen, an average of the length estimation for each possible position was used for the analyses.

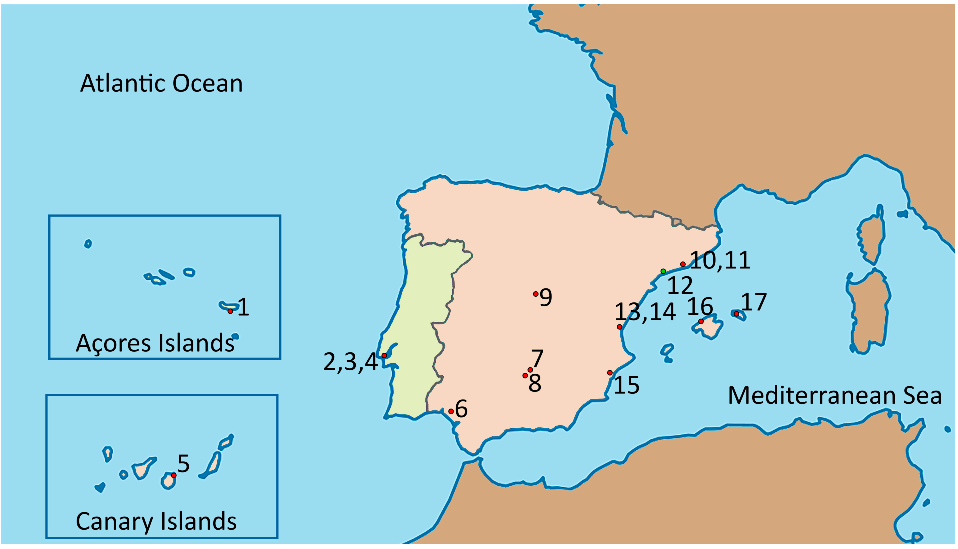

Figure 1. Institutions from where the specimens were compiled into the database. Observatorio Vulcanológico e Geotérmico dos Açores (1), Laboratório Nacional de Energia e Geologia (2), Museo Décio Thadeu, Universidade de Lisboa (3), Museu Nacional de História Natural e da Ciência (4), Universidad de Las Palmas de Gran Canaria (5), Universidad de Huelva (6), Museo de La Carolina (7), Universidad de Jaén (8), Museo Nacional de Ciencias Naturales (9), Museu de Geologia del Seminari de Barcelona (10), Museu de Ciències Naturals de Barcelona (11), Museu Cau del Tauró (12), Museo Universitat de València Historia Natural (13), El Paleontològic-Museo de Colecciones Naturales (14), Museo Paleontológico de Elche Fundación Cidaris (15), Museu Balear de Ciències Naturals (16) and Centre de Geologia de Menorca (17). The location of the previously described nursery is marked by a circle.

Table 1. Linear regression equations for specific tooth positions in *C. carcharias*, extracted from Shimada [47]. TL, estimated total body length; CH, crown height.

dental position	upper jaw	lower jaw
A1	TL = 5.234 + 11.522*(CH)	TL = −8.216 + 14.895 *(CH)
A2	TL = −2.160 + 12.103*(CH)	TL = −7.643 + 13.597*(CH)
I1	TL = 19.162 + 15.738*(CH)	TL = −10.765 + 17.616*(CH)
L1	TL = 5.540 + 14.197*(CH)	TL = 9.962 + 17.437*(CH)
L2	TL = 4.911 + 13.433*(CH)	TL = 1.131 + 19.204*(CH)
L3	TL = 0.464 + 14.550*(CH)	TL = −30.947 + 25.132*(CH)
L4	TL = 5.569 + 17.658*(CH)	TL = −51.765 + 35.210*(CH)
L5	TL = −5.778 + 26.381*(CH)	TL = −73.120 + 55.262*(CH)
L6	TL = −71.915 + 50.205*(CH)	TL = −117.456 + 96.971*(CH)
L7	TL = −48.696 + 69.292*(CH)	TL = −64.732 + 138.350*(CH)
L8	TL = −84.781 + 104.968*(CH)	TL = −137.593 + 231.411*(CH)
L9	TL = −62.050 + 142.142*(CH)	

(b) Chronological and geographical grouping

Specimens were assigned stratigraphic ages (Lower, Middle and Upper Miocene, and Pliocene) based on a review and update of the corresponding institutional records. For statistical purposes, however, all specimens were grouped by oceanic basin—Atlantic *versus* Mediterranean—regardless of age, which is a common practice in the field when temporal resolution is limited (e.g. [48]). This decision was made to maximize sample size and because body-size stasis has been demonstrated for †*O. megalodon* throughout its entire stratigraphic range [46]. Specimens from southern Spain (Guadalquivir Basin and post-orogenic basins), representing a transitional corridor between Atlantic and Mediterranean, were excluded due to uncertain affinity. The Middle Miocene Reverté quarry assemblage, interpreted as a potential nursery site, was analysed separately from the rest of the Mediterranean sample.

(c) Statistical analyses

From the total dataset, 48 anterior teeth met the selection criteria and were included in statistical analyses: 25 from the Atlantic, 15 from the Mediterranean and 8 from the Reverté site. Body-length distributions were visualized with beanplots [49]. We first assessed groupwise normality with Shapiro–Wilk tests and variance homogeneity with the robust Fligner–Killeen test. Global differences among the three groups were evaluated with Welch's ANOVA (unequal variances) and, non-parametrically, with the Kruskal–Wallis test. Pairwise differences were then tested for all three contrasts—Atlantic versus Mediterranean, Atlantic versus

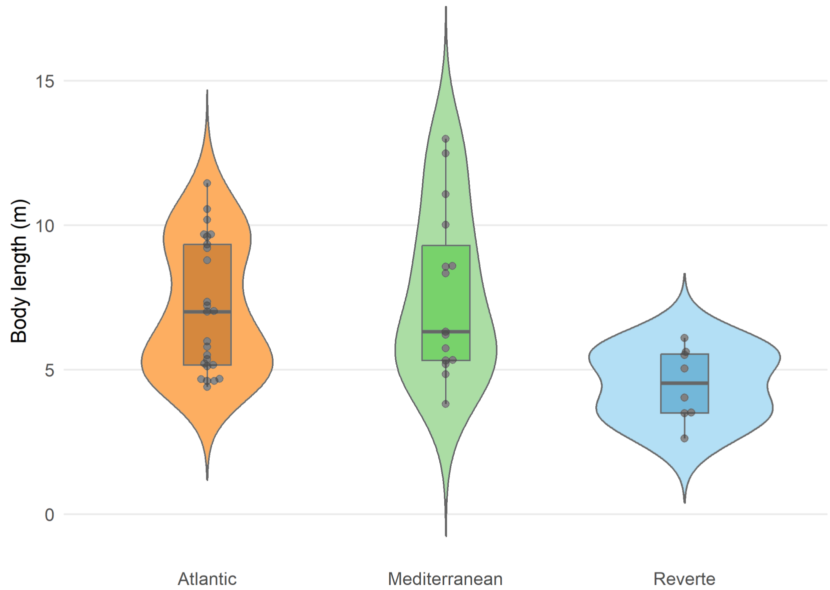

Figure 2. Body-length distribution in †*O. megalodon* populations in the Neogene of Spain and Portugal, beanplots represent the interquartile range (IQR), horizontal lines indicate the median (Atlantic = 7.00; Mediterranean = 6.31; Reverté quarries = 4.54), whiskers extend to 1.5 × IQR, and points represent individual data values. The Reverté quarries represent a population previously described in a potential nursery area [21].

Reverté and Mediterranean versus Reverté—using Welch-style *t*-tests and Wilcoxon rank-sum tests, with Holm correction for multiple comparisons. Descriptive statistics (sample size, mean, standard deviation (s.d.), median, interquartile range and min–max) were computed per group and exported. All analyses were performed in R v. 4.5.1 [50] using base statistics functions, with readxl [51] for data import and ggplot2 [52] for visualization (electronic supplementary material, data S3).

3. Results

The compiled dataset consisted of a total of 335 †*O. megalodon* teeth fragments in different preservation categories: category 1 (n = 43); category 2 (n = 80); category 3 (n = 73); category 4 (n = 97); and category 5 (n = 42). Regarding tooth positions among all categories, 39 upper anterior teeth and 42 lower anterior teeth, 95 upper lateral and 52 lower lateral, 3 posterior and 70 unidentified or unclear teeth were classified in total. Most of the specimens belong to the Middle Miocene (n = 156), whereas samples from the Lower Miocene (n = 53), Upper Miocene (n = 12) and Pliocene (n = 4) are less represented. Specific temporal data were unavailable for 95 fragments. Additional classifications for each category, as well as specimens lacking temporal, geographical or morphological data can be consulted in the full database (electronic supplementary material, data S1).

Body-size distributions for †*O. megalodon* were broadly similar between the Atlantic and the non-Reverté Mediterranean occurrences (means 7.13 m and 7.65 m, ranges 4.40–11.46 m and 3.81–12.99 m, respectively), whereas the Reverté assemblage was markedly smaller (mean 4.49 m, range 2.61–6.09 m; figure 2). Assumption checks indicated partial non-normality for the Atlantic sample (Shapiro–Wilk, W = 0.89099, p = 0.01174), near-normality for the Mediterranean sample (W = 0.9111, p = 0.1408) and no departure from normality for Reverté (W = 0.945, p = 0.639). Group variances did not differ (Fligner–Killeen, χ^2 = 3.85, d.f. = 2, p = 0.146).

Global tests detected overall differences among the three groups (Welch's ANOVA, F = 11.07, p = 0.0004; Kruskal–Wallis, χ^2 = 7.029, p = 0.0142). Pairwise contrasts with Holm correction showed no difference between Atlantic and Mediterranean (Welch t, p = 0.5532; Wilcoxon, p = 0.615). In contrast, Reverté differed significantly from both Atlantic (Welch t, p = 0.0012; Wilcoxon, p = 0.0260) and Mediterranean (Welch t, p = 0.0032; Wilcoxon, p = 0.0260). Collectively, these results indicate comparable body-size structure in Atlantic and non-Reverté Mediterranean populations, while Reverté is significantly size-shifted toward smaller individuals.

4. Discussion

This study provides the most extensive published dataset of †*O. megalodon* teeth from the Iberian Peninsula and one of the largest regional compilations worldwide. Such efforts are particularly valuable given that most ecological and palaeobiological reconstructions of this species have relied on extensive collections from the Americas (e.g. [46]). By integrating 335 specimens from Spain and Portugal, we expand the fossil record beyond the American continent, enabling more balanced cross-continental comparisons and reducing the sampling bias that has long constrained interpretations of †*O. megalodon* ecology and life history.

The Iberian Peninsula offers a uniquely powerful testbed for palaeobiogeographical, ecological, life-history and evolutionary hypotheses in †*O. megalodon* because it spans two adjacent basins—the Atlantic and the Mediterranean—in close geographical contiguity. This side-by-side configuration minimizes potential regional confounds, such as large-scale climatic or environmental differences, and allows a direct assessment of basin effects on body size and population structure. Within this framework,

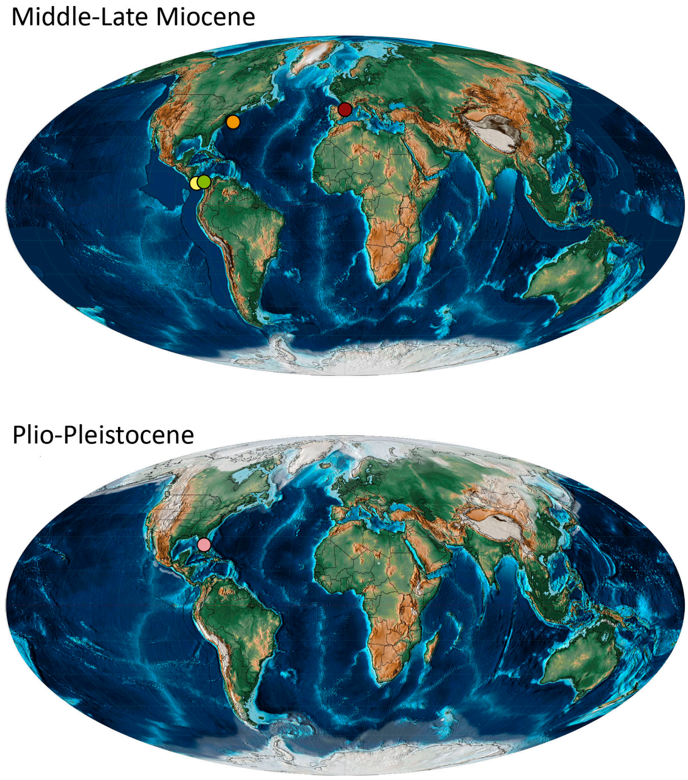

Figure 3. Worldwide distribution of previously described potential †*O. megalodon* nursery areas throughout the Miocene and Pliocene: with the age distribution being: Langhian (Reverté quarries, red circle; Calvert Formation, orange circle), Serravallian–Tortonian (Gatún Formation, yellow circle), Tortonian (Chucunaque Formation, green circle) and Zanclean (Bone Valley, pink circle). Modified from Herraiz *et al.* [21] & Scotese [53].

the Middle Miocene Reverté quarries have been described as a nursery area, complementing other well-documented nurseries from the Americas (figure 3) [21]. Under this view, widespread nursery use across space and time could have been central to †*O. megalodon*'s life history, supporting juvenile survival and contributing to its ecological success. An alternative interpretation invokes Bergmann's rule to explain geographical size variation, specifically proposing that the smaller Mediterranean samples reflect dwarfism rather than localized nursery behaviour [23]. Our Iberian compilation directly evaluates these competing ideas. Mediterranean occurrences excluding Reverté quarries do not differ in body size from the Atlantic, whereas those of Reverté quarries are significantly smaller than both basins. This pattern highlights the uniqueness of Reverté quarries within the Mediterranean and demonstrates that a basin-wide small-body signal does not exist. Consequently, the dwarfism scenario for Mediterranean †*O. megalodon* is refuted by our data, while the Reverté quarries signal is consistent with a localized nursery.

More broadly, our results undermine a Bergmann-type cline in †*O. megalodon*. The Iberian pattern is nursery-driven, not latitudinal: once Reverté is treated as a distinct locality, Atlantic and non-Reverté Mediterranean assemblages show no size shift, while Reverté alone is significantly smaller. Evidence for Bergmann's rule in sharks is limited and mixed (with isolated support in *Mustelus schmitti* [54]), and basin-scale oceanography—currents, productivity regimes and thermal structure—can decouple temperature from latitude, eroding any simple Bergmann expectation [55–57]. In contrast, the repeated occurrence of geographically dispersed nursery assemblages in the Americas and Europe offers a coherent, process-based explanation for the observed size structure and aligns with nursery use as a key reproductive strategy in many extant sharks, including *Carcharodon carcharias* and *Carcharhinus brachyurus*, which employ similar habitats today.

In summary, these data not only expand the global record of †*O. megalodon* but also highlight the reproductive strategies, such as the use of nursery areas, underpinning its evolutionary success. The recognition of a nursery area in the Mediterranean, consistent with patterns observed elsewhere, reinforces the view that juvenile protection and resource availability were central to the species's biology. By bridging a major geographical gap, our dataset provides a stronger foundation for future comparative studies of population dynamics, ecology and extinction in one of the ocean's most iconic predators.

5. Conclusions

This study presents the most extensive compilation of †*O. megalodon* teeth from the Iberian Peninsula, substantially expanding the species's fossil record beyond the Americas. By integrating specimens from numerous institutional collections, we provide one of the most comprehensive datasets available for this taxon.

Our analyses reveal that †*O. megalodo*n populations from the Atlantic and Mediterranean basins share broadly similar body-size distributions once the proposed nursery at the Reverté quarries is excluded. The markedly smaller size of individuals from this locality supports its interpretation as a nursery area, consistent with life-history strategies documented in both fossil and extant sharks.

These results challenge explanations based on Bergmann's rule or simple latitudinal temperature gradients. Instead, they highlight the central role of nursery habitats in shaping †*O. megalodon* population dynamics, offering new insights into the ecological strategies that may have facilitated its Miocene–Pliocene cosmopolitan distribution.

More broadly, this work underscores the importance of assembling and re-examining diverse collections for palaeobiological research. The Iberian dataset provides a critical foundation for future comparative studies across continents and ocean basins, advancing our understanding of †*O. megalodon*'s life history, ecology and biogeographical patterns.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data available from the Figshare repository: https://doi.org/10.6084/m9.figshare.29693333. Supplementary material is available online [58].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.L.H.: conceptualization, data curation, formal analysis, investigation, writing—original draft; H.G.F.: conceptualization, methodology, supervision, writing—review and editing; H.B.: supervision, writing—review and editing; M.R.: data curation, investigation, writing—review and editing; C.M.-P.: conceptualization, data curation, funding acquisition, investigation, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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