[Original report]

# The relationship between the tooth size and total body length in the sandtiger shark, *Carcharias taurus* (Lamniformes : Odontaspididae)

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## Abstract

The relationship between the height of tooth crown (CH) and total body length (TL) in the modern sandtiger shark, *Carcharias taurus* Rafinesque (Lamniformes : Odontaspididae) is examined using regression analyses. The results suggest : 1) that an increase in the CH of each tooth through replacement is proportional to the increase in the TL, 2) that the CH can be used to predict the TL, and 3) that distally located teeth develop faster through replacement compared to mesially located teeth. The quantitative dental data presented here can be used to infer the TL for modern *Carcharias* jaws without specimen data and for fossil odontaspidid individuals.


Key words : dentition, fossil, growth, lamnoid, odontaspidid

## Introduction

Sharks generally occupy one of the highest trophic positions in any given marine ecosystem. Therefore, paleobiological inferences of extinct sharks, as simple as estimating their body size, are important for the reconstruction of ancient marine ecology. Odontaspidid sharks, which belong to the order Lamniformes, are common in the post-Jurassic fossil record worldwide (Cappetta, 1987), but like most other fossil elasmobranchs, most of them are known only by their teeth (e.g., Ward, 1988; Cvancara and Hoganson, 1993 ; Siverson, 1992 ; Welton and Farish, 1993 ; Shimada *et al.*, 2004). Thus, paleontologists must usually depend on the size of teeth to estimate their body size.

Lahille (1928), Applegate (1965), and Sadowsky (1970) noted the correlation between body length and tooth size in the modern odontaspidid shark, *Carcharias taurus* Rafinesque (sandtiger shark; Lamniformes : Fig. 1A), that reach to about 318 cm in total body length (for its biology, see Compagno, 1984). In particular, Applegate (1965) graphically showed that the increase in tooth height is directly

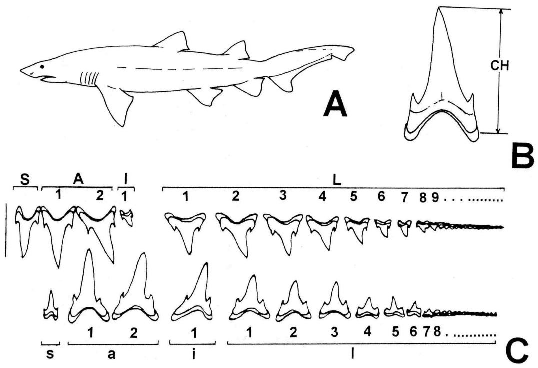


Fig. 1. Modern sandtiger shark, *Carcharias taurus* Rafinesque. A, adult individual (after Compagno, 1984 ; see text for size). B, tooth in labial view showing the measured variable, crown height (CH ; see text for definition ; not to scale). C, upper and lower dental series in labial view (mesial to the left ; vertical line = position of upper jaw symphysis ; illustration modified from Compagno, 1984). Tooth types based on Shimada (2002a) : A, upper anterior tooth; a, lower anterior tooth; I, upper intermediate tooth; i, lower intermediate tooth; L, upper lateral tooth; l, lower lateral tooth; S, upper symphyseal tooth ; s, lower symphyseal tooth.

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proportional to the increase in TL in this species. However, Applegate's (1965) study was not rigorous in the assessment of dental homologies and in the analysis.

The recent assessment of dental homologies in modern lamniform sharks (Shimada, 2002a) offers an opportunity to statistically investigate the relationship between the tooth size and body size in modern *Carcharias taurus*. In this paper, I present the quantitative relationship between the height of tooth crown (CH = the maximum vertical enameloid height on the labial side : Fig. 1B) and total body length (TL) for each tooth in the species. The data presented here help to deciphering the ontogenetic pattern of dental development though tooth replacement. The tooth-based TL estimation method presented here, which is an extension of Applegate's (1965) work, is anticipated to be useful for fossil shark research (e.g., see Randall, 1973; Gottfried *et al.*, 1996 ; Hamm and Shimada, 2002 ; Shimada, 2002b, 2003 ; Shimada *et al.*, 2004).

## Materials and methods

Ten, non-embryonic jaw samples of *Carcharias taurus*, each with a known TL, were examined (Appendix). One is housed in the American Museum of Natural History (AMNH), New York, New York, U.S.A., seven are in the Natural History Museum of Los Angeles County (LACM), California, U.S.A., and two are a part of Gordon Hubbell collection (GH : JAWS International) in Gainesville, Florida, U.S.A. Tooth types (Fig. 1C) were identified in each jaw specimen based on the method presented by Shimada (2002a). The CH of fully mineralized ("functional"), 18 upper teeth (S, A1-A2, I1, and L1-L14) and 17 lower teeth (s, a1-a2, i1, and l1-l13) in each sample was measured (Appendix; for tooth types, see Fig. 1). Then, the relationship between the CH and TL was examined using regression analysis (least squares method ; simple linear regression, $y = a + bx$, where a is the constant and b is the slope of the line ; $x$ = CH in mm ; $y$ = TL in cm ; $\alpha = 0.05$ ; for statistics, see Zar, 1996). The null hypothesis is : The CH does not predict the TL.

Table 1. Regression analyses between tooth crown height (CH) and total body length (TL) among 10 individuals of *Carcharias taurus* (x = CH in mm [for tooth types, see Fig. 1] ; y = TL in cm ; degrees of freedom = 1,8). Statistical notations : r, correlation coefficient ; p, probability of estimates ; s.e., standard error of estimates.

| x | Regression equation | r | F-ratio | p | s.e. |
|---|---|---|---|---|---|
| Upper teeth | | | | | |
| S | y = − 11.581+12.883x | 0.995 | 785.208 | <0.001 | 7.520 |
| A1 | y = − 26.665+12.499x | 0.996 | 1093.165 | <0.001 | 6.382 |
| A2 | y = − 27.489+13.913x | 0.990 | 391.826 | <0.001 | 10.592 |
| I1 | y=47.725+26.039x | 0.902 | 35.110 | <0.001 | 32.257 |
| L1 | y = − 9.355+17.708x | 0.989 | 347.560 | <0.001 | 11.232 |
| L2 | y = − 25.189+18.270x | 0.990 | 401.656 | <0.001 | 10.464 |
| L3 | y = − 29.736+19.371x | 0.994 | 632.962 | <0.001 | 8.366 |
| L4 | y = − 32.095+22.283x | 0.970 | 126.924 | <0.001 | 18.233 |
| L5 | y = − 17.994+27.130x | 0.983 | 233.759 | <0.001 | 13.621 |
| L6 | y = − 1.487+35.056x | 0.960 | 94.940 | <0.001 | 20.875 |
| L7 | y=15.962+39.214x | 0.960 | 95.015 | <0.001 | 20.867 |
| L8 | y=44.069+43.013x | 0.980 | 193.247 | <0.001 | 14.930 |
| L9 | y=55.610+51.719x | 0.947 | 69.377 | <0.001 | 24.077 |
| L10 | y=85.554+47.282x | 0.854 | 21.487 | 0.002 | 39.003 |
| L11 | y=44.706+81.703x | 0.958 | 88.761 | <0.001 | 21.531 |
| L12 | y=80.678+62.434x | 0.893 | 31.573 | <0.001 | 33.668 |
| L13 | y=57.063+95.029x | 0.919 | 43.526 | <0.001 | 29.505 |
| L14 | y=85.820+68.800x | 0.870 | 24.798 | 0.001 | 36.982 |

| x | Regression equation | r | F-ratio | p | s.e. |
|---|---|---|---|---|---|
| Lower teeth | | | | | |
| s | y=18.407+16.732x | 0.953 | 78.337 | <0.001 | 22.794 |
| a1 | y=−24.722+10.305x | 0.993 | 451.233 | <0.001 | 9.037 |
| a2 | y=−14.280+10.189x | 0.990 | 376.626 | <0.001 | 10.799 |
| i1 | y=−2.201+11.847x | 0.981 | 206.030 | <0.001 | 14.477 |
| l1 | y=0.515+15.938x | 0.989 | 358.708 | <0.001 | 11.060 |
| l2 | y=−1.099+17.820x | 0.990 | 382.465 | <0.001 | 10.718 |
| l3 | y=−15.189+21.495x | 0.989 | 350.907 | <0.001 | 11.179 |
| l4 | y=−15.809+25.098x | 0.982 | 212.346 | <0.001 | 14.268 |
| l5 | y=−5.312+32.568x | 0.963 | 103.144 | <0.001 | 20.089 |
| l6 | y=21.017+41.496x | 0.891 | 30.661 | 0.001 | 34.062 |
| l7 | y=51.702+46.690x | 0.803 | 14.548 | 0.005 | 44.602 |
| l8 | y=81.402+43.436x | 0.811 | 15.393 | 0.004 | 43.789 |
| l9 | y=64.595+60.694x | 0.841 | 19.358 | 0.002 | 40.492 |
| l10 | y=87.850+51.039x | 0.830 | 17.781 | 0.003 | 41.712 |
| l11 | y=82.952+70.403x | 0.702 | 7.788 | 0.024 | 53.303 |
| l12 | y=−87.513+69.608x | 0.814 | 15.672 | 0.004 | 43.530 |
| l13 | y=−89.341+72.650x | 0.849 | 20.595 | 0.002 | 39.607 |

## Results

The results of the regression analyses are provided in Table 1. All regression lines show positive correlation. Whereas the position of y-intercept varies widely, the slope of the lines tends to increase from mesially located teeth to distally located teeth for both upper and lower dental series (Fig. 2). The correlation coefficient (r) for each line is high (all >0.800, except l11 which is 0.702), indicating that the bivariate plots are clustered closely along each regression line. The standard error of estimate (s.e.) for each regression suggests that some degree of scattering of plots around the line exists. The probability of error (p) is low for all teeth (all $p \leq 0.024$; i.e., showing a high statistical significance).

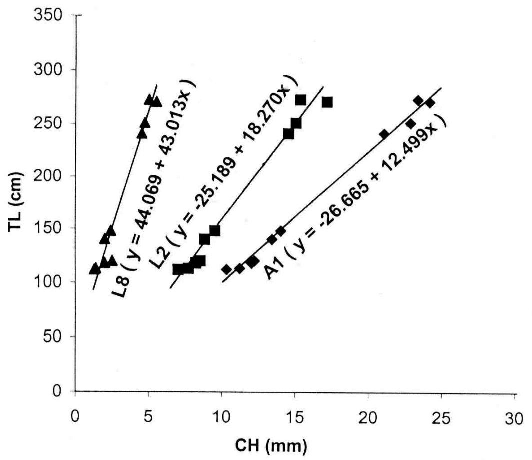


Fig. 2. Bivariate scatter with regression line between crown height (CH) and total body length (TL) for the first upper anterior tooth (A1 : diamond), second upper lateral tooth (L2 : square), and eighth upper lateral tooth (L8 : triangle) in modern *Carcharias taurus* (n=10 ; for measurements, see Appendix ; for statistics of regression line, see Table 1).

## Discussion

A high r-value and a low p-value for all regression lines suggest that, in *Carcharias taurus*, the CH can be used to estimate the TL. A positive relationship for each regression line indicates that an increase in the CH through replacement is proportional to increases in the TL. The tendency of the increase in the slope of regression lines from mesially located teeth to distally located teeth suggests that, through replacement, the rate of size increase of distally located teeth is greater than that of mesially located teeth : i.e., a negative allometry of mesially located teeth relative to the distally located teeth.

Shimada (2002a) noted that the exact homology of symphyseal teeth ("S" and "s") is uncertain due to their lack of definable anatomical markers. Thus, the linear relationship between the CH of the symphyseal teeth and the TL may be artificial. However, it should be noted that the high correlation coefficient between the two variables for each symphyseal tooth is intriguing (r=0.995 for "S" and r=0.953 for "s": Table 1).

The estimation should be regarded as first approximation due to some statistical concerns. First, the sample size is small. Second, whether or not the CH-TL relationship is linear needs to be further examined. Third, the present data lack measurements from shark individuals ranging between 148 and 241 cm TL, which may be partially responsible for showing high correlation coefficients. In addition, it should be pointed out that the examined specimens come from different localities and sexes (see Appendix), and whether or not sexual and geographic variations in CH-TL relationship are present is unknown at the present time. For example, Lucifora *et al.* (2003) found a statistically significant geographic difference in the number of distally located teeth in *Carcharias taurus* between the individuals from East China Sea and those from Argentina (cf. Applegate, 1965; Sadowsky, 1970; Taniuchi, 1970).

The regression equations may be used to infer the TL of fossil *Carcharias* individuals, which are commonly represented only by their teeth. For example, Cvancara and Hoganson (1993) reported teeth of Paleocene *C. taurus*, and the largest tooth illustrated was a large "lateral tooth" (Cvancara and Hoganson, 1993, figs. 2N, 2O). It has a total tooth height of 30.3 mm, and its CH is extrapolated to be about 25 mm. A conservative estimate of TL is possible for the fossil individual that carried the tooth based on three assumptions: 1) that the tooth represent the largest lateral tooth on the jaws (i.e., the L2; see Shimada, 2002a); 2) that the CH of the tooth has the same relationship to the TL as modern *C. taurus*; and 3) that it is admissible to extend the regression line below the lowest plot and above the highest plot (e.g., the same assumption implicit in the work by Randall [1973] and Gottfried *et al.* [1996]). If the regression equation for the L2 in modern *C. taurus* (Table 1) is used to estimate the TL of fossil *C. taurus*, it is suggested that the tooth comes from a fish about 432 cm TL. Some recent phylogenetic studies have suggested that the family Odontaspididae may not be monophyletic (Compagno, 1990; Naylor *et al.*, 1997). However, to note, such a quantitative operation (based on a precursor of this present study: Shimada, 1999) was applied to a tooth of a Cretaceous odontaspidid taxon, *Johnlongia* sp., which suggested that the shark was very small (47 cm TL, if a linear CH-TL relationship in *C. taurus* is assumed: Shimada *et al.*, 2004).

Jaw specimens of modern *Carcharias taurus* are common in museum collections, but most of them lack basic biological data (Shimada, personal observation). The lack of TL and sex data is particularly severe. There seems to be a bias in the record keeping where jaws of more common lamniform species, such as *C. taurus*, tend to have "poor" data, compared to more uncommon species (e.g., great white shark, *Carcharodon carcharias*). Whereas the regression equations presented here can be used to "restore" missing TL data for such modern *C. taurus* jaws (e.g., Lucifora *et al.* [2001], which is based on a precursor of this present study: i.e., Shimada, 1999), I believe the progress in future comparative studies and paleobiological applications of shark dentitions depends on "good" record keeping of modern shark jaw specimens.

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## Appendix.

Examined specimens (with TL, sex, and locality data) and crown height of each tooth (in mm; for tooth types, see Fig. 1; value in parenthesis = estimated measurement).

AMNH 79962SD (241 cm TL; male; caught off New Jersey, U.S.A.), left dentition: S, 19.3; A1, 21.0; A2, 20.0; I1, 4.8; L1, 14.5; L2, 14.5; L3, 13.6; L4, 12.1; L5, 9.6; L6, (6.4); L7, (5.7); L8, 4.5; L9, 3.8; L10, 2.7; L11, 2.7; L12, 2.4; L13, 1.7; L14, 1.8; s, 11.1; a1, (24.5); a2, (26.3); i1, (22.0); l1, 15.5; l2, 14.3; l3, 11.8; l4, 10.9; l5, (7.9); l6, 4.9; l7, 2.6; l8, 3.2; l9, 2.2; l10, 2.1; l11, 1.2; l12, 1.4; l13, 1.4.

LACM 39334-2 (273 cm TL; female; caught off Delaware, U.S.A.), right dentition: S, 21.5; A1, (23.3); A2, 20.5; I1, 7.5; L1, 15.3; L2, 15.3; L3, 15.1; L4, 13.1; L5, 10.6; L6, 7.5; L7, 6.3; L8, 5.0; L9, 4.0; L10, 2.5; L11, 2.3; L12, 2.2; L13, 1.7; L14, 1.9; s, 14.0; a1, (29.0); a2, 28.0; i1, 21.5; l1, 15.8; l2, 14.3; l3, 12.6; l4, (11.0); l5, 7.3; l6, 4.5; l7, 3.7; l8, 2.2; l9, 2.1; l10, 2.1; l11, 1.3; l12, 1.5; l13, 1.5.

LACM 39335-1 (112 cm TL; male; caught off New Jersey, U.S.A.), right dentition: S, 9.2; A 1, 10.3; A2, 9.6; I1, 3.1; L1, 6.0; L2, 7.0; L3, 7.0; L4, 5.7; L5, 4.3; L6, 3.1; L7, 2.3; L8, 1.3; L9, 1.0; L10, 0.7; L11, 0.7; L12, 0.6; L13, 0.5; L14, 0.5; s, 4.7; a1, 13.0; a2, 12.3; i1, 9.3; l1, 6.6; l2, 5.7; l3, 5.6; l4, 4.7; l5, 3.1; l6, 2.5; l7, 1.5; l8, 1.3; l9, 1.0; l10, 1.0; l11, 0.9; l12, 0.8; l13, 0.6.

LACM 39336-1 (113 cm TL; female; caught off New Jersey, U.S.A.), right dentition: S, 9.3; A1, 11.2; A2, 9.0; I1, 3.0; L1, 7.1; L2, 7.7; L3, 7.6; L4, 6.6; L5, 4.7; L6, 2.9; L7, 2.2; L8, 1.4; L9, 1.1; L10, 1.0; L11, 0.9; L12, 0.7; L13, 0.6; L14, 0.6; s, 5.5; a1, 14.0; a2, (13.1); i1, 10.0; l1, 6.9; l2, 6.5; l3, 6.2; l4, 5.1; l5, 3.9; l6, 1.8; l7, 1.2; l8, 1.0; l9, 0.8; l10, 0.7; l11, 0.7; l12, 0.6; l13, 0.5.

LACM 39336-2 (118 cm TL; male; caught off New Jersey, U.S.A.), right dentition: S, 10.5; A 1, 12.0; A2, 11.4; I1, 4.0; L1, 8.0; L2, 8.2; L3, 7.8; L4, 7.0; L5, 5.7; L6, 4.4; L7, 3.2; L8, 2.0; L9, 1.3; L10, 1.1; L11, 1.0; L12, 0.8; L13, 0.7; L14, 0.7; s, 7.6; a1, 14.0; a2, 14.1; i1, 11.4; l1, 8.0; l2, 7.1; l3, 6.7; l4, 6.0; l5, 4.5; l6, 2.8; l7, 2.4; l8, 1.6; l9, 1.3; l10, 1.0; l11, 1.0; l12, 0.9; l13, 0.8.

LACM 39336-3 (140 cm TL; female; caught off New Jersey, U.S.A.), right dentition: S, (11.5); A1, 13.4; A2, 12.0; I1, 2.8; L1, 7.8; L2, 8.8; L3, 8.6; L4, 7.0; L5, 5.1; L6, 3.8; L7, 2.9; L8, 2.0; L9, 1.6; L10, 1.3; L11, 1.2; L12, 1.0; L13, 0.8; L14, 0.7; s, 6.8; a1, 14.8; a2, 15.2; i1, 12.1; l1, 8.9; l2, 7.5; l3, 7.0; l4, 5.9; l5, 4.2; l6, 3.2; l7, 1.9; l8, 1.3; l9, 1.2; l10, 1.0; l11, 1.0; l12, 0.9; l13, 0.7.

LACM 39336-4 (148 cm TL; male; caught off New Jersey, U.S.A.), left dentition: S, 13.5; A1, 14.0; A2, 13.2; I1, 4.3; L1, 9.5; L2, 9.5; L3, 9.0; L4, 9.9; L5, 6.3; L6, 3.9; L7, 2.8; L8, 2.4; L9, 2.0; L10, 1.6; L11, 1.3; L12, 1.3; L13, 1.3; L14, 1.3; s, 8.1; a1, 18.3; a2, 13.7; i1, 10.7; l1, 8.7; l2, 8.5; l3, 8.1; l4, 7.2; l5, 5.3; l6, 4.3; l7, 3.8; l8, 2.1; l9, 2.3; l10, 1.8; l11, 1.7; l12, 1.1; l13, 1.2; l11, 0.9; l12, 0.9; l13, 0.8.

LACM 39455-2 (120 cm TL; female; caught off Uruguay), right dentition: S, 10.9; A1, 12.2; A2, 11.1; I1, 3.1; L1, (7.6); L2, 8.5; L3, 8.2; L4, 7.3; L5, 5.9; L6, 4.3; L7, 3.8; L8, 2.5; L9, (1.8); L10, (3.1); L11, (1.1); L12, (1.0); L13, (1.0); L14, (0.9); s, (7.7); a1, 13.9; a2, 13.7; i1, 11.3; l1, 8.1; l2, (7.4); l3, 6.0; l4, (5.3); l5, (3.7); l6, 2.1; l7, 1.5; l8, 1.3; l9, 1.1; l10, 1.0; l11, 0.8; l12, 0.6; l13, 0.5.

GH-Eug1-01 (251 cm TL; female; caught off Florida, U.S.A.), right dentition: S, 21.3; A1, 22.8; A2, 19.8; I1, 8.4; L1, 14.2; L2, 15.0; L3, 14.4; L4, 12.2; L5, 9.7; L6, 6.8; L7, 5.8; L8, 4.7; L9, 2.7; L10, 2.5; L11, 2.2; L12, 1.9; L13, 1.9; L14, 1.7; s, 13.8; a1, 27.2; a2, 25.5; i1, 21.1; l1, 15.5; l2, 14.1; l3, 12.1; l4, 9.8; l5, 7.8; l6, 5.6; l7, 4.1; l8, 3.1; l9, 3.0; l10, 2.6; l11, 2.0; l12, 2.0; l13, 2.0.

GH-Eug1-02 (271 cm TL; female; caught off South Carolina, U.S.A.), right dentition: S, 21.8; A1, 24.1; A2, 21.6; I1, 9.3; L1, 16.2; L2, 17.1; L3, 16.3; L4, 13.7; L5, 10.6; L6, 8.3; L7, 6.5; L8, 5.5; L9, 4.5; L10, 5.0; L11, 3.0; L12, 3.8; L13, 2.6; L14, 3.4; s, 16.5; a1, 28.7; a2, 27.5; i1, 23.3; l1, 17.8; l2, 15.5; l3, 14.1; l4, 11.6; l5, 8.8; l6, 6.1; l7, 4.5; l8, 5.3; l9, 3.8; l10, 4.5; l11, 3.0; l12, 3.3; l13, 3.1.