

## TRACING THE ANCESTRY OF THE GREAT WHITE SHARK, *CARCHARODON CARCHARIAS*, USING MORPHOMETRIC ANALYSES OF FOSSIL TEETH

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**ABSTRACT**—The evolutionary origin of the great white shark (*Carcharodon carcharias*) is unclear, with debate centering around two principal hypotheses. The first, based on similarity in tooth shape, claims that *C. carcharias* originated from a group of extinct mako sharks that includes *Isurus hastalis*. The second hypothesis, based mostly on cladistic evidence, claims that *C. carcharias* originated from the same lineage as the giant megatoothed sharks, sharing a close evolutionary ancestor with the extinct *Carcharodon megalodon*. To distinguish between the two hypotheses we performed several morphometric analyses. In the first analysis, we used Procrustes method and principal components analysis to quantify variation between *C. carcharias*, *I. hastalis*, and *C. megalodon* in four different positions within the dentition. The results indicate no significant difference in tooth shape between *C. carcharias* and *I. hastalis*. In the second analysis, correlating tooth size with age, we analyzed teeth from upper anterior and lower anterior positions. For both tooth positions, we show that the growth rate of *C. carcharias* is more congruent with the growth rate of *I. hastalis* than that of *C. megalodon*. Finally, we used scanning electron microscopy to show that the tooth serrations of *C. carcharias* are distinct from those of the megatooths and more similar in size to those of slightly serrated mako teeth. Taken together, these results indicate that *C. carcharias* originated from an extinct group of mako sharks and not from the megatoothed sharks.

### INTRODUCTION

Despite more than a century of scrutiny, the evolutionary origin of the great white shark, *Carcharodon carcharias*, is still in dispute. The two leading hypotheses posit an ancestry on the one hand from the extinct megatooth sharks, including *Carcharodon megalodon*, and on the other from *Isurus hastalis*, an extinct mako shark. It is difficult to argue effectively that one species is directly descended from another, particularly in the case of fossil sharks with their dearth of diagnostic material, so we will describe the two theories in terms of sharing more recent common ancestors (Smith, 1994).

The older and more accepted hypothesis is that *C. carcharias* is descended from the extinct megatooth sharks that include species such as *Carcharodon auriculatus*, *Carcharodon subauriculatus*, and *C. megalodon*. In other words, this hypothesis proposes that *C. carcharias* shares a more recent common ancestor with *C. megalodon* than with *I. hastalis*, a view shared by Applegate and Espinosa-Arubarrena (1996), Gottfried and colleagues (1996), and Purdy and colleagues (2001). We will refer to this as the *megalodon* hypothesis (Fig. 1A). The more recent hypothesis is that *C. carcharias* is descended from the extinct mako sharks that include *I. hastalis*. That is, *C. carcharias* shares a more recent common ancestor with *I. hastalis* than with *C. megalodon*, a view that is shared by Casier (1960), Muizon and DeVries (1985), and Cappetta (1987). We will subsequently refer to this as the *hastalis* hypothesis (Fig. 1B).

In 1835, Louis Agassiz formally introduced *Carcharodon megalodon* based on morphological similarity of tooth shape with *C. carcharias*. Since then, several lines of evidence have been advanced to support the *megalodon* hypothesis. Applegate and Espinosa-Arubarrena (1996), Gottfried and colleagues (1996), and Purdy and colleagues (2001) identified tooth shape

similarities in *C. carcharias* and *C. megalodon*, including shared symmetries of particular positions and orientation of root lobes. While no formal cladistic analysis has been performed on these species, several non-shape synapomorphies also support the *megalodon* hypothesis (Applegate and Espinosa-Arubarrena, 1996; Gottfried et al., 1996; Purdy et al., 2001).

Proponents of the *megalodon* hypothesis view the evolution of *C. carcharias* from the megatooth sharks as a case of heterochrony, where large *C. carcharias* teeth are similar in morphology to similar sized teeth in *C. megalodon* and other megatooth sharks (Gottfried et al., 1996). This could explain the lack of lateral denticles in juvenile *C. megalodon* versus the presence of lateral denticles in juvenile *C. carcharias* (Applegate and Espinosa-Arubarrena, 1996).

Although both *C. carcharias* and *C. megalodon* have serrated teeth, Purdy and colleagues (2001) maintain that this is not a useful character for establishing phylogenetic relationships because serrations have evolved many times independently (Applegate, 1967; Compagno, 1988). Purdy and colleagues (2001) also argue that the transition from the extinct makos to *C. carcharias* is not possible because a key hypothesized transitional fossil (Muizon and DeVries, 1987) is from the late Miocene, after the emergence of early *C. carcharias* in the middle Miocene. Furthermore, Purdy (1996) suggests that a similarity in tooth shape between *C. carcharias* and *I. hastalis* could be due to convergent evolution in response to shared pinniped predation.

Casier (1960) submitted the first legitimate challenge to *C. megalodon*'s ascription in the genus *Carcharodon*. Noting the similarity in overall shape, he argued that the serrated-toothed *C. carcharias* evolved from the smooth-toothed broad-form *I. hastalis*, a subset of *I. hastalis* teeth categorized as *I. xiphodon* by Purdy and colleagues (2001). Casier pointed to a shared labio-lingual flattening in both *C. carcharias* and *I. hastalis* as a shared, derived character distinct from *C. megalodon*. He also noted the appearance of marginal serrations in some specimens of *I. hastalis*, which look suspiciously like the teeth of *C. carcharias*, and believed he had identified a possible transition species, *Oxyrin-*

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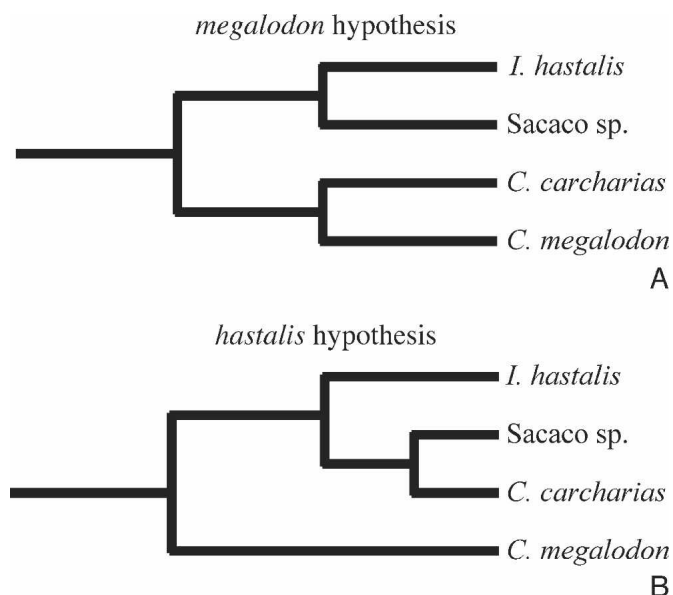


FIGURE 1. Phylogenies of possible *C. carcharias* origination. **A**, *megalodon* hypothesis proposes that *C. carcharias* descends from the megalodon sharks. **B**, *hastalis* hypothesis proposes that *C. carcharias* descends from the prehistoric mako sharks. Sacaco sp. refers to the slightly serrated prehistoric mako teeth found in the Sacaco region of Peru.

*chus escheri*. (Casier used the genus *Oxyrinchus* in place of the genus *Isurus*.)

Weakly serrated teeth from the genus *Isurus* are usually identified as *I. escheri* (Agassiz, 1843), although there is a growing consensus that the teeth commonly referred to as *I. escheri* are in fact derived from two distinct species. Specimens found along the Atlantic seaboard of Europe, which both Agassiz and Casier referred to, are the true *I. escheri*. The other weakly serrated *Isurus* form is from the Pisco Formation (late Pliocene) in the Sacaco region of Peru (Muizon and DeVries, 1985). We will refer to this unnamed species, which is clearly related to *I. hastalis*, as the Sacaco species. The focus of the *hastalis* hypothesis is now

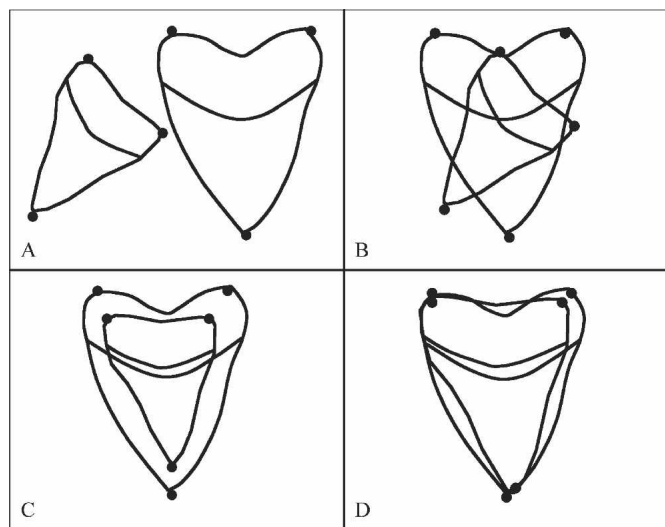


FIGURE 2. Procrustes method of superimposition. **A**, landmark points are determined in two objects. **B**, objects are translated. **C**, objects are mirror reflected, if needed and rotated. **D**, objects are scaled for best fit. (Modified from Peres-Neto, P. R., and D. A. Jackson. 2001. *Oecologia*. 129:169–178.)

centered on this species. Muizon and DeVries (1985) detailed a possible transition from *I. hastalis* to *C. carcharias* based on individual teeth. More importantly, an articulated dentition was found with weakly serrated edges and a slightly distal pointing intermediate tooth. The overall tooth shape is similar to both *C. carcharias* and *I. hastalis*.

While qualitative shape descriptions and cladistic characters have been used to compare *C. carcharias* to other species of lamniforms, quantitative methods have not been used to compare tooth shape among species. We used morphometric methods to compare not only general tooth shape, but also the shape of the more conserved roots. We implemented the generalized Procrustes method to capture and compare the shapes of individual teeth and principal components analysis (PCA) to illustrate the variation in shape between teeth and roots in general in four different areas of the dentition. We also examined the specific arguments about individual tooth shape that support the *megalodon* hypothesis. We examined a wide range of tooth sizes to address the heterochrony component argument of the *megalodon* hypothesis. Finally, we used scanning electron microscopy (SEM) to analyze the serrations of *C. carcharias*, *C. megalodon*, and the Sacaco species. All of our analyses point to the same conclusion: *C. carcharias* is more closely related to *I. hastalis* than *C. megalodon*.

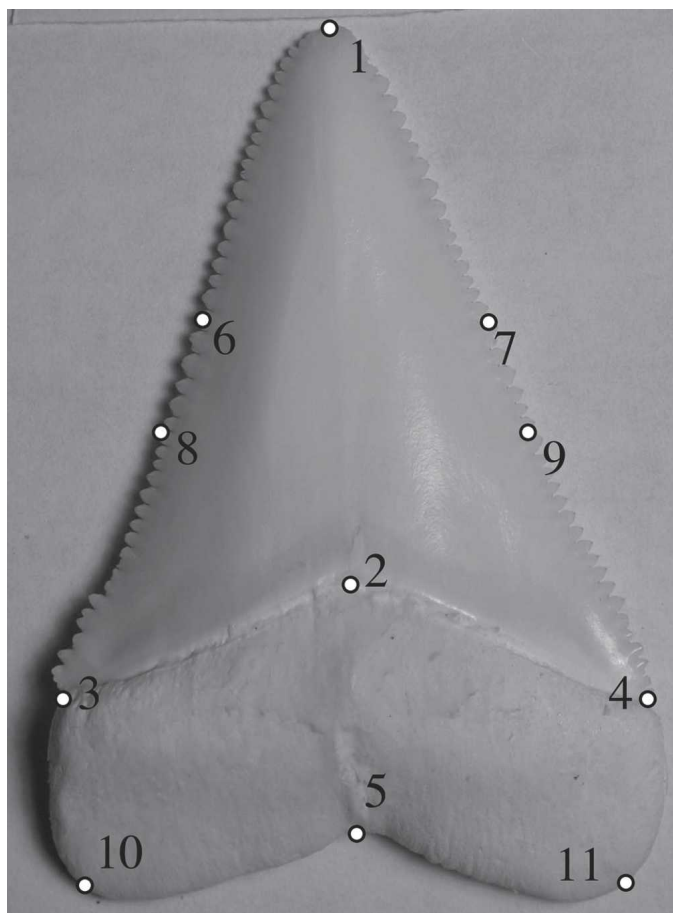


FIGURE 3. Eleven landmark points used for Procrustes analysis. 1, tip of the crown; 2, center of the inner edge of the root; 3, distal junction point of crown and root; 4, mesial junction point of crown and root; 5, center of the outer edge of the root; 6, half the distance between points 1 and 2 on distal edge; 7, half the distance between points 1 and 2 on mesial edge; 8, half the distance between points 1 and 5 on distal edge; 9, half the distance between points 1 and 5 on mesial edge; 10, outermost tip of the distal root lobe; 11, outermost top of the mesial root lobe.

## MATERIALS AND METHODS

Our analyses required an extensive sampling of shark teeth from all three species and at different ontogenetic stages of all sizes, including the largest *C. megalodon*. We used both individual teeth as well as associated dentitions from the collections at the North Carolina Museum of Natural Sciences in Raleigh, NC, the Smithsonian Institute's Museum of Natural History in Washington, D.C., and the private collection of Gordon Hubbell (JAWS International, Gainesville, FL).

The North Carolina Museum of Natural Sciences provided individual teeth from all three species, with most specimens derived from the Lee Creek Mine locality in northeastern North Carolina as well as other localities along the mid-Atlantic coast of the United States. This material includes one associated dentition of *C. megalodon*.

The Smithsonian Institute provided several individual teeth from *C. megalodon* and *C. carcharias* and a large number of individual teeth from *I. hastalis* (there catalogued as *I. xiphodon*). These teeth were mostly collected from Lee Creek along with other localities along the mid-Atlantic coast.

Gordon Hubbell provided extensive specimens of individual teeth from each species from his personal collection, with the majority of specimens of *I. hastalis* collected in the southeastern United States, including the Lee Creek area, and all specimens of *C. megalodon* collected in Florida. The majority of individual specimens from *C. carcharias* were collected in Peru, particularly from the Sacaco formation. Hubbell also provided numerous

associated dentitions including: one *C. megalodon* from the Four Corners Phosphate Mine in Florida, one *C. megalodon* from Lee Creek, and one juvenile *C. megalodon* from Chile; four extant *C. carcharias* at different ontogenetic stages, one *C. carcharias* and two *I. hastalis* from Sacaco, Peru; and the aforementioned Sacaco dentition.

We took digital photographs of the lingual views of each individual tooth and then used Quickimage 1.62 to digitize the photos, produce coordinate landmark points, and measure distances (Walker). We used Microsoft Excel 11.0.0 to compile data and Paleontological Statistics 1.31 (PAST) for both Procrustes analysis and PCA (Hammer, 2002). Software for reduced major axis regression (RMA 1.17) was used for generating regression lines (Bohonak, 2004).

We conducted three types of analyses: morphometric comparisons of complete teeth and roots, an analysis of tooth allometry in teeth, and a comparison of fine detail in serrations. First, using specimens from *C. carcharias*, *C. megalodon*, *I. hastalis*, and the Sacaco species, we used the generalized Procrustes method followed by PCA to compare overall tooth shape between the species in four different positions: upper and lower anterior tooth positions and upper and lower lateral tooth positions. These positions can be compared to an illustrated dentition by Applegate and Espinosa-Arrubarrena (1996). The generalized Procrustes method involves translation, rotation, and scaling of multiple images to achieve an 'average' image (Fig. 2). Individual specimens can then be quantitatively compared to the 'average' image. For a detailed explanation of the generalized Procrustes

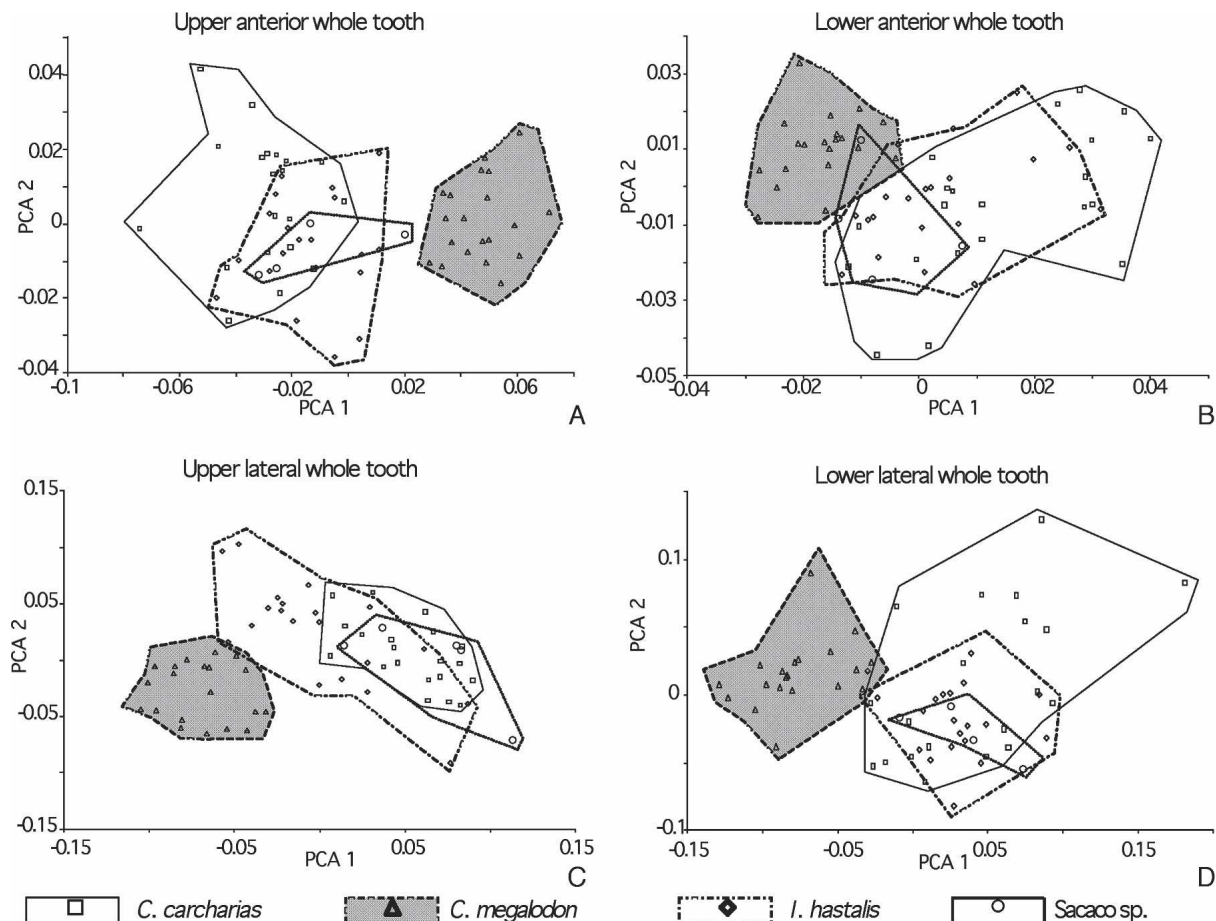


FIGURE 4. PCA analysis of Procrustes residuals for the entire tooth representing variations in shape. **A**, upper anterior positions. **B**, Lower anterior positions. **C**, upper lateral positions. **D**, lower lateral positions. Polygons outline all specimens from each species. Note that the specimens from *C. megalodon* cluster distinctly from the specimens of the other three species.

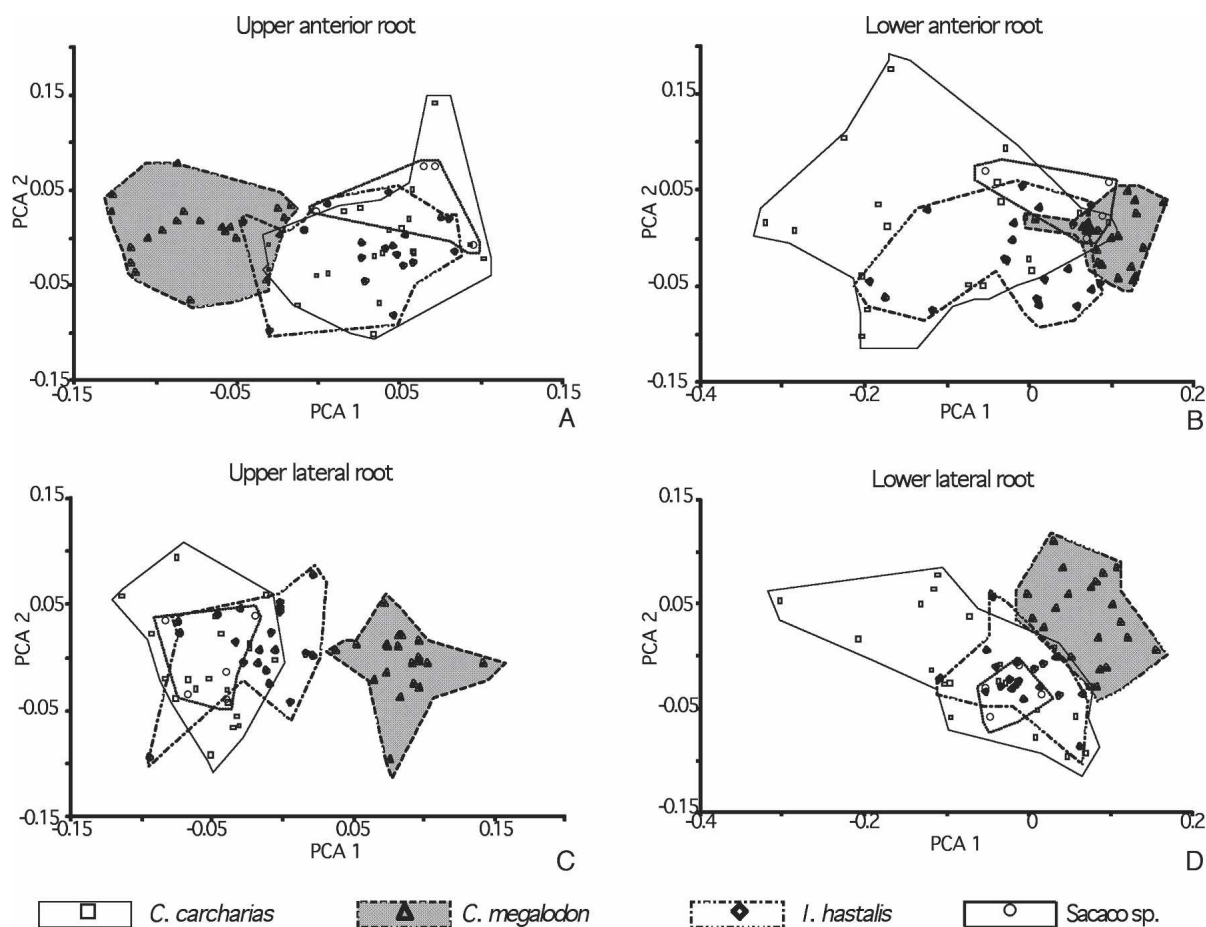


FIGURE 5. PCA analysis of Procrustes residuals for the root (points 2, 3, 4, 5, 10, and 11 from Figure 3). **A**, upper anterior positions. **B**, lower anterior positions. **C**, upper lateral positions. **D**, lower lateral positions. Again, note that the specimens of *C. megalodon* cluster distinctly from the specimens of the other three species.

method, see Rohlf and Slice (1990) and Peres-Neto and Jackson (2001).

The specimens we examined had all been identified to species independently, but we confirmed these identifications with reference to Cappetta (1987), Kent (1994), and Purdy and colleagues (2001). Placement along the anterior-posterior axis can generally be accomplished by examining the asymmetry of the crown in conjunction with the height of the crown relative to the root. Lateral teeth are highly asymmetrical, with the crown tip pointing to the posterior. While the upper anteriors of *I. hastalis* will show asymmetry, they can be identified as anterior by both a lessened degree of asymmetry as compared to the laterals and the relative height of their crowns. Dignathic heterodonty exists in both these species that is useful in placing teeth in the upper or lower dentition (Purdy et al., 2001). Upper teeth have broader and thinner crowns than their lower counterparts. Lower teeth possess better-developed root toruses and both their crown edges tend to be more concave than those of upper teeth (Purdy et al., 2001).

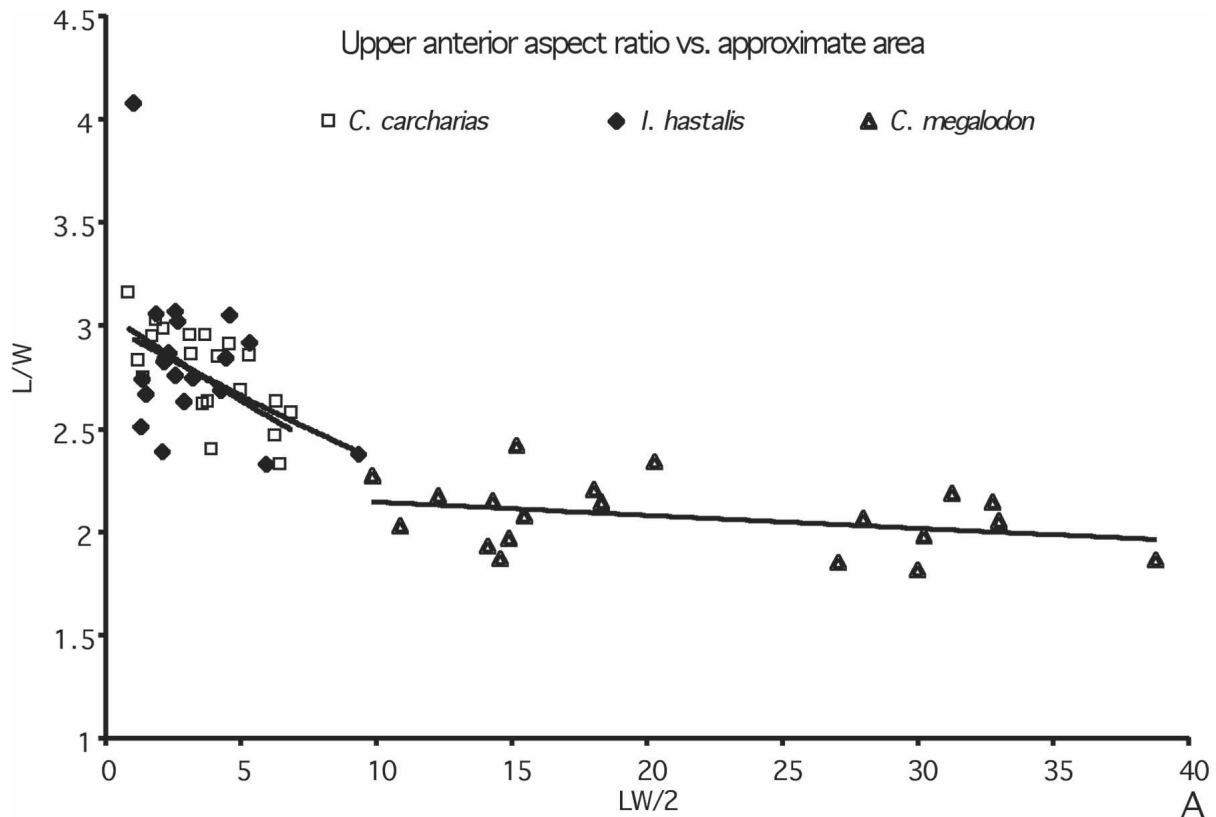
Positional placements were confirmed morphometrically using the generalized Procrustes method and PCA using extant sets of *C. carcharias* (Supplementary Data Fig. S1, [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)) and associated sets of *I. hastalis* (Supplementary Data Fig. S2, [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)) and *C. megalodon* (Supplementary Data Fig. S3, [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)) as standards. Lower and uppers cluster discretely along the first two principal components, with

one notable exception in the laterals of *C. megalodon*. Interestingly, both upper lateral and lower lateral *C. megalodon* specimens from associated sets cluster in the same region along even the first three principal components, suggesting that the two-dimensional profile may not be sufficient to distinguish between upper and lower lateral teeth in this species. Alternatively, the overlap may indicate a need to reexamine established methods of positional identification in *C. megalodon*. This overlap, however, does not affect our study, as we will discuss subsequently.

We used eleven landmark points to capture not only the distinct anatomical points on the teeth, but also to capture the curvature of the crown blades (Fig. 3). Applegate and Espinosa-Arribarrena (1996), Gottfried and colleagues (1996), and Purdy and colleagues (2001) all contend that there are synapomorphies in the roots of *C. carcharias* and *C. megalodon* that would support the *megalodon* hypothesis. We also tested these arguments using the generalized Procrustes method on the six root landmarks in isolation.

Sample sizes for each study are 20 individual teeth from each position of *C. carcharias*, *I. hastalis*, and *C. megalodon*. We used four teeth from the Sacaco species from each position with the exception of the upper laterals, in which we used five teeth.

Second, we tested the hypothesis of heterochronic change between *C. carcharias* and *C. megalodon*. Strictly speaking, heterochronic analysis requires knowing the age of the individual from which each tooth came. In the absence of definitive staging



Species	RMA Intercept (95%)	RMA Slope (95%)	R <sup>2</sup>
<i>C. carcharias</i>	3.236±0.148	-0.121±0.0318	0.471±0.288
<i>I. hastalis</i>	3.109±0.815	-0.261±0.095	0.231±0.229
<i>C. megalodon</i>	2.181±0.452	-0.00340±0.0217	0.193±0.192

B

FIGURE 6. RMA analysis of ontogenetic growth rates at the 95% confidence level of upper anterior teeth in *C. carcharias*, *I. hastalis*, and *C. megalodon*. **A**, plot of aspect ratio ( $L/W$ ) versus approximated area ( $1/2 LW$ ). **B**, range of values at the 95% confidence level for RMA intercept and RMA slope. Note that the intercept and the rate of aspect ratio change in *C. megalodon* are significantly different from the intercepts and the rates of change in *C. carcharias* and *I. hastalis*.

criteria, size is often used as a proxy for age in studies of fossil material. To the degree that size and age are correlated, allometric relationships between the three species provide a fair approximation of heterochronic relationships (McKinney and McNamara, 1991). For this analysis, we only used the upper and lower anterior teeth which exhibit much less variability within species than the lateral teeth (Purdy et al., 2001). To estimate size, we approximated the area of the tooth as a triangle ( $1/2 LW$ ; where  $L$  is the distance between landmark points 1 and 5, and  $W$  is the distance between landmarks 3 and 4) and examined the change in the aspect ratio (length over width) as the size increases in each species. We statistically tested our data using RMA analysis at the 95% confidence level.

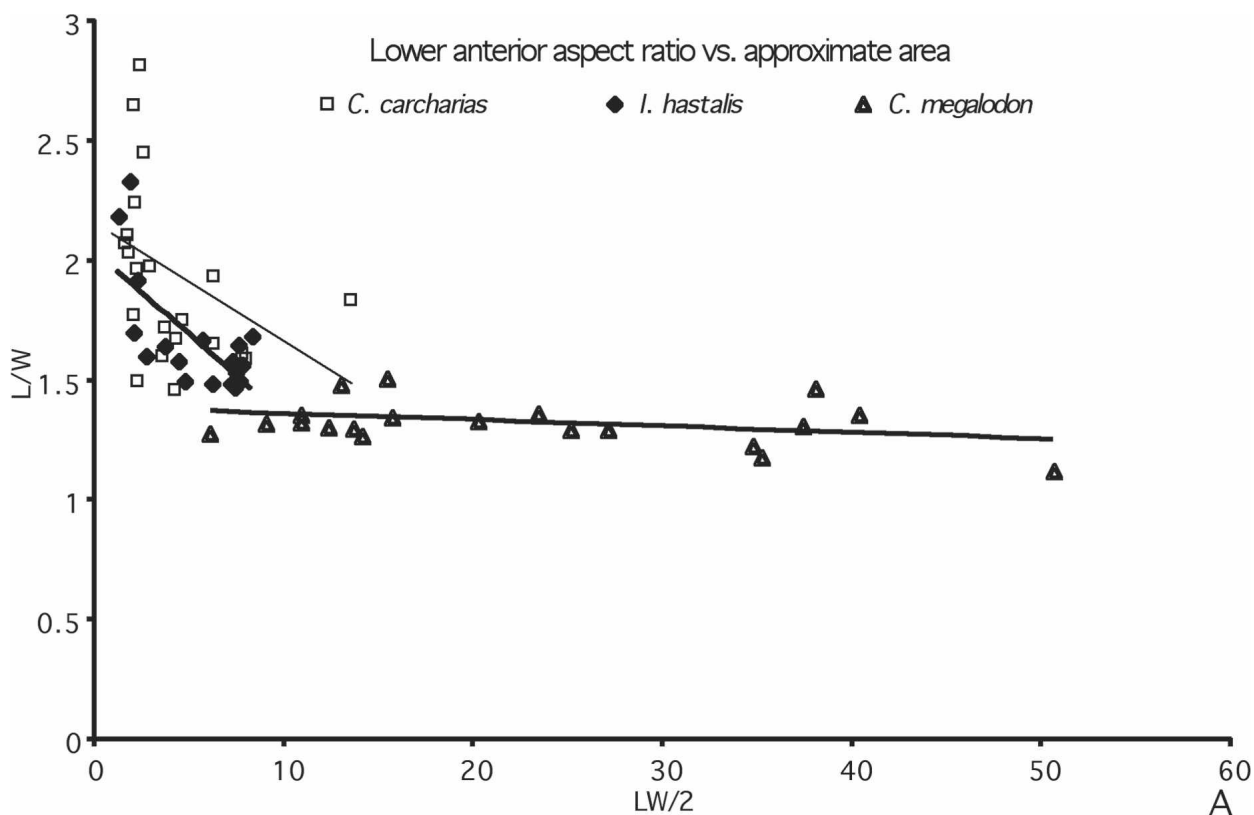
Third, we used scanning electron microscopy to examine the shapes of the serrations of *C. carcharias*, *C. megalodon*, the Sacaco species, and the megatooth sharks *Carcharodon auriculatus* and *Carcharodon subauriculatus* in detail. We calculated the distances between serration tips along different points on the blades and compared the distances among species.

## RESULTS

Using the generalized Procrustes method, we first compared individual teeth from four different positions within the dentition in *C. carcharias*, *I. hastalis*, *C. megalodon*, and the Sacaco species using the eleven landmark points indicated in Figure 3.

We obtained the residuals from this Procrustes analysis first in the upper anteriors and then used those as variables in a PCA analysis (Fig. 4A): 63.2% of the variance in shape was resolved into the first principal component, and nearly 75% of the overall variance can be represented in the plot of the first two principal components. *C. megalodon* clusters distinctly from *C. carcharias*, *I. hastalis*, and the Sacaco species. The range of variation of *C. carcharias* is almost completely overlapped by the wide range of variation in *I. hastalis*. One of the Sacaco specimens comes nearest to approaching the shape of *C. megalodon*.

The PCA analysis plot generated from the residuals of a Procrustes analysis of lower anterior teeth (Fig. 4B) shows a more tightly clustering group of *C. megalodon* teeth and a more vari-



Species	RMA Intercept (95%)	RMA Slope (95%)	R <sup>2</sup>
<i>C. carcharias</i>	2.138±0.228	-0.0900±0.0358	0.502±0.253
<i>I. hastalis</i>	2.494±0.361	-0.170±0.103	0.244±0.214
<i>C. megalodon</i>	1.378±0.199	-0.000896±0.00918	0.260±0.260

B

FIGURE 7. RMA analysis of ontogenetic growth rates at the 95% confidence level of lower anterior teeth in *C. carcharias*, *I. hastalis*, and *C. megalodon*. **A**, plot of aspect ratio ( $L/W$ ) versus approximated area ( $1/2LW$ ). **B**, range of values at the 95% confidence level for RMA intercept and RMA slope. Note that the intercept and the rate of aspect ratio change in *C. megalodon* are significantly different from the intercepts and the rates of change in *C. carcharias* and *I. hastalis*.

able shape in the other three species. While the first two principal components capture again about 75% of the variance, only 35.5% of the variance is resolved by the first principal component. Still, *C. megalodon* clusters distinctly from the other species, with only one Sacaco tooth and one *C. carcharias* tooth clustering within its range. *C. carcharias* shows nearly as much range as *I. hastalis* in the lower anteriors.

The PCA analysis of the upper laterals (Fig. 4C) shows, once again, that *C. megalodon* clusters distinctly with its unique variation. Only one specimen of *C. carcharias* approaches the range of *C. megalodon*. The Sacaco species overlaps with *C. carcharias* and *I. hastalis*. In contrast to both plots for anterior teeth, in the upper laterals, *C. carcharias* shows the largest range of variation. A little over 60% of the variance is resolved upon the first two principal components.

A PCA analysis of the lower lateral teeth (Fig. 4D) shows enormous variation within *I. hastalis*, though the Sacaco species and *C. carcharias* cluster together through about one-third of the range of *I. hastalis*. *C. megalodon* again clusters distinctly with only one specimen of *C. carcharias* overlapping its range. Nearly

60% of the variance is covered by the first two principal components.

In addition, we ran a Procrustes and PCA analysis with all lateral teeth, both upper and lower specimens, to address potential concerns stemming from the overlap between upper and lower lateral teeth in *C. megalodon* (Supplementary Data Fig. S4, [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)). Specimens from *C. carcharias* and *I. hastalis* cluster together, separate from the lateral specimens from *C. megalodon*. Approximately 57% of the variance is resolved by the first two principal components.

We also used the generalized Procrustes method followed by PCA analysis from the roots for the same four species in the same four dentition positions. The landmark points used for the root analysis were 2, 3, 4, 5, 10, and 11 (Fig. 3).

The PCA plots for the roots alone from all four positions are similar to those for the entire tooth (Fig. 5). In all four positions, *C. carcharias*, *I. hastalis*, and the Sacaco species cluster together, with little or no overlap from the uniquely shaped *C. megalodon*. The PCA plots for the roots alone capture much of the variance at all four positions, with first principal component and first two

principal components as follows: upper anterior teeth (49.5%, 70.9%), lower anterior teeth (67.2%, 78.9%), upper lateral teeth (47.9%, 66.4%), lower lateral teeth (50.8%, 68.1%). In summary, at least two-thirds of the total variance is represented by the PCA analysis plots for all four dentition positions, both for the entire tooth and the root. Thus, we can quantitatively argue that the tooth and root shapes of *C. carcharias*, *I. hastalis*, and the Sacaco species are remarkably similar and are all distinct from the tooth and root shapes of *C. megalodon*.

We plotted aspect ratio (L/W) versus approximate size ( $1/2LW$ ) for twenty individual teeth from *C. carcharias*, *I. hastalis*, and *C. megalodon* in both the upper and lower anterior teeth (Fig. 6A and Fig. 7A). Using RMA analysis to generate regression statistics (Fig. 6B and Fig. 7B), we found that the growth trajectories of *C. carcharias* and *I. hastalis* are not significantly different at the 95% confidence level for either the upper or lower anterior teeth. In both tooth positions, there is no statistical significance between the slopes or intercepts of *C. carcharias* and *C. megalodon*.

We used SEM to examine the crown serrations several specimens in each of five species of sharks: *C. auriculatus* (2 specimens), *C. subauriculatus* (2 specimens), *C. megalodon* (4 specimens), *C. carcharias* (3 specimens), and the Sacaco species (3 specimens) (Fig. 8). Members of the megatooth shark species had more regular, rounded serrations while the serrations of *C. carcharias* and the Sacaco species were triangular and pointed with more irregular spacing. The roundedness of the megatooth shark species is a morphological aspect and not due to wear.

To quantify these differences, we measured the distances between serration tips in each SEM image and compiled the data into histograms (Fig. 9). The spacings between serrations of the megatooth sharks have a narrow range of 0.5 to 1.0 mm between serration tips. The spacings between serrations of *C. carcharias* and the Sacaco species exist over a wider range, with a maximum spacing of 0.6 to 1.5 mm in *C. carcharias* and 0.5 to 1.2 mm in the Sacaco species. Although sample sizes in this analysis are smaller than the morphometric analyses presented earlier, the results indicate similar spacing of serrations in the megatooth shark species and distinct spacings in *C. carcharias* and the Sacaco species.

## DISCUSSION

Procrustes analyses demonstrate that the overall tooth shape and root shape of *C. carcharias*, *I. hastalis*, and the Sacaco species are remarkably similar and collectively quite distinct from the tooth and root shape of *C. megalodon* and the megatooth sharks. Although these similarities support the *hastalis* hypothesis, they do not outright invalidate the *megalodon* hypothesis, for two reasons. First, the shared tooth shape of *C. carcharias* and *I. hastalis* could be a primitive trait shared by the common ancestor of the genera *Carcharodon* and *Isurus*, with the megatooth sharks branching off from earlier *Carcharodon*.

Proponents of the *megalodon* hypothesis, however, are more likely to attribute similarities in tooth shape in *C. carcharias* and *I. hastalis* as convergence, perhaps due to predation on similar pinniped prey (Purdy, 1996). There is no evidence, however, of a correlation between the *C. carcharias*/*I. hastalis* tooth shape and increased success on pinniped predation, particularly with respect to the shape typical of the megatooth sharks.

The morphometric analyses presented here do not support earlier claims of similarity in tooth shape that have been offered in support of the *megalodon* hypothesis. In particular, Applegate and Espinosa-Arrubarrena's (1996) claim that the lower anteriors of *I. hastalis* are more 'spike-like' than those of *C. carcharias* is rejected (Fig. 4B). The same is true of their claim that the root interspaces are significantly shallower in *I. hastalis* than in *C. carcharias* (Fig. 5A and 5C). Similarly, our morphometric analy-

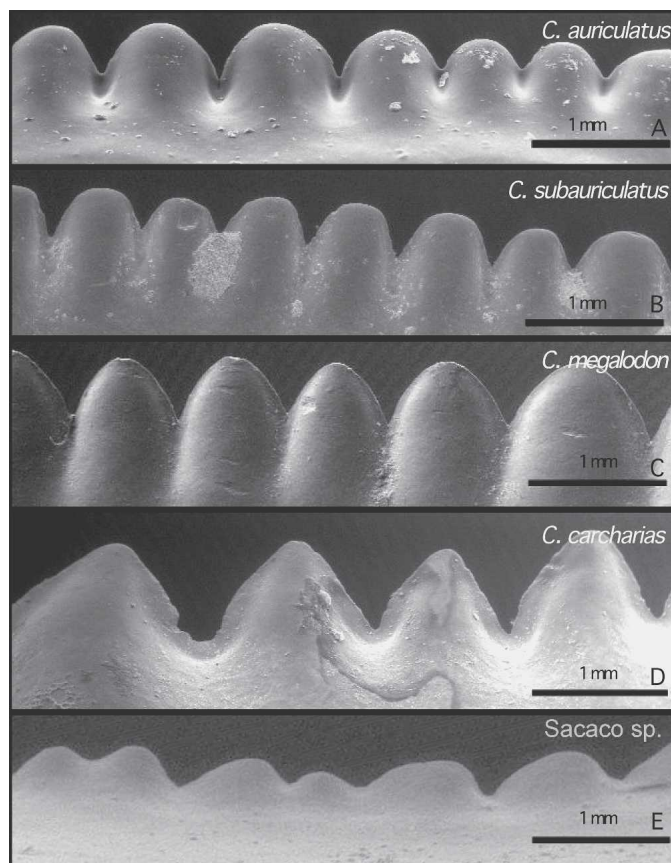


FIGURE 8. SEM photographs of tooth serrations in five species. **A**, *C. auriculatus*. **B**, *C. subauriculatus*. **C**, *C. megalodon*. **D**, *C. carcharias*. **E**, Sacaco species. Serrations in *C. auriculatus*, *C. subauriculatus*, and *C. megalodon* are highly regular and more lobed than those of *C. carcharias* and the Sacaco species. Serrations in *C. carcharias* have a more pointed tip, and serrations in the Sacaco species are highly irregular. Scale bar equals 1 mm.

ses reject Gottfried and colleagues' (1996) claim that the root lobes of *I. hastalis* are more angular than the lobes of *C. carcharias*.

Shimada (2002) challenged Applegate and Espinosa-Arrubarrena's (1996) claim that there is a shared symmetry between *C. carcharias* and *C. megalodon* in the first upper anterior tooth. He calculated the degree of symmetry in several first upper anteriors of *C. carcharias* by finding the ratio of the mesial crown edge length to the distal crown edge length (MCL/DCL). Shimada found a mean value of 1.06 for this ratio in the first upper anterior and determined that the difference between symmetrical and nearly symmetrical teeth is not easy to determine on a numerical basis. Furthermore, he challenged Applegate and Espinosa-Arrubarrena's (1996) qualitative observations by pointing out that the mean value for symmetry in the second upper anterior tooth is also 1.06, which calls into question their claim that the first upper anterior tooth is more symmetrical than the second upper anterior tooth in *C. carcharias*. Hubbell (1996) found that the degree of slant in the second upper anterior is actually less than that of the first upper anterior in *C. carcharias*. These quantitative analyses demonstrate that the first upper anteriors of *C. carcharias* are not symmetrical, undermining another suggested synapomorphy between *C. carcharias* and *C. megalodon*.

Our RMA regression analyses based on the growth series of upper and lower anteriors (Fig. 6 and Fig. 7) do not support

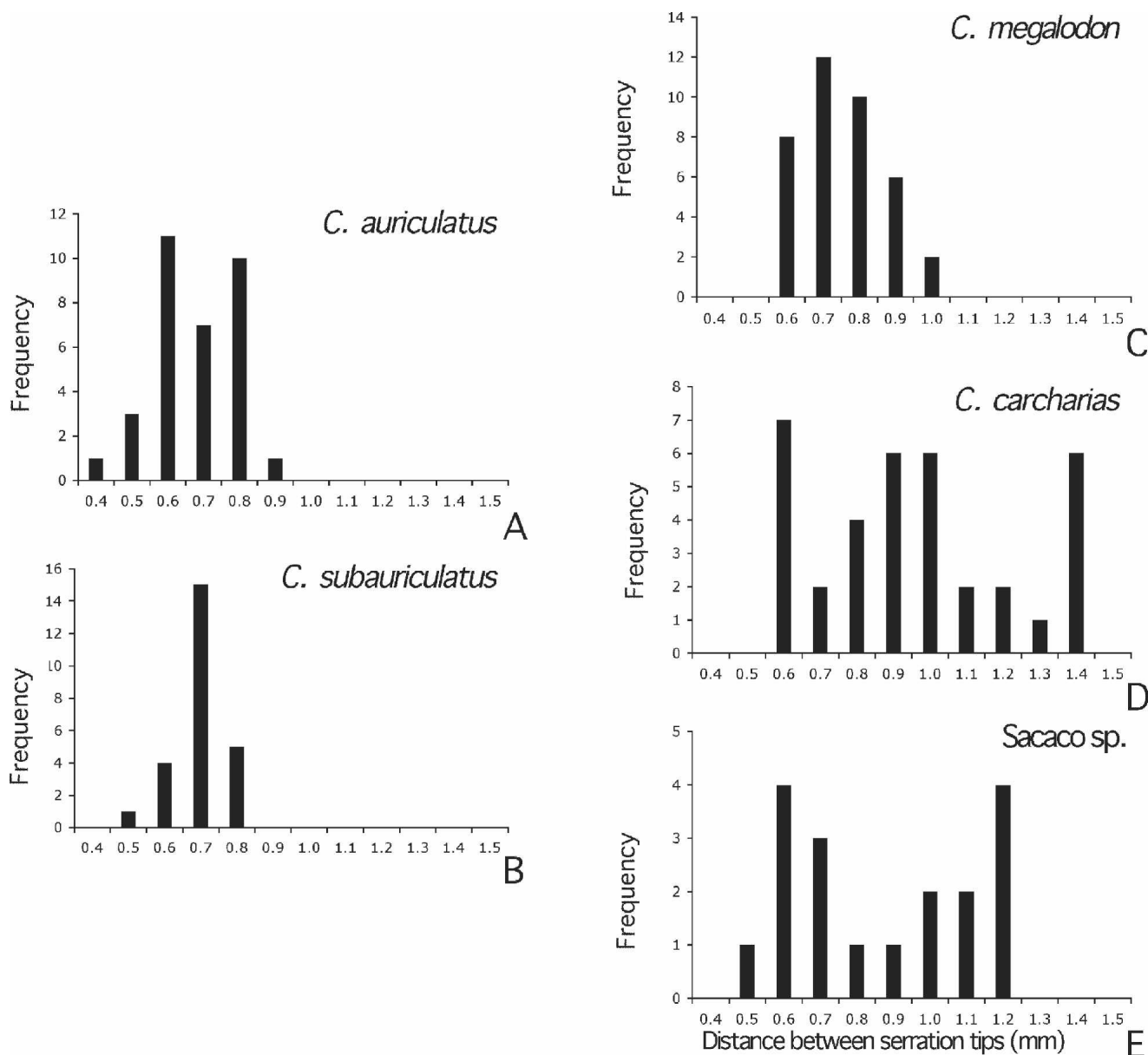


FIGURE 9. Frequency of distances between serrations in five species. **A**, *C. auriculatus*. **B**, *C. subauriculatus*. **C**, *C. megalodon*. **D**, *C. carcharias*. **E**, *Sacaco* species. Note the similarities in range and frequency between *C. auriculatus*, *C. subauriculatus*, and *C. megalodon* and the similarities in range and frequency between *C. carcharias* and the *Sacaco* species. *I. hastalis* is not included because it lacks serrations.

Gottfried and colleagues' (1996) claim of heterochronic change linking the tooth shapes of *C. carcharias* and *C. megalodon*. We found that the growth rates of *C. carcharias* and *C. megalodon* are significantly different, while the growth rates of *C. carcharias* and *I. hastalis* do not show a significant difference. If the teeth of *C. carcharias* and *C. megalodon* were linked by a simple allometric change, then teeth of similar size should have similar shapes in the two species. The regression analyses clearly show that this is not the case.

We also considered other arguments that support the *megalodon* hypothesis and found little evidence in its favor. After analyzing hundreds of specimens of *C. carcharias* over the course of our study, we failed to observe the chevron-shaped dental band that Applegate and Espinosa-Arrubarrena (1996) attribute to *C. carcharias*, similar to the ones commonly found on *C. auriculatus*, *C. subauriculatus*, and *C. megalodon*. Purdy and colleagues' (2001) observation that the second upper anterior is the

largest tooth in *C. carcharias* and *C. megalodon* versus the second lower anterior in *I. hastalis* is also problematic, particularly in *C. carcharias* (data not shown), as tooth size in these species is highly variable.

Perhaps the most widely cited synapomorphy between *C. carcharias* and *C. megalodon* concerns the third tooth from the upper symphysis, known as the intermediate tooth. Applegate and Espinosa-Arrubarrena (1996), Gottfried and colleagues (1996), and Purdy and colleagues (2001) argue that this tooth points mesially in *C. carcharias* and *C. megalodon*, as opposed to the distal-pointing intermediate tooth of *I. hastalis* and earlier lamniforms. However, no articulated dentitions of *C. megalodon* have been described. Thus, we do not know with certainty the positioning of every tooth in an associated set. The orientation of the mesially pointed intermediate tooth in *C. megalodon* was apparently modeled using the dentition of *C. carcharias*. To then use this character to posit a shared evolutionary relationship



between the two species is circular reasoning. We conclude that the intermediate teeth of associated megatooth dentitions are most likely out of position. The intermediate tooth of USNM 411881 (*C. subauriculatus*) appears to be a lower lateral, and the intermediate tooth of NCSM 13073 (*C. megalodon*) appears to be an upper anterior that, despite its designation as an intermediate tooth, is fairly symmetrical and does not point mesially.

Frazzetta (1988) pointed out that smooth and narrow teeth are more efficient at puncturing, but serrated teeth are more efficient at cutting. If the broad-tooth form *I. hastalis*, with a larger point area than the slimmer teeth of the narrow-tooth form *I. hastalis*, developed slight serrations, we find it entirely conceivable that those serrations would offer a significant advantage for pinniped predation. We recognize the possibility of the Sacaco species as a transitional species, but do not maintain its necessity to support the *hastalis* hypothesis. It does, along with *I. escheri*, show the potential of members of the *I. hastalis* lineage to develop serrations that are similar in size and density to the serrations of *C. carcharias*, and it is not improbable that serrations evolved independently in parallel in *C. carcharias*, *I. escheri*, and the Sacaco species.

The scanning electron micrographs reveal remarkable similarities in serration density, size, and regularity among the megatooth species, while *C. carcharias* and the Sacaco species have similar serration densities and show a similar variation in serration size. These results from our limited sampling highlight the need for further studies of serrations throughout the Lamnidae.

Finally, Purdy and colleagues (2001) argue that the Sacaco species cannot be a transitional form to *C. carcharias* because it is out of temporal sequence: the earliest known Sacaco specimens date from the late Miocene, after the earliest known specimens of *C. carcharias* in the middle Miocene. Temporal incongruence alone does discount the *hastalis* hypothesis, however. The existence of the Sacaco species (or its ancestors) earlier in the Miocene, for instance in another locality, is certainly possible, as stratigraphic gaps are not uncommon in the fossil record (Smith, 1994).

## CONCLUSION

The great white shark, *C. carcharias*, evolved from an extinct lineage of mako sharks, and not from the megatooth sharks. We present several lines of evidence consistent with this hypothesis based on morphometric analyses and the fine structure of teeth. We also re-examine several proposed synapomorphies linking *C. carcharias* with the megatoothed sharks, and find that most are problematic.

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