化石研究会会誌 Journal of Fossil Research, Vol. 39(1), 7-11(2006)

[Original report]

The relationship between the tooth size and total body length in the common thresher shark, *Alopias vulpinus* (Lamniformes : Alopiidae)

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Abstract

The relationship between the height of tooth crown (CH) and total body length (TL) in the modern common thresher shark, *Alopias vulpinus* (Bonnaterre) (Lamniformes : Alopiidae), 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 regression equations presented here can be used to estimate the TL of fossil *Alopias*.

Key words : alopiid, dentition, elasmobranch, fossil, growth, lamnoid

Introduction

The common thresher, *Alopias vulpinus* (Bonnaterre, 1788) (Fig. 1A), is the most common alopiid shark (Lamniformes) caught nearly worldwide in circumtropical regions. The largest reliably measured individual appears to be 573 cm TL (Cailliet *et al*., 1983), although it is said to reach up to 600-610 cm TL (Compagno, 2001) or possibly more (e.g., 762 cm TL in Paust and Smith, 1986). This shark commonly feeds on small schooling teleosts, such as herring and mackerel, as well as on cephalopods (squids and octopi), pelagic crustaceans (crabs and shrimps), and seabirds (Bigelow and Schroeder, 1948 ; Compagno, 2001). It uses its elongated tail (Fig. 1A) as a stunning device to assist in prey capture (Gubanov, 1972).

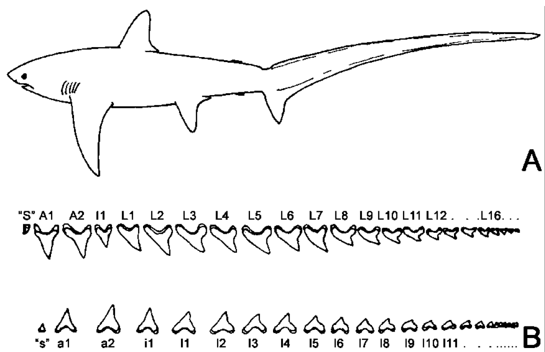

Fig. 1. Modern common thresher shark, *Alopias vulpinus* (Bonnaterre). A, adult individual (after Compagno, 2001 ; see text for size). B, upper and lower dental series in labial view (mesial to the left : see Appendix 1 for size ; after Bass *et al*., 1975). Tooth types based on Shimada (2002a): A, upper anterior tooth; a, lower anterior tooth ; I, upper intermediate tooth ; i, lower intermediate tooth ; L, upper lateral tooth ; l, lower lateral tooth ; "S", upper symphysial tooth ; "s", lower symphysial tooth (parentheses denote the uncertainty in homology : see Shimada, 2002a).

In this paper, I examine the quantitative relationship between tooth crown height (CH) and total body length (TL) in modern *Alopias vulpinus*. This study constitutes the first attempt to demonstrate the correlation between tooth size and body size for

Received : 11th October, 2005, Accepted : 30th May, 2006

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this species. Isolated teeth possibly referable to *A. vulpinus* occur in the fossil record (e.g., Purdy *et al*., 2001), and my ultimate goal is to apply my quantitative data to fossil forms for TL estimation.

Materials and methods

Even though *Alopias vulpinus* is a relatively common alopiid shark, complete specimens with readily measurable teeth as well as jaw specimens with accurate TL data are rare. Nevertheless, I was able to examine a total of eight, non-embryonic jaw samples of *A. vulpinus*, each with a known TL (Appendix 1). They are housed in the following collections: California Academy of Sciences (CAS), San Francisco; Gordon Hubbell collection (GH: JAWS International, Gainsville, Florida) referred to in several scientific papers (e.g., Gruber and Compagno, 1981; Randall, 1987; Purdy *et al*., 2001; Shimada, 2002a); Natural History Museum of Los Angeles County (LACM), California; and Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts. All samples in LACM are housed in its Ichthyology Section except the one labeled as "LACM VP", which is a comparative specimen in the Vertebrate Paleontology Section.

I followed Shimada's (2002a) dental terminology and tooth type identification made for *Alopias vulpinus* (Fig. 1B). Using a calliper, a CH measurement (i.e., the maximum vertical enameloid height on the labial side: Appendix 1) of each tooth in the first (= labialmost or most functional) tooth series was taken from one side of each jaw specimen. When the labialmost tooth was not measurable, the second tooth of the same tooth row (i.e., nearly identical to the first series in CH development) was used to estimate the CH of the first tooth. Then, the CH-TL relationship in 19 upper teeth (A1, A2, I1, and L1-L16) and 17 lower teeth (a1, a2, i1, and l1-l14) was examined using least squares linear regression ($y = a + bx$, where y = TL in cm, x = CH in mm, and a and b constants; $\alpha = 0.05$; see Zar, 1996). The null hypothesis for the analysis was that the CH cannot predict the TL.

Results

The results of the regression analyses are presented in Table 1. All regression lines exhibit positive correlation where the position of y-intercept varies widely. The slope of the lines generally increases from mesially located teeth to distally located teeth for both upper and lower dental series. The correlation coefficient (r) for each line is high (all >0.930), indicating that the bivariate plots are clustered closely along each regression line (e.g., see Fig. 2). The standard error of estimate (SE) 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 <0.005; i.e., showing high statistical significance).

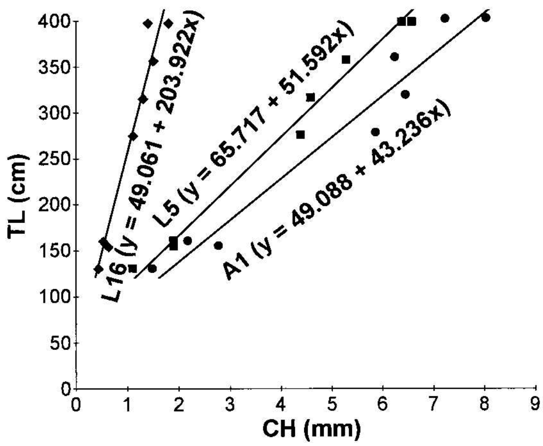

Fig. 2. Bivariate scatter with regression line between crown height (CH) and total body length (TL) for the first upper anterior tooth (A1: circle), fifth upper lateral tooth (L5: square), and sixteeth upper lateral tooth (L 16: diamond) in modern *Alopias vulpinus* (n = 8; for measurements, see Appendix 1; for statistics of regression line, see Table 1).

Discussion

A high r-value and a low p-value in all regression lines (Table 1) suggest that the CH can be used to estimate the TL in *Alopias vulpinus*, although this estimation should be regarded as a first approximation due to the small sample size (n = 8). A positive correlation for each regression line indicates that an increase in the CH through replacement is proportional to increases in the TL. The general increase in the slope of regression lines from mesially located teeth to distally located teeth (e.g., Fig. 2) suggests that, through replacement, the rate of size increase for distally located teeth is greater than that of mesially located teeth.

The regression equations presented here can be used to infer the TL of fossil *Alopias* individuals,

Table 1. Regression analyses between tooth crown height (CH) and total body length (TL) among individuals of *Alopias vulpinus* (n = 8 ; cf. Fig. 2 ; for tooth types, see Fig. 1B ; x = CH in mm ; y = TL in cm ; degrees of freedom = 1,6). Statistical notations : r, correlation coefficient ; p, probability of estimates ("0.000" means <0.001 ; asterisk indicates probability with <5% chance of error) ; SE, standard error of estimates.

x	Regression equation	r	F-ratio	p	SE
Upper teeth					
A1	y = 49.088 + 43.236 x	0.977	128.213	0.000*	25.319
A2	y = 53.080 + 41.663 x	0.982	161.248	0.000*	22.681
I1	y = 100.441 + 56.933 x	0.966	83.192	0.000*	31.059
L1	y = 56.382 + 50.027 x	0.954	60.543	0.000*	35.958
L2	y = 42.895 + 47.892 x	0.988	243.053	0.000*	18.587
L3	y = 62.569 + 49.025 x	0.987	222.757	0.000*	19.394
L4	y = 65.279 + 49.400 x	0.984	178.160	0.000*	21.615
L5	y = 65.717 + 51.592 x	0.994	518.699	0.000*	12.805
L6	y = 75.236 + 50.968 x	0.980	145.471	0.000*	23.833
L7	y = 77.996 + 55.427 x	0.985	200.988	0.000*	20.388
L8	y = 81.364 + 57.966 x	0.980	147.916	0.000*	23.643
L9	y = 84.469 + 67.769 x	0.971	97.545	0.000*	28.826
L10	y = 83.540 + 76.316 x	0.962	74.257	0.000*	32.742
L11	y = 89.181 + 82.321 x	0.964	78.876	0.000*	31.839
L12	y = 98.792 + 87.841 x	0.935	41.718	0.001*	42.463
L13	y = 88.525 + 108.735 x	0.967	85.516	0.000*	30.662
L14	y = 103.377 + 118.259 x	0.935	41.727	0.001*	42.459
L15	y = 109.808 + 132.175 x	0.883	21.205	0.004*	56.237
L16	y = 49.061 + 203.922 x	0.993	421.173	0.000*	14.192
Lower teeth					
a1	y = 82.881 + 46.891 x	0.959	68.953	0.000*	33.881
a2	y = 59.661 + 48.710 x	0.993	400.962	0.000*	14.540
i1	y = 53.643 + 53.593 x	0.995	563.042	0.000*	12.296
l1	y = 68.936 + 54.336 x	0.986	211.573	0.000*	19.886
l2	y = 71.072 + 56.787 x	0.986	215.576	0.000*	19.706
l3	y = 64.433 + 62.371 x	0.990	284.000	0.000*	17.225
l4	y = 62.767 + 68.213 x	0.985	198.518	0.000*	20.511
l5	y = 62.748 + 72.630 x	0.984	178.455	0.000*	21.598
l6	y = 58.089 + 83.606 x	0.990	284.825	0.000*	17.200
l7	y = 70.694 + 90.584 x	0.990	297.939	0.000*	16.825
l8	y = 75.375 + 99.000 x	0.990	288.779	0.000*	17.084
l9	y = 83.214 + 111.859 x	0.965	80.621	0.000*	31.517
l10	y = 71.527 + 140.416 x	0.957	65.718	0.000*	34.637
l11	y = 55.188 + 176.313 x	0.954	60.684	0.000*	35.920
l12	y = 81.940 + 174.032 x	0.934	41.242	0.001*	42.676
l13	y = 62.089 + 201.225 x	0.970	96.087	0.000*	29.031
l14	y = 65.676 + 227.615 x	0.947	51.942	0.000*	38.535

which are represented only by isolated teeth (e.g., Cappetta, 1987). For example, Purdy *et al.* (2001) reported teeth of Neogene "*A.* cf. *A. vulpinus*". The fossil teeth ranged up to 15 mm in total tooth height, and Purdy *et al.* (2001) estimated that those teeth probably came from individuals that ranged up to about 6 m TL. However, they did not provide any explanations as to how they derived their estimates. Purdy *et al.* (2001) did not give the CH of those fossil teeth, but the maximum CH is extrapolated to be approximately 13 mm (cf. Fig. 1B). A conservative TL estimate is possible for fossil individuals that carried those teeth based on three assumptions : 1) that those teeth represent the largest teeth on the jaws (generally the A1 or A2) ; 2) that the CH of those teeth has a similar relationship to the TL as modern *A. vulpinus* ; and 3) that it is admissible to extend the regression line below the lowest plot and above the highest plot. When the CH of 13 mm is applied to the regression equation for the A1 and A2 (Table 1), the TL of the fossil "*A.* cf. *A. vulpinus*" is estimated to be about 611 cm and 595 cm, respectively, agreeing well with the estimation made by Purdy *et al.* (2001). However, unlike Purdy *et al.*'s (2001) study, the use of regression equations here provides a powerful justification that was not possible in the past. To note, such quantitative inferences about the body length of sharks from their teeth are found not only useful to paleontology but also to modern sharks which are represented only by jaw specimens from individuals of unknown length. Some recent studies demonstrating this practice include papers by Randall (1987), Lucifora *et al.* (2001), Shimada (2002b, 2003, 2005), and Shimada and Seigel (2005).

Acknowledgments

I thank the following individuals involved in access to the shark specimens: D. Catania, T. Iwamoto (CAS); G. Hubbell (JAWS International); J. Seigel, J. D. Stewart (LACM); and K. E. Hartel (MCZ). I also wish to thank the following individuals for their direct and/or indirect assistance for this study: D. Bardack, L. Grande, W. S. Greaves, K. Hubbell, R. Plotnick, and T. Poulson, and L. K. Shimada.

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Appendix 1

Examined *Alopias vulpinus* 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).

CAS 65976 (155 cm TL ; female ; off California, U.S.A.), left dental series : A1, 2.9 ; A2, 2.7 ; I1, 1.0 ; L1, 2.6 ; L2, 2.7 ; L3, 2.2 ; L4, 2.2 ; L5, 1.9 ; L6, 1.9 ; L 7, 1.7 ; L8, 1.6 ; L9, 1.4 ; L10, 1.3 ; L11, 1.2 ; L12, 1.0 ; L13, 0.9 ; L14, 0.8 ; L15, 0.7 ; L16, 0.6 ; L17, 0.5 ; "s", 0.8 ; a1, 2.0 ; a2, 2.1 ; i1, 1.9 ; l1, 1.6 ; l2, 1.6 ; l3, 1.6 ; l 4, 1.6 ; l5, 1.6 ; l6, 1.3 ; l7, 1.1 ; l8, 1.0 ; l9, 0.9 ; l10, 0.8 ; l11, 0.7 ; l12, 0.6 ; l13, 0.6 ; l14, 0.5.

LACM 39325-1 (356 cm TL ; sex unknown ; off California, U.S.A.), left dental series : A1, 6.4 ; A2, 6.9 ; I1, 3.5 ; L1, 5.0 ; L2, 6.1 ; L3, 5.7 ; L4, (5.4) ; L5, 5.3 ; L6, 4.7 ; L7, 4.5 ; L8, 4.2 ; L9, 3.6 ; L10, 3.2 ; L11, 3.0 ; L12, 2.5 ; L13, 2.1 ; L14, 1.8 ; L15, 1.5 ; L16, 1.5 ; L17, 1.5 ; L18, 1.1 ; L19, 1.0 ; L20, 1.0 ; L21, 0.9 ; a1, (4.8) ; a2, 5.5 ; i1, 5.2 ; l1, (4.7) ; l2, (4.4) ; l3, 4.2 ; l4, 3.8 ; l5, 3.6 ; l6, 3.2 ; l7, (3.0) ; l8, 2.6 ; l9, 2.0 ; l10, 1.6 ; l11, 1.4 ; l12, 1.1 ; l13, 1.2 ; l14, 1.2 ; l15, 1.1 ; l16, 1.1 ; l17, 1.0 ; l18, 1.0 ; l19, 0.8 ; l20, 0.6

LACM 39342-1 (131 cm TL ; male ; locality unknown), left dental series : A1, 1.6 ; A2, 1.7 ; I1, 0.8 ; L1, 1.4 ; L2, 1.8 ; L3, 1.2 ; L4, 1.1 ; L5, 1.1 ; L6, 1.1 ; L7, 1.0 ; L8, 1.0 ; L9, 0.9 ; L10, 0.8 ; L11, 0.7 ; L 12, 0.6 ; L13, 0.5 ; L14, 0.4 ; L15, 0.4 ; L16, 0.4 ; s, 0.7 ; a1, 1.2 ; a1, 1.5 ; i1, 1.5 ; l1, 1.3 ; l2, 1.0 ; l3, 0.9 ; l4, 0.9 ; l5, 0.8 ; l6, 0.7 ; l7, 0.6 ; l8, 0.5 ; l9, 0.5 ; l10, 0.5 ; l 11, 0.5 ; l12, 0.4 ; l13, 0.4 ; l14, 0.4.

LACM VP (161 cm TL; female; locality unknown), right dental series : A1, 2.3 ; A2, 2.6 ; I1, 1.3 ; L1, 2.2 ; L2, 2.3 ; L3, 2.1 ; L4, 2.0 ; L5, 1.9 ; L6, 1.7 ; L7, 1.5 ; L8, 1.4 ; L9, 1.1 ; L10, 1.0 ; L11, 0.8 ; L 12, 0.8 ; L13, 0.6 ; L14, 0.5 ; L15, 0.5 ; L16, 0.5 ; s, 0.9 ; a1, 1.9 ; a2, 2.2 ; i1, 2.0 ; l1, 2.0 ; l2, 1.9 ; l3, 1.8 ; l4, 1.6 ; l5, 1.5 ; l6, 1.3 ; l7, 1.1 ; l8, 0.9 ; l9, 0.7 ; l10, 0.6 ; l 11, 0.5 ; l12, 0.4 ; l13, 0.4 ; l14, 0.3.

MCZ 36089 (397 cm TL ; sex unknown ; off Massachusetts, U.S.A.), left dental series : A1, 8.2 ; A 2, (8.8) ; I1, 5.5 ; L1, 6.8 ; L2, 7.8 ; L3, 6.6 ; L4, (6.5) ; L 5, (6.4) ; L6, (6.3) ; L7, (6.2) ; L8, (6.1) ; L9, 5.3 ; L10, 4.8 ; L11, 4.3 ; L12, 4.1 ; L13, 3.2 ; L14, (3.0) ; L15, 2.7 ; L16, 1.8 ; L17, 1.5 ; s, 3.1 ; a1, (6.1) ; a2, (7.1) ; i1, (6.7) ; l1, (6.4) ; l2, 6.0 ; l3, (5.5) ; l4, (5.0) ; l5, (4.5) ; l6, (4.1) ; l 7, (3.9) ; l8, 3.5 ; l9, 3.2 ; l10, 2.6 ; l11, 2.1 ; l12, 2.0 ; l 13, 1.8 ; l14, 1.6 ; l15, 1.1 ; l16, 0.9 ; l17, 0.8.

GH-Alop2-01 (397 cm TL ; sex unknown ; off United Kingdom), left dental series : A 1, 7.4 ; A 2, 7.5 ; I1, 5.5 ; L1, 7.1 ; L2, 7.2 ; L3, 7.2 ; L4, 7.1 ; L5, 6.6 ; L6, 6.8 ; L7, 5.8 ; L8, 5.3 ; L9, 4.3 ; L10, 3.6 ; L11, 3.3 ; L12, 2.7 ; L13, 2.6 ; L14, 2.1 ; L15, 1.5 ; L16, 1.4 ; L17, 1.4 ; L18, 0.5 ; s, 2.5 ; a1, 7.8 ; a2, 7.2 ; i1, 6.3 ; l1, 6.3 ; l2, 6.0 ; l3, 5.5 ; l4, 5.2 ; l5, 5.0 ; l6, 4.0 ; l7, 3.5 ; l8, 3.2 ; l9, 2.6 ; l10, 2.2 ; l11, 1.7 ; l12, 1.7 ; l13, 1.6 ; l14, 1.2 ; l15, 0.9 ; l16, 0.5.

GH-Alop2-02 (315 cm TL; male; off New York, U.S.A.), right dental series : S, 1.6 ; A1, 6.6 ; A 2, 6.0 ; I1, 3.2 ; L1, 4.3 ; L2, 5.3 ; L3, 4.6 ; L4, 4.6 ; L5, 4.6 ; L6, 4.3 ; L7, 3.8 ; L8, 3.7 ; L9, 3.0 ; L10, 2.8 ; L11, 2.7 ; L12, 2.4 ; L13, 2.2 ; L14, 1.5 ; L15, 1.4 ; L16, 1.3 ; L17, 1.3 ; L18, 1.3 ; L19, 1.1 ; L20, 1.0 ; s, 1.5 ; a1, 4.5 ; a2, 5.3 ; i1, 5.0 ; l1, 4.2 ; l2, 4.0 ; l3, 3.8 ; l4, 3.4 ; l5, 3.4 ; l6, 3.3 ; l7, 2.5 ; l8, 2.3 ; l9, 2.1 ; l10, 1.6 ; l11, 1.6 ; l12, 1.3 ; l13, 1.3 ; l14, 1.0 ; l15, 1.0 ; l16, 0.9 ; l17, 0.8 ; l18, 0.7 ; l19, 0.7.

GH-Alop2-03 (275 cm TL ; sex unknown ; off California, U.S.A.), left dental series : A1, 6.0 ; A2, 6.1 ; I1, 3.5 ; L1, 5.3 ; L2, 5.3 ; L3, 4.8 ; L4, 4.8 ; L5, 4.4 ; L6, 4.3 ; L7, 3.7 ; L8, 3.2 ; L9, 2.7 ; L10, 2.4 ; L11, 1.9 ; L12, 1.8 ; L13, 1.5 ; L14, 1.4 ; L15, 1.2 ; L16, 1.1 ; L17, 1.0 ; L18, 1.0 ; L19, 0.8 ; L20, 0.7 ; L21, 0.6 ; a1, 4.2 ; a2, 4.2 ; i1, 4.2 ; l1, 3.6 ; l2, 3.6 ; l3, 3.5 ; l4, 3.2 ; l 5, 2.8 ; l6, 2.7 ; l7, 2.2 ; l8, 2.0 ; l9, 1.6 ; l10, 1.6 ; l11, 1.4 ; l12, 1.3 ; l13, 1.1 ; l14, 1.1 ; l15, 1.1 ; l16, 1.0 ; l17, 0.9 ; l18, 0.6 ; l19, 0.6 ; l20, 0.6 ; l20, 0.4.

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