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［Original report］

Tooth sizes as a proxy for estimating body lengths in the porbeagle shark, *Lamna nasus*

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Abstract

The porbeagle shark, *Lamna nasus* (Bonnaterre), is an extant lamniform shark. We used linear regression analysis to quantitatively examine the relationships between the total body length (TL) and height of the tooth crown (CH) of each tooth in 19 *Lamna nasus* individuals ranging 104-244 cm TL from northern Atlantic Ocean. We obtained a total of 25 independent regression equations, and they all suggest that increase in CH of each tooth through tooth replacements is proportional to increase in TL with a high correlation coefficient between TL and CH. Our regression equations can increase the efficiency of the TL data collection from captured individuals useful for ecological monitoring. They can also be used to extrapolate the TL of fossil *L. nasus* from teeth that would help paleoecological inferences.

Key words: dentition, fossil, growth, jaw, Lamniformes, Lamnidae

Introduction

Lamna nasus (Bonnaterre) (porbeagle shark: Fig. 1A), is a coastal-oceanic lamniform shark that has been heavily fished commercially in the North Atlantic and Mediterranean for human consumption (Compagno, 2001; Hurley, 1998). Although commercial fishing of the porbeagle at least in Northwest Atlantic is carefully monitored for stock management, population structures of the species in other regions, including cold-temperate regions of the Southern Hemisphere, are not well understood because the species is generally caught sporadically as bycatch through longline fishery (Campana *et al.*, 2008).

One biological parameter that is usually

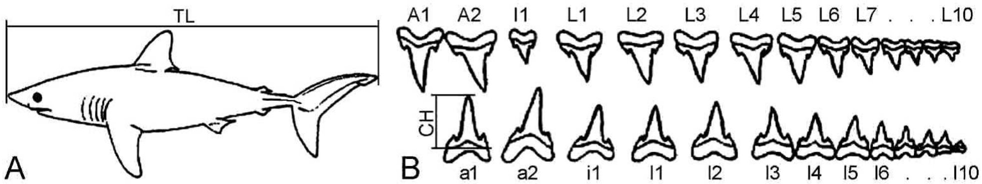

Fig. 1. Porbeagle shark, *Lamna nasus* (Bonnaterre). A, Adult individual showing total length (TL) measurement ; B, Upper and lower dental series in labial view (mesial to the left) showing tooth types and crown height (CH) measurement. Tooth types based on Shimada (2002a) : A, upper anterior tooth ; a, lower anterior tooth ; I, upper intermediate tooth ; i, lower intermediate tooth ; L, upper lateral tooth ; l, lower lateral tooth. Illustrations modified after Bigelow and Schroeder (1948).

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important for population studies is the size information of individuals in each population. This is particularly true for large top predators that affect lower trophic levels. *Lamna nasus* is considered to be such a predator because it opportunistically feeds on a variety of fishes and may reach up to 370 cm TL (Bigelow and Schroeder, 1948; Compagno, 2001). In this paper, we examine the relationship of the total body length (TL: Fig. 1A) with the tooth crown height (CH: Fig. 1B) in non-embryonic, modern *L. nasus*. Whereas ontogenetic changes in dental morphology between embryonic and non-embryonic individuals of *L. nasus* have been examined previously (Shimada, 2002c; Purdy and Francis, 2007), this study constitutes the first attempt to demonstrate the correlation between tooth size and body size for this species. Our quantitative data can be used as a powerful tool to estimate the body length of porbeagle individuals for ecological and paleoecological studies of the species.

Materials and Methods

Lamna nasus is a relatively common shark in northern Atlantic, but complete specimens with readily measurable teeth and jaw specimens with accurate TL data are rare. Nevertheless, we were able to examine a total of 19 jaw samples of *L. nasus*, each with a known TL (Appendix 1). They are housed in the following two collections: Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, and Gordon Hubbell collection (GH: JAWS International, Gainesville, Florida; Hubbell, 1996).

We followed Shimada's (2002a) dental terminology and tooth type identification made for *Lamna nasus* (Fig. 1B). Using a caliper, a CH measurement (i.e., the maximum vertical enameloid height on the labial surface) 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 was used to estimate the CH of the first tooth. Then, the CH-TL relationship in 13 upper teeth (A1, A2, I1, and L1-L10) and 12 lower teeth (a1, a2, i1, and l1-l9) 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 ≥ 0.798), 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 ≤ 0.002 indicating high statistical significance).

Table 1. Regression analyses between tooth crown height (CH) and total body length (TL) among individuals of *Lamna nasus* (n = 19; 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 (asterisk indicates probability with <5% chance of error).

x	Regression equation	r	p
Upper teeth			
A1	y = −54.608 + 20.677x	0.963	0.001*
A2	y = −51.640 + 21.794x	0.953	0.001*
I1	y = 53.266 + 27.772x	0.873	0.002*
L1	y = −2.410 + 22.428x	0.874	0.001*
L2	y = −23.952 + 23.105x	0.921	0.0009*
L3	y = −32.514 + 24.920x	0.947	0.001*
L4	y = −20.456 + 25.461x	0.934	0.001*
L5	y = −6.063 + 25.800x	0.931	0.001*
L6	y = 7.672 + 27.383x	0.915	0.001*
L7	y = 27.137 + 29.859x	0.895	0.001*
L8	y = 24.342 + 37.848x	0.856	0.001*
L9	y = 55.288 + 39.547x	0.798	0.001*
L10	y = 52.800 + 51.737x	0.869	0.001*
Lower teeth			
a1	y = −50.561 + 18.892x	0.900	0.001*
a2	y = −73.273 + 20.533x	0.907	0.001*
i1	y = −47.737 + 23.788x	0.949	0.001*
l1	y = −16.904 + 21.647x	0.923	0.001*
l2	y = −30.356 + 23.944x	0.932	0.001*
l3	y = −26.651 + 25.176x	0.918	0.002*
l4	y = −41.766 + 28.861x	0.937	0.001*
l5	y = −5.562 + 27.912x	0.887	0.001*
l6	y = 6.792 + 30.330x	0.867	0.001*
l7	y = 47.681 + 30.980x	0.867	0.001*
l8	y = 34.430 + 42.785x	0.920	0.001*
l9	y = 28.175 + 68.315x	0.814	0.001*

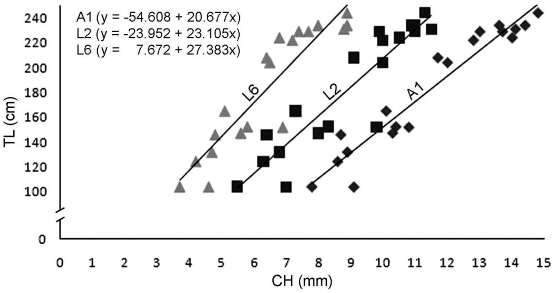

Fig. 2. Bivariate scatter with regression line between tooth crown height (CH) and total body length (TL) for the first upper anterior tooth (A1 : diamond), second upper lateral tooth (L2 : square), and sixth upper lateral tooth (L6 : triangle) in *Lamna nasus* from the northern Atlantic Ocean (n = 19; for tooth types, see Fig. 1B ; for statistics of regression lines, see Table 1 ; for measurements, see Appendix 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 *Lamna nasus*. A positive correlation for each regression line indicates that an increase in the CH through replacement is proportional to increases in the TL (Fig. 2). The general increase in the slope of regression lines from mesially located teeth to distally located teeth suggests that, through replacement, the rate of size increase for distally located teeth is greater than that of mesially located teeth. It is noteworthy that the same trend is also present in several other lamniform species in which CH-TL relationships are examined to date (Shimada, 2002b, 2003, 2005, 2006 ; Shimada and Seigel, 2005).

Because of a directed fishery for *Lamna nasus* (Hurley, 1998), the porbeagle population may be under stress in the northern Atlantic (Campana *et al*., 2008). Stock monitoring is critical for any conservation effort, and gathering basic biological information, including body size data, for the species is vital for such effort. Because of their high TL predictability, our tooth-based regression equations have the potential to increase the efficiency of the TL data collection from captured individuals because of some advantages. For example, teeth are durable, and collecting and preserving them are relatively easy. Therefore, TL measurements can be taken later in time without the need of preserving the whole body. Because individual teeth are small, the impact to the weight of each shark by the removal of teeth is negligibly small which in turn does not affect the commercial value of the shark. The collection of teeth is also possible after decapitation of the head after the rest of the body is sold on market. It is also noteworthy that our regression equations can also be used to extrapolate the TL of porbeagle individuals represented only by their jaws without any body size data, including specimens housed in museum collections.

Sharks have been top predators in marine ecosystems through geologic time, and estimating the size of fossil sharks is vital for deciphering paleoecological dynamics of prehistoric seas (e.g., Shimada, 2008). The genus *Lamna* was apparently in existence by the Oligocene (Cappetta, 1987), and remains of *L. nasus* are known sporadically in post-Oligocene marine deposits (e.g., Mollen, 2010). For example, Herman *et al*. (1974) described two fossil teeth of *L. nasus*. The larger tooth (Herman *et al*., 1974, pl. 2, fig. 3a) that has a CH of 7 mm is considered to be a mesially located lateral tooth, such as one from the upper second lateral tooth row (L2). A conservative TL estimate is possible for the fossil individual that carried the tooth based on two assumptions: 1) that the tooth represents the largest lateral tooth on the jaws, and 2) that the CH of the tooth has a similar relationship to the TL as modern *L. nasus*. By using the regression equation for L2, our calculation suggests that the fossil tooth came from an individual that likely measured about 137.8 cm TL. Such a calculation demonstrates the usefulness of our regression equations, not only for applications to ecological studies, but also to paleontological applications.

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Appendix 1.

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

MCZ 36251 (165 cm TL ; sex unknown ; Gulf of Maine) : A1, 10.1 ; A2, 9.2 ; I1, 3.5 ; L1, 7.0 ; L2, 7.3 ; L3, 7.4 ; L4, 7.0 ; L5, 6.0 ; L6, 5.1 ; L7, 4.5 ; L8, 3.9 ; L9, 3.3 ; L10, 2.2 ; L11, 1.7 ; a1, 10.9 ; a2, 11.1 ; i1, 7.9 ; l1, 7.8 ; l2, 7.7 ; l3, 7.2 ; l4, 7.1 ; l5, 5.8 ; l6, 4.8 ; l7, 4.1 ; l8, 2.6 ; l9, 2.1 ; l10, 1.5.

MCZ 36252 (146 cm TL ; sex unknown ; Gulf of Maine) : A1, 8.7 ; A2, 8.2 ; I1, 2.6 ; L1, 6.0 ; L2, 6.4 ; L3, 6.5 ; L4, 6.3 ; L5, 4.9 ; L6, 4.8 ; L7, 3.1 ; L8, 2.8 ; L9, 2.0 ; L10, 1.5 ; L11, 1.0 ; a1, 10.2 ; a2, 10.5 ; i1, 7.3 ; l1, 6.9 ; l2, 7.1 ; l3, 6.5 ; l4, 6.3 ; l5, 5.3 ; l6, 4.5 ; l7, 3.0 ; l8, 2.3 ; l9, 1.5.

MCZ 36253 (104 cm TL ; sex unknown ; Gulf of Maine) : A1, 7.8 ; A2, 7.3 ; I1, 2.9 ; L1, 4.9 ; L2, 5.5 ; L3, 5.7 ; L4, 4.9 ; L5, 4.6 ; L6, 3.7 ; L7, 3.3 ; L8, 2.7 ; L9, 2.2 ; L10, 1.3 ; L11, 1.0 ; a1, 9.3 ; a2, 8.7 ; i1, 6.4 ; l1, 6.0 ; l2, 5.7 ; l3, 5.7 ; l4, 5.5 ; l5, 4.5 ; l6, 3.8 ; l7, 2.8 ; l8, 2.2 ; l9, 1.6 ; l10, 0.9 ; l11, 0.4.

MCZ 36254 (147 cm TL ; sex unknown ; Gulf of Maine) : A1, 10.3 ; A2, 9.8 ; I1, 3.8 ; L1, 7.5 ; L2, 8.0 ; L3, 7.6 ; L4, 6.8 ; L5, 6.6 ; L6,5.6 ; L7, 4.9 ; L8, 3.7 ; L9, 3.2 ; L10, 1.8 ; L11, 1.3 ; L12, 1.2 ; L13, 1.0 ; a1, 10.5 ; a2, 11.3 ; i1, 8.6 ; l1, 8.5 ; l2, 7.7 ; l3, 7.7 ; l4, 7.3 ; l5, 6.5 ; l6, 5.8 ; l7, 4.3 ; l8, 3.7 ; l9, 2.4 ; l10, 1.1.

MCZ 36255 (124 cm TL ; sex unknown ; Gulf of Maine) : A1, 8.6 ; A2, 7.7 ; I1, 2.2 ; L1, 5.2 ; L2, 6.3 ; L3, 6.4 ; L4, 6.0 ; L5, 5.2 ; L6, 4.2 ; L7, 3.5 ; L8, 2.5 ; L9, 1.7 ; L10, 1.5 ; L11, 1.0 ; a1, 9.0 ; a2, 10.0 ; i1, 7.7 ; l1, 7.0 ; l2, 6.6 ; l3, 6.3 ; l4, 5.8 ; l5, 4.7 ; l6, 4.2 ; l7, 2.8 ; l8, 2.2 ; l9, 1.5 ; l10, 1.0.

MCZ 36257 (132 cm TL ; sex unknown ; Gulf of Maine) : A1, 8.9 ; A2, 8.3 ; I1, 3.1 ; L1, 6.0 ; L2, 6.8 ; L3, 6.5 ; L4, 5.8 ; L5, 5.2 ; L6, 4.7 ; L7, 2.7 ; L8, 2.9 ; L9, 1.6 ; L10, 1.7 ; L11, 1.2 ; L12, 1.0 ; a1, 9.6 ; a2, 9.6 ; i1, 7.7 ; l1, 6.8 ; l2, 6.9 ; l3, 6.1 ; l4, 5.6 ; l5, 4.8 ; l6, 4.3 ; l7, 3.0 ; l8, 2.3 ; l9, 1.5 ; l10, 1.2.

MCZ 36258 (152 cm TL ; sex unknown ; Gulf of Maine) : A1, 10.4 ; A2, 9.8 ; I1, 4.5 ; L1, 7.8 ; L2, 8.3 ; L3, 7.7 ; L4, 7.3 ; L5, 6.6 ; L6, 5.8 ; L7, 4.8 ; L8, 4.0 ; L9, 3.0 ; L10, 3.0 ; L11,2.3 ; a1,11.6 ; a2, 11.8 ; i1, 9.0 ; l1, 8.0 ; l2, 8.3 ; l3, 7.5 ; l4, 7.4 ; l5,6.1 ; l6, 5.2 ; l7, 3.9 ; l8, 3.3 ; l9, 2.5 l10, 1.5.

GH-Lamn 1-03 (234 cm TL ; female ; "north Atlantic") : A1, 14.4 ; A2,13.8 ; I1, 7.2 ; L1, 10.6 ; L2, 11.0 ; L3, 10.8 ; L4, 10.3 ; L5, 9.6 ; L6, 8.9 ; L7, 7.2 ; L8, 5.2 ; L9, 4.3 ; L10, 3.6 ; L11, 2.4 ; L12, 1.5 ; a1, 15.8 ; a2, 15.8 ; i1, 12.2 ; l1, 12.5 ; l2, 11.8 ; l3, 11.6 ; l4, 10.4 ; l5, 10.3 ; l6, 9.3 ; l7, 7.6 ; l8, 4.9 ; l9, 3.3 ; l10, 2.2 ; l11, 1.8.

GH-Lamn 1-04 (229 cm TL ; male ; "north Atlantic") : A1, 13.0 ; A2, 12.2 ; I1, 6.3 ; L1, 8.0 ; L2, 9.9 ; L3, 9.4 ; L4, 8.5 ; L5, 8.4 ; L6, 7.4 ; L7, 6.1 ; L8, (5.0) ; L9, 3.7 ; L10, 2.7 ; L11, 1.8 ; a1, 13.2 ; a2, 13.6 ; i1, 11.1 ; l1, 11.0 ; l2, 10.1 ; l3, 9.0 ; l4, 8.5 ; l5, 7.7 ; l6, 6.5 ; l7, 5.0 ; l8, 3.9 ; l9, 2.7 ; l10, 1.6 ; l11, 1.0.

GH-Lamn 1-10 (234 cm TL ; male ; "north Atlantic") : A1, 13.6 ; A2, (12.2) ; I1, 5.8 ; L1, 10.1 ; L 2, 10.9 ; L3, 10.5 ; L4, 9.8 ; L5, 8.7 ; L6, 8.0 ; L7, 6.9 ; L8, 5.4 ; L9, 4.3 ; L10, 3.3 ; L11, 2.4 ; a1, 13.1 ; a2, 12.7 ; i1, 11.6 ; l1, 12.0 ; l2, 12.0 ; l3, 10.9 ; l4, 9.8 ; l5, 8.1 ; l6, 7.6 ; l7, 6.2 ; l8, 5.0 ; l9, 2.9 ; l10, 2.3.

GH-Lamn 1-11 (229 cm TL ; female ; "north Atlantic") : A1, 13.7 ; A2, 12.6 ; I1, 7.0 ; L1, 10.1 ; L2, 11.0 ; L3, 10.3 ; L4, 9.7 ; L5, 8.6 ; L6, 7.7 ; L7, 6.6 ; L8, 5.0 ; L9, 3.5 ; L10, 2.9 ; L11, 2.0 ; a1, 15.1 ; a2, 14.9 ; i1, 11.2 ; l1, 11.1 ; l2, 10.6 ; l3, 9.5 ; l4, 9.3 ; l5, 8.0 ; l6, 6.5 ; l7, 5.4 ; l8, 4.6 ; l9, 2.6 ; l10, 2.2.

GH-Lamn 1-12 (231 cm TL ; female ; "north Atlantic") : A1, 14.1 ; A2, (13.0) ; I1, 6.0 ; L1, 10.7 ; L2, 11.5 ; L3, 11.5 ; L4, 10.8 ; L5, 9.9 ; L6, 8.8 ; L7, 6.9 ; L8, 5.8 ; L9, 4.7 ; L10, 3.2 ; L11, 2.7 ; a1, 14.6 ; a2, 14.4 ; i1, 12.2 ; l1, 11.3 ; l2, 10.9 ; l3, 10.2 ; l4, 9.0 ; l5, 8.0 ; l6, (7.0) ; l7, (5.3) ; l8, 4.0 ; l9, 2.1 ; l10, 2.0.

GH-Lamn 1-20 (224 cm TL ; male ; "north Atlantic") : A1, 14.0 ; A2, 13.1 ; I1, 6.7 ; L1, 9.6 ; L2, 10.5 ; L3, 10.0 ; L4, 8.5 ; L5, 8.0 ; L6, 6.8 ; L7, 5.8 ; L8, 4.8 ; L9, (3.7) ; L10, 3.0 ; L11, 1.8 ; a1, 15.3 ; a2, (15.3) ; i1, 12.2 ; l1, 10.3 ; l2, 10.0 ; l3, (9.1) ; l4, 8.7 ; l5, 7.1 ; l6, 6.5 ; l7, (5.0) ; l8, 4.3 ; l9, 2.2 ; l10, 1.7.

GH-Lamn 1-21 (244 cm TL ; female ; "north Atlantic") : A1, 14.8 ; A2, (13.9) ; I1, 4.8 ; L1, 10.5 ; L2, (11.3) ; L3, 11.2 ; L4, 10.8 ; L5, 10.0 ; L6, 8.9 ; L7, 7.7 ; L8, 6.3 ; L9, 5.1 ; L10, 4.2 ; L11, 2.8 ; a1, (16.6) ; a2, (16.0) ; i1, 12.0 ; l1, 12.6 ; l2, 11.6 ; l3, 10.6 ; l4, 10.5 ; l5, 9.2 ; l6, 7.3 ; l7, 6.2 ; l8, 5.1 ; l9, 3.1.

GH-Lamn 1-28 (152 cm TL ; female ; "north Atlantic") : A1, 10.8 ; A2, 10.2 ; I1, 4.1 ; L1, 9.5 ; L2, 9.8 ; L3, 8.9 ; L4, 8.2 ; L5, 7.9 ; L6, 6.9 ; L7, 5.3 ; L8, 4.3 ; L9, 3.5 ; L10, 2.7 ; L11, 2.0 ; L12, 1.5 ; a1, 10.8 ; a2, 12.1 ; i1, 8.2 ; l1, 8.2 ; l2, 8.0 ; l3, 7.0 ; l4, 6.5 ; l5, 6.0 ; l6, 4.7 ; l7, 3.5 ; l8, 2.8 ; l9, 2.3 ; l10, 0.9.

GH-Lamn 1-34 (208 cm TL ; female ; "north Atlantic") : A1, 11.7 ; A2, 11.5 ; I1, 5.2 ; L1, 8.6 ; L2, 9.1 ; L3, 9.1 ; L4, 8.5 ; L5, 7.5 ; L6, 6.4 ; L7, 5.3 ; L8, 3.8 ; L9, (2.9) ; L10, 2.7 ; L11, 1.5 ; a1, 12.8 ; a2, 12.4 ; i1, 10.1 ; l1, 8.6 ; l2, 8.4 ; l3, 8.1 ; l4, 7.9 ; l5, 6.9 ; l6, 5.8 ; l7, 3.8 ; l8, 3.6 ; l9, 2.7.

GH-Lamn 1-39 (204 cm TL ; male ; "north Atlantic") : A1, (12.0) ; A2, 11.2 ; I1, 5.1 ; L1, (9.6) ; L2, (10.0) ; L3, 9.7 ; L4, (8.2) ; L5, (8.0) ; L6, (6.5) ; L7, (5.3) ; L8, (3.4) ; L9, (2.5) ; L10, (2.3) ; L11, 1.3 ; L12, 1.2 ; a1, (13.6) ; a2, (13.6) ; i1, 10.5 ; l1, 10.3 ; l2, 9.5 ; l3, 9.8 ; l4, 8.3 ; l5, 6.7 ; l6, 5.9 ; l7, (4.6) ; l8, 3.5 ; l9, 2.2 ; l10, 1.0.

GH-Lamn 1-43 (222 cm TL ; male ; "north Atlantic") : A1, 12.8 ; A2, 12.2 ; I1, 5.0 ; L1, 9.2 ; L2, 10.0 ; L3, 9.3 ; L4, 9.0 ; L5, 8.3 ; L6, 7.2 ; L7, 5.6 ; L8, 4.9 ; L9, 3.8 ; L10, 3.0 ; a1, 12.5 ; a2, (13.2) ; i1, 10.8 ; l1, 9.5 ; l2, (9.5) ; l3, 9.1 ; l4, 8.3 ; l5, 7.4 ; l6, 6.3 ; l7, 4.3 ; l8, (4.1) ; l9, (2.7) ; l10, (1.8).

GH-Lamn 1-44 (104 cm TL ; male ; "north Atlantic") : A1, 9.1 ; A2, 8.8 ; I1, 3.3 ; L1, 6.6 ; L2, 7.0 ; L3, 6.2 ; L4, 5.8 ; L5, 5.6 ; L6, 4.6 ; L7, 4.0 ; L8, 3.5 ; L9, 2.6 ; L10, 1.4 ; a1, 10.9 ; a2, 10.6 ; i1, 8.0 ; l1, 7.5 ; l2, 7.3 ; l3, 6.7 ; l4, 6.1 ; l5, 5.6 ; l6, 4.7 ; l7, 2.5 ; l8, 1.8 ; l9, 1.3 ; l10, 0.5.