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[Original report]

# The relationship between the tooth size and total body length in the goblin shark, *Mitsukurina owstoni* (Lamniformes: Mitsukurinidae)

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## Abstract

The goblin shark, *Mitsukurina owstoni* Jordan (Lamniformes: Mitsukurinidae) is a rarely caught but widely distributed shark. Based on four specimens from Japan (110-335 cm total body length, TL), the relationship between tooth crown height (CH) and TL for each tooth in *M. owstoni* is examined using regression analysis. The results suggest that the CH for most teeth can be used to predict the TL, where an increase in the CH of each tooth through replacement is proportional to the increase in TL. Distally located teeth show a proportionally greater size increase in comparison to mesially located teeth.

Most mitsukurinid fossils are represented only as isolated teeth. The regression equations obtained in this study may be used to estimate the TL of extinct mitsukurinids (e.g., *Scapanorhynchus* Woodward) from their teeth. Calculations suggest that most *Scapanorhynchus* individuals did not exceed 415 cm TL, although some individuals may have attained 670 cm TL.

The sole specimen of eastern Pacific *Mitsukurina owstoni* is represented only by the head. Previous TL estimates of this individual ranged from 2.18 m TL to 3.75 m TL. A reassessment of its TL based on our 36 independent, tooth-based regression equations strongly suggests that the shark was about 2.7 m TL.

Key words: dentition, fossil, growth, jaw, lamnoid, mitsukurinid

## Introduction

Within an elasmobranch species, teeth of smaller individuals are usually smaller than those of larger individuals. Using *Carcharias taurus* (Rafinesque) (Lamniformes: Odontaspididae) as a model, Applegate (1965) pioneered a quantitative method to show the correlation between the tooth height and body length in a form of bivariate plots. For extinct sharks, teeth are usually the very few body parts that are preserved as fossils. Thus, Applegate's (1965) study gave hope to paleontologists that such neontological data can be used to quantitatively estimate the body length of extinct sharks from their teeth. The method has indeed been applied to a few fossil sharks: e.g., Mio-Pliocene lamniforms, *Carcharocles megalodon* (Agassiz) and *Isurus hastalis* (Agassiz), based on the modern white shark, *Carcharodon carcharias* (Linnaeus) (Randall, 1973; Uyeno *et al*., 1990; Gottfried *et al*., 1996). 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 (e.g., Randall, 1987; Lucifora *et al*., 2001). This is because it is not uncommon for fishers and/or ichthyologists to save only the jaws or head of large

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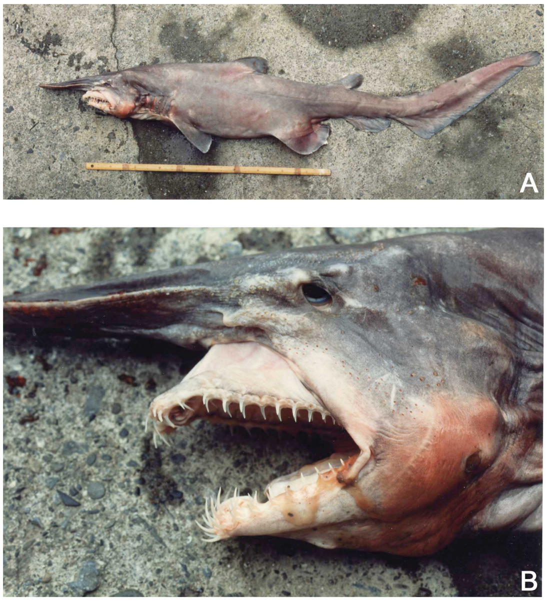


Fig. 1. Goblin shark, *Mitsukurina owstoni* Jordan (jaws preserved as TUDM-unnumbered, 208 cm TL, male), from Suruga Bay, Shizuoka Prefecture, Japan, shortly after capture in June of 1990. A, whole body in lateral view (scale = 1 m) ; B, close-up view of head (note teeth and highly protracted jaws). Photographs courtesy of H. Ida and M. Goto.

sharks.

In this paper, we examine the quantitative relationship between tooth crown height (CH) and total body length (TL) for each tooth in the modern goblin shark, *Mitsukurina owstoni* Jordan, 1898 (Fig. 1). This study constitutes the first attempt to demonstrate the correlation between tooth size and body size for this lamniform species. Although available samples are limited, *M. owstoni* is examined because this species is the only living representative of the Family Mitsukurinidae, where teeth of mitsukurininds are relatively common in the fossil record (e.g., see Cappetta, 1987). Our ultimate goal is two-fold. First, we apply our quantitative data to the "largest known" fossil mistukurinids, which are represented only by their teeth, for a TL estimation. Second, we apply our dental data to a modern *M. owstoni* head specimen without an accurate TL record to extrapolate its TL.

## Materials and methods

*Mitsukurina owstoni* is a widely distributed but rarely seen shark (Compagno, 1984, 2001 ; Stevens and Paxton, 1985 ; Last and Stevens, 1994 ; Duffy, 1997; Ugoretz and Seigel, 1999; Parsons *et al*., 2002). Therefore, specimens of *M. owstoni* are rare and scattered throughout the world, and there are few specimens with measurable teeth and accurate TL data. Our study is based on four specimens from Japan, all with known TL (Appendix 1): CAS 113888 (120 cm TL, female); MCZ 1279 (110 cm TL, female); USNM 50972 (335 cm TL, female); and TUDM-unnumbered (208 cm TL, male ; Fig. 1), Department of Anatomy, School of Dental Medicine, Tsurumi University, Japan.

The teeth of *Mitsukurina owstoni* are similar in both jaws (Nobre, 1935 ; Gomon *et al*., 1994) and are apparently suited to grasping fish and squid (Stevens and Paxton, 1985 ; Yanagisawa, 1991 ; Duffy, 1997 ; Ugoretz and Seigel, 1999 : Fig. 2). The first 12-15 teeth from the jaw symphysis are long, slender, and lanceolate, whereas distally located teeth are small with sharp crowns (Last and Stevens, 1994). We followed Shimada's (2002a) dental terminology and tentative tooth type identification made for *M. owstoni* (Fig. 2). Using a calliper, a CH measurement (i.e., the maximum vertical enameloid height on the labial side) of each tooth on the first (= labialmost or most functional) tooth series was taken from one side of jaws in the four *M. owstoni* specimens. 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 was examined using least squares linear

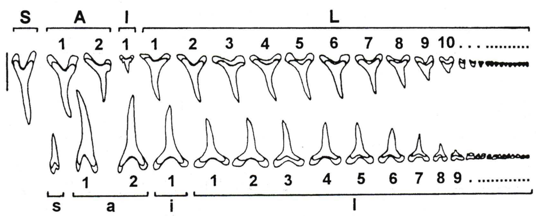


Fig. 2. Upper and lower tooth series of the goblin shark, *Mitsukurina owstoni* Jordan (mesial to the left ; labial view ; vertical line = position of jaw symphysis). Tooth types: A, upper anterior tooth; a, lower anterior tooth ; I, upper intermediate tooth ; i, lower intermediate tooth ; L, upper lateral tooth ; l, lower lateral tooth ; S, upper symphysial tooth ; s, lower symphysial tooth. Illustration modified from Compagno (1984); tooth type identification based on Shimada (2002a).

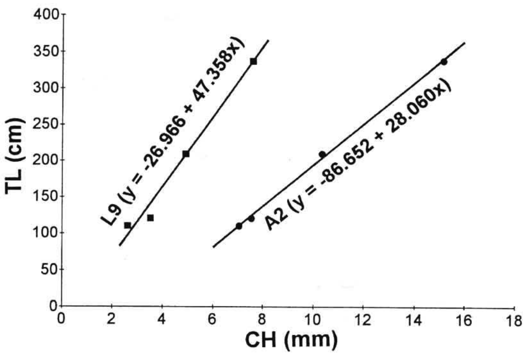


Fig. 3. Bivariate scatter with regression line between crown height (CH) and total body length (TL) for the second upper anterior tooth (A2: circle) and ninth upper lateral tooth (L9: square) in *Mitsukurina owstoni* Jordan (n=4 ; see Appendix 1 for measurements ; see Table 1 for statistics of regression line).

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 provided in Table 1. All regression lines show positive correlation. Whereas the position of y-intercept varies widely, the slope of the lines generally increase from mesially located teeth to distally located teeth for both upper and lower tooth series. The correlation coefficient (r) for each line is high (all >0.900), indicating that the bivariate plots are clustered closely along each regression line (e.g., see Fig. 3). 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 (i.e., showing high statistical significance), except for the A1, L10-L12, a1, and l8.

## Discussion

*Quantitative data*.--A high r-value and a low p-value for most regression lines suggest that, in *Mitsukurina owstoni*, the CH of most teeth can be used to estimate the TL. However, this estimation should be regarded as a first approximation because 1) the sample size is small and 2) a slight shortening of TL (ca. 3% ; see Duffy, 1997) might have occurred for preserved specimens (e.g., CAS 113888 and MCZ 1279). Dental variations are present in *M. owstoni* (presence or absence of basal cusps: e.g., Duffy,

Table 1. Regression analyses between tooth crown height (CH) and total body length (TL) among individuals of *Mitsukurina owstoni* (n = 4, except for I1 ; for tooth types, see Fig. 2 ; x = CH in mm ; y = TL in cm ; degrees of freedom = 1,2). Statistical notations : r, correlation coefficient ; p, probability of estimates (asterisk indicates probability with <5% chance of error) ; SE, standard error of estimates.

| x | Regression equation | r | F-ratio | p | SE |
|---|---|---|---|---|---|
| Upper teeth | | | | | |
| S | y=-104.477+20.116x | 0.998 | 500.910 | 0.002* | 8.052 |
| A1 | y= -61.314+18.547x | 0.933 | 13.466 | 0.067 | 45.916 |
| A2 | y= -86.652+28.060x | 0.999 | 1290.907 | 0.001* | 5.022 |
| I1 | (analysis not applicable due to n = 1) | | | | |
| L1 | y= -52.621+25.217x | 0.980 | 47.661 | 0.020* | 25.624 |
| L2 | y= -96.910+28.035x | 0.995 | 206.977 | 0.005* | 12.491 |
| L3 | y= -89.936+27.561x | 0.993 | 146.207 | 0.007* | 14.833 |
| L4 | y= -51.878+25.077x | 0.993 | 137.529 | 0.007* | 15.287 |
| L5 | y= -68.826+28.256x | 0.990 | 98.594 | 0.010* | 18.004 |
| L6 | y= -66.938+30.701x | 0.974 | 37.146 | 0.026* | 28.861 |
| L7 | y= -60.081+32.478x | 0.985 | 67.349 | 0.015* | 21.684 |
| L8 | y= -49.155+36.728x | 0.983 | 59.036 | 0.017* | 23.113 |
| L9 | y= -26.966+47.358x | 0.991 | 115.075 | 0.009* | 16.689 |
| L10 | y= 39.975+40.603x | 0.926 | 12.071 | 0.074 | 48.138 |
| L11 | y= 55.471+50.561x | 0.938 | 14.702 | 0.062 | 44.184 |
| L12 | y= 0.505+98.843x | 0.918 | 10.655 | 0.082 | 50.759 |
| L13 | y= -6.218+122.750x | 0.968 | 29.697 | 0.032* | 32.074 |
| L14 | y=-51.321+168.670x | 0.975 | 38.840 | 0.025* | 38.840 |

| x | Regression equation | r | F-ratio | p | SE |
|---|---|---|---|---|---|
| L15 | y=-65.917+199.359x | 0.975 | 38.595 | 0.025* | 28.341 |
| L16 | y=-78.160+230.988x | 0.997 | 335.182 | 0.003* | 9.834 |
| L17 | y=-77.071+257.449x | 0.998 | 501.341 | 0.002* | 8.049 |
| L18 | y=-31.963+230.988x | 0.997 | 335.182 | 0.003* | 9.834 |
| L19 | y= 8.864+230.988x | 0.997 | 335.182 | 0.003* | 9.834 |
| Lower teeth | | | | | |
| s | y= -17.075+20.773x | 0.988 | 83.060 | 0.012* | 19.579 |
| a1 | y= -55.323+14.818x | 0.934 | 13.737 | 0.066 | 45.519 |
| a2 | y= -93.164+16.948x | 0.963 | 25.470 | 0.037* | 34.453 |
| i1 | y= -88.861+20.480x | 0.996 | 222.097 | 0.004* | 12.062 |
| l1 | y= -66.812+24.024x | 0.996 | 262.239 | 0.004* | 11.108 |
| l2 | y= -99.985+27.026x | 0.977 | 341.530 | 0.023* | 27.369 |
| l3 | y= -78.928+26.619x | 0.991 | 111.572 | 0.009* | 16.944 |
| l4 | y= -76.447+27.804x | 0.986 | 68.342 | 0.014* | 21.530 |
| l5 | y= -65.515+28.912x | 0.991 | 106.790 | 0.009* | 17.312 |
| l6 | y= -36.810+31.407x | 0.994 | 160.091 | 0.006* | 14.183 |
| l7 | y= -53.246+43.628x | 0.949 | 36.889 | 0.026* | 28.956 |
| l8 | y= -30.879+62.258x | 0.900 | 8.566 | 0.100 | 55.552 |
| l9 | y= 25.673+72.859x | 0.998 | 547.355 | 0.002* | 7.704 |
| l10 | y= 24.200+98.000x | 0.999 | 888.895 | 0.001* | 6.050 |
| l11 | y= 8.028+125.574x | 1.000 | 14472.387 | 0.000* | 1.501 |
| l12 | y=-17.090+175.283x | 0.999 | 1663.092 | 0.001* | 4.425 |
| l13 | y=-34.855+212.191x | 0.988 | 84.766 | 0.012* | 19.386 |
| l14 | y=-45.824+239.074x | 0.973 | 35.430 | 0.027* | 29.515 |
| l15 | y=-11.429+221.274x | 0.986 | 70.163 | 0.014* | 21.257 |
| l16 | y=-26.793+251.478x | 0.992 | 125.397 | 0.008* | 15.998 |
| l17 | y=-19.882+258.342x | 0.978 | 44.406 | 0.022* | 26.502 |
| l18 | y=-14.280+276.707x | 0.981 | 51.704 | 0.019* | 24.640 |
| l19 | y=-34.950+326.000x | 0.989 | 88.080 | 0.011* | 19.026 |

1997; Ugoretz and Seigel, 1999). However, CH variability, at least through ontogeny, appears to be minimal based on our statistical results (e.g., high r-value and low p-value) for most regression equations.

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 suggests that, through replacement, the rate of size increase for distally located teeth is greater than that of mesially located teeth.

Among the teeth with a low predictability (p> 0.05) and a high SE-value (i.e., the A1, L10-L12, a1, and l8), the L10-L12 and l8 represent the transition area between teeth traditionally called "lateral" (e.g., Compagno, 1984) and "posterior" (see Shimada, 2002a). The reason for their low predictability is uncertain but may be due to the small sample size. Shimada (2002a) noted that the exact homology of symphysial teeth ("S" and "s") is uncertain due to their lack of definable anatomical markers. The linear relationship between the CH of the symphysial teeth and the TL may be artificial. However, the high correlation coefficient between the two variables for each symphysial tooth is intriguing (r=0.998 for "S" and r =0.988 for "s": Table 1).

*Paleontological application*.--Some skeletal remains of mitsukurinids are known in the fossil record (Cappetta, 1980). However, most mitsukurinid fossils, which are typically found in Cretaceous marine deposits worldwide, are represented by isolated teeth (e.g., Cappatta, 1987; Welton and Farish, 1993). Therefore, the number of extinct mitsukurinid taxa and their taxonomy are in a state of flux. Nevertheless, fossil mitsukurinids include the following three genera: *Anomotodon* Arambourg, *Mitsukurina* Jordan, and *Scapanorhynchus* Woodward (Cappetta, 1987; Siverson, 1992).

Teeth of *Anomotodon* and fossil *Mitsukurina* attain only about 3 cm in tooth height (Cappetta, 1987; Siverson, 1992). On the other hand, the total tooth height (crown + root) of anterior teeth of *Scapanorhynchus* measure up to 6 cm high (Cappetta, 1987). Although Cappetta (1987) did not illustrate such gigantic teeth, the CH for these teeth is extrapolated to be about 45 mm because the CH takes up approximately 75% of the total tooth height in mitsukurinid anterior teeth (e.g., Welton and Farish, 1993). A conservative TL estimate is possible for fossil individuals that carried those large teeth based on three assumptions: 1) that those teeth represent the largest teeth on the jaws (the a1 or a 2); 2) that the CH of those teeth has a similar relationship to the TL as modern *M. owstoni* (assuming that the body form of *Scapanorhynchus* is interpreted to be similar to that of the modern *Mitsukurina*: Cappetta, 1980); and 3) that it is admissible to extend the regression line below the lowest plot and above the highest plot.

When the regression equation for the a2 in *Mitsukurina owstoni* (which has a higher statistical significance than that of the a1: Table 1) is used to estimate the TL of *Scapanorhynchus*, it is suggested that these teeth are from fish almost 670 cm TL. However, the CH of anterior teeth in *Scapanorhynchus* commonly do not exceed 30 mm (e.g., Welton and Farish, 1993; Hamm and Shimada, 2002). Based on the equation for the a2 of *M. owstoni* a CH of 30 mm would indicate a TL of 415 cm for *Scapanorhynchus*. In addition, whereas the largest known modern *Mitsukurina* is 384 cm TL (Stevens and Paxton, 1985), most teeth of fossil *Mitsukurina* are less than 30 mm in total tooth height (Cappetta, 1987). Therefore, the extinct forms of the genus *Mitsukurina* were probably much smaller than 415 cm TL (note: the same interpretation also applies to *Anomotodon*, which is represented only by extinct taxa).

*Neontological application*.--Ugoretz and Seigel (1999) described the first eastern Pacific record of *Mitsukurina owstoni* (LACM 47362-1, male). It is represented only by the head, as the local fishers who caught the shark discarded the body immediately after capture. The fisher's recollection of the TL of the shark was 2.7 m. Ugoretz and Seigel (1999, p. 119) estimated the shark's TL as "between 2.18 m and 3.75 m (mean 3.26 m)." Their conclusion was based on the comparison of five separate measurements

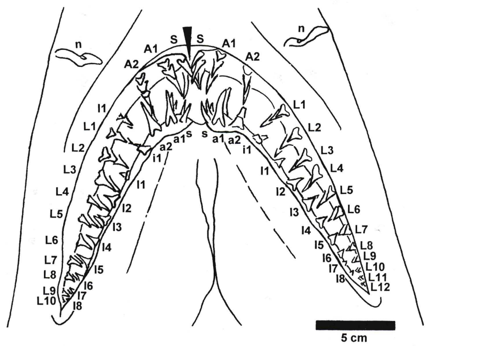


Fig. 4. Mouth of *Mitsukurina owstoni* (LACM 47362-1) showing identified tooth rows. (anterior to the top; "n" = naris; arrow points to the upper jaw symphysis); see Fig. 2 for abbreviations of tooth types).

from three goblin sharks taken by Stevens and Paxton (1985): 1) distance between the tip of snout and inner nostrils, 2) distance between the tip of snout and eye, 3) distance between the tip of snout and mouth, 4) mouth width, and 5) eye diameter.

Based on Shimada's (2002a) tooth identification scheme (Fig. 2), we identified the teeth in LACM 47362-1 (Fig. 4) and measured their CH (Appendix 2). The tooth-based regression equations (Table 1) were then used to reassess the TL of LACM 47362-1. Equations for the following teeth were not used: "S" and "s" due to their tenuous homology (see above); "I1" due to the lack of an equation; those that gave an equation with a low predictability ($p > 0.05$: see Table 1); those that are not measurable in LACM 47362-1; and those that are not present in LACM 47362-1 (see Appendix 2). After these exclusions, a total of 36 independent equations were available and were used for the TL estimation.

Each estimated TL-value and the mean of the TL-values for each jaw quadrant are shown in Table 2. Whereas the estimated TL-values range from 237.3745 cm to 308.994 cm (note: both extreme values occur on the left upper jaw), the mean of the four means is 271.7818 cm TL (standard deviation = 16.5712). Therefore, our TL estimation is nearly identical to the fisher's recollection of the shark's TL.

## Conclusions

In reference to shark paleontology, Shimada (1997, p. 234) stated that "[b]ecause of the nature of fossils, deciphering the paleobiology of extinct organisms from limited observational information is a never-ending challenge to paleontologists." Sharks generally occupy one of the highest trophic positions in any marine ecosystem (Hamm and Shimada, 2002), so paleobiological inferences of fossil sharks, as simple as estimating their TL, are important for the reconstruction of marine paleoecology. As such, the tooth-based TL estimation method presented here, which can be viewed as the extension of Applegate's (1965) work, is expected to be useful for fossil shark research (e.g., see Hamm and Shimada, 2002 ; Shimada, 2002b, 2003, 2005).

The use of tooth-based, multiple, extrapolated TL values for an incomplete modern *Mitsukurina* specimen (LACM 47362-1) presented in this study is novel. Whereas previously extrapolated values based on soft-tissue anatomy range widely (2.18-3.75 m by Ugoretz and Seigel, 1999), the range of our 36 estimated TL-values for the same specimen is much narrower (2.37-3.09 m). Furthermore, the average value of the 36 independently derived values (2.72 m) is nearly identical to the fisher's recollection (2.7 m). Although the exact TL of the shark individual would never be known, the closeness of our value to the fisher's recollection is striking. It is interpreted here that, for a TL estimation, the use of dental measurements may be more reliable than the measurements based on soft-tissue anatomy. This is because teeth as hard, mineralized tissue generally do not suffer distortion and shrinkage (e.g., Duffy, 1997) regardless of the condition of the specimen. The compelling result of our case study suggests that the method (i.e., to extrapolate the TL of a shark based on multiple dental data) is promising and powerful.

Table 2. Total length values estimated from dental measurements (Appendix 2) for *Mitsukurina owstoni* (LACM 47362-1) based on regression equations presented in Table 1. Abbreviations: AE, absence of equation; ELP, equation with low predictability ; SD = standard deviation ; TNM, tooth not measurable ; TNP = tooth not present ; UH, analysis not applicable due to uncertain homology.

| Upper tooth | Right (TL) | Left (TL) | Lower tooth | Right (TL) | Left (TL) |
|---|---|---|---|---|---|
| S | UH | UH | s | UH | UH |
| A1 | ELP | ELP | a1 | ELP | ELP |
| A2 | TNM | 308.9940 | a2 | 294.9452 | TNM |
| I1 | AE | AE | i1 | 273.6350 | (259.2990) |
| L1 | (247.4613) | (237.3745) | l1 | 283.9384 | (252.7072) |
| L2 | (270.3485) | 264.7415 | l2 | 291.8920 | (291.8920) |
| L3 | (268.3570) | 257.3326 | l3 | 280.4285 | (267.1190) |
| L4 | (271.6153) | 254.0614 | l4 | (257.2010) | 259.9814 |
| L5 | 270.2460 | 270.2460 | l5 | 264.0818 | 264.0818 |
| L6 | 289.1936 | 289.1936 | l6 | (292.9635) | (292.9635) |
| L7 | 293.9292 | 274.4424 | l7 | 252.1500 | 252.1500 |
| L8 | 266.7058 | 252.0146 | l8 | ELP | ELP |
| L9 | 290.3326 | 276.1252 | l9 | TNM | TNM |
| L10 | ELP | ELP | l10 | TNM | TNM |
| L11 | ELP | ELP | l11 | TNM | TNM |
| L12 | ELP | ELP | l12 | TNM | TNM |
| L13 | TNM | TNM | l13 | TNM | TNM |
| L14 | TNM | TNM | l14 | TNM | TNM |
| L15 | TNM | TNM | l15 | TNM | TNM |
| L16 | TNM | TNM | l16 | TNM | TNP |
| L17 | TNM | TNM | l17 | TNP | TNP |
| L18 | TNM | TNM | l18 | TNP | TNP |
| L19 | TNP | TNM | l19 | TNP | TNP |
| Average | 274.2433 | 268.4526 | Average | 276.8039 | 267.5242 |
| SD | 13.8110 | 19.3710 | SD | 15.0773 | 15.1386 |

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## Appendix 1.

Tooth crown heights (mm) in four *Mitsukurina owstoni* specimens (for tooth types, see Fig. 2 ; parenthesis = estimated value).

CAS 113888 (left dentition) : S, 11.7 ; A1, 11.7 ; A2, 7.5 ; L1, 7.9 ; L2, 8.2 ; L3, 8.2 ; L4, 7.5 ; L5, 7.4 ; L6, 7.2 ; L7, 6.3 ; L8, 5.3 ; L9, 3.5 ; L10, 3.2 ; L11, 2.2 ; L12, 1.8 ; L13, 1.3 ; L14, 1.2 ; L15, 1.1 ; L16, 0.9 ; L17, 0.8 ; L18, 0.7 ; L19, 0.6 ; L20, 0.6 ; s, 7.4 ; a1, 14.3 ; a2, 15.0 ; i1, 10.5 ; l1, 8.1 ; l2, 9.3 ; l3, 8.2 ; l4, 7.8 ; l5, 7.1 ; l6, 5.5 ; l7, 4.6 ; l8, 3.2 ; l9, 1.2 ; l10, 1.0 ; l11, 0.9 ; l12, 0.8 ; l13, 0.8 ; l14, 0.7 ; l15, 0.6 ; l16, 0.6 ; l17, 0.5 ; l18, 0.5 ; l19, 0.5.

MCZ 1279 (right dentition): S, (10.5); A1, 10.0 ; A2, 7.0 ; I1, 2.6 ; L1, 6.2 ; L2, 7.2 ; L3, 7.0 ; L4, 5.9 ; L5, 5.8 ; L6, 5.2 ; L7, 4.9 ; L8, 3.8 ; L9, 2.6 ; L10, 1.7 ; L11, 1.0 ; L12, 1.0 ; L13, 0.9 ; L14, 0.9 ; L15, 0.8 ; L16, 0.8 ; L17, 0.7 ; L18, 0.6 ; L19, 0.5 ; s, 6.1 ; a1, 12.0 ; a2, 10.9 ; i1, 9.2 ; l1, 7.4 ; l2, 7.3 ; l3, 6.6 ; l4, 6.0 ; l5, 5.6 ; l6, 4.3 ; l7, 3.7 ; l8, 1.7 ; l9, 1.2 ; l10, 0.9 ; l11, 0.8 ; l12, 0.7 ; l13, 0.6 ; l14, 0.6 ; l15, 0.5 ; l16, 0.5 ; l17, 0.5 ; l18, 0.4 ; l19, 0.4 ; l20, 0.4.

USNM 50972 (left dentition): S, 22.0; A1, 21.5 ; A2, 15.1 ; L1, 15.5 ; L2, 15.5 ; L3, 15.5 ; L4, 15.3 ; L5, 14.2 ; L6, 13.0 ; L7, 12.2 ; L8, 10.3 ; L9, 7.6 ; L10, 7.2 ; L11, 5.5 ; L12, 3.3 ; L13, 2.8 ; L14, 2.3 ; L15, 2.0 ; L16, 1.8 ; L17, 1.6 ; L18, 1.6 ; L19, 1.5 ; L20, 1.5 ; L21, 1.4 ; L22, 1.4 ; L23, 1.3 ; L24, 1.3 ; s, 17.2 ; a1, 26.5 ; a2, 25.0 ; i1, 20.4 ; l1, 16.9 ; l2, 16.1 ; l3, 15.5 ; l4, 14.5 ; l5, 13.8 ; l6, 11.8 ; l7, 9.0 ; l8, 5.2 ; l9, 4.2 ; l10, 3.2 ; l11, 2.6 ; l12, 2.0 ; l13, 1.7 ; l14, 1.5 ; l15, 1.5 ; l16, 1.4 ; l17, 1.3 ; l18, 1.2 ; l19, 1.1 ; l20, 1.1 ; l21, 1.0 ; l22, 1.0 ; l23, 0.9 ; l24, 0.9 ; l25, 0.8 ; l26, 0.8.

TUDM-unnumbered (left dentition) : S, 15.4 ; A1, 11.7 ; A2, 10.3 ; L1, 9.4 ; L2, 10.5 ; L3, 10.4 ; L4, 10.4 ; L5, 9.7 ; L6, 8.5 ; L7, 7.8 ; L8, 7.0 ; L9, 4.9 ; L10, 3.0 ; L11, 2.2 ; L12, 1.7 ; L13, 1.5 ; L14, 1.4 ; L15, 1.3 ; L16, 1.2 ; L17, 1.1 ; L18, 1.0 ; L19, 0.9 ; L20, 0.9 ; L21, 0.8 ; L22, 0.8 ; L23, 0.8 ; s, 9.8 ; a1, (14.3) ; a2, (16.7) ; i1, 15.0 ; l1, 10.9 ; l2, 10.7 ; l3, (10.6) ; l4, 10.5 ; l5, 9.3 ; l6, 7.7 ; l7, 5.3 ; l8, 4.3 ; l9, 2.6 ; l10, 1.8 ; l11, 1.6 ; l12, 1.3 ; l13, 1.2 ; l14, 1.2 ; l15, 1.1 ; l16, 1.0 ; l17, 1.0 ; l18, 0.9 ; l19, 0.8 ; l20, 0.7 ; l21, 0.7.

## Appendix 2.

Tooth crown heights (mm) in *Mitsukurina owstoni* (LACM 47362-1, male, TL unknown) ; for tooth types, see Figs. 2, 4. Notations : parenthesis = estimated value ; ? = not measurable due to extensive damage or inaccessible tooth position ; - = not present.

Right dentition : S, 19.5 ; A1, (19.0) ; A2, ? ; I1, 6.0 ; L1, (11.9) ; L2, (13.1) ; L3, (13.0) ; L4, (12.9) ; L5, 12.0 ; L6, 11.6 ; L7, 10.9 ; L8, 8.6 ; L9, 6.7 ; L10, 4.5 ; L11, 2.7 ; L12, (1.5) ; L13, ? ; L14, ? ; L15, ? ; L16, ? ; L17, ? ; L18, ? ; s, 13.8 ; a1, ? ; a2, 22.9 ; i1, 17.7 ; l1, 14.6 ; l2, 14.5 ; l3, 13.5 ; l4, (12.0) ; l5, 11.4 ; l6, (10.5) ; l7, 7.0 ; l8, (4.7) ; l9, ? ; l10, ? ; l11, ? ; l12, ? ; l13, ? ; l14, ? ; l15, ? ; l16, ?.

Left dentition : S, 19.1 ; A1, 18.0 ; A2, 14.1 ; I1, - ; L1, (11.5) ; L2, 12.9 ; L3, 12.6 ; L4, 12.2 ; L5, 12.0 ; L6, 11.6 ; L7, 10.3 ; L8, 8.2 ; L9, (6.4) ; L10, (4.5) ; L11, (3.1) ; L12, (1.6) ; L13, ? ; L14, ? ; L15, ? ; L16, ? ; L17, ? ; L18, ? ; L19, ? ; s, (13.7) ; a1, (23.0) ; a2, ? ; i1, (17.0) ; l1, (13.3) ; l2, (14.5) ; l3, (13.0) ; l4, 12.1 ; l5, 11.4 ; l6, (10.5) ; l7, 7.0 ; l8, 4.6 ; l9, ? ; l10, ? ; l11, ? ; l12, ? ; l13, ? ; l14, ? ; l15, ?.