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Dental variations in the crocodile shark, *Pseudocarcharias kamoharai* (Lamniformes: Pseudocarchariidae): implications for fossil *Pseudocarcharias*

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Abstract

The crocodile shark, *Pseudocarcharias kamoharai* (Matsubara), is an extant lamniform shark. Whereas the genus is represented in the fossil record by isolated teeth found primarily in Miocene deposits nearly worldwide, many biological aspects, even for the extant *Pseudocarcharias*, are still poorly understood, including the ontogenetic development of teeth. In this study, we used linear regression analyses to examine the relationship between the total body length (TL) and tooth crown height (CH) or enameloid height of each tooth in 14 individuals of extant *P. kamoharai* collected from the Pacific and Indian Oceans. The resulting regression equations suggest that the increase in CH of teeth through replacement is generally proportional to an increase in TL, with high predictability of TL from CH ($p<0.0001$) found in teeth located mesially (the so-called "anterior teeth"). In addition, we used two-sample t-tests to investigate sexual and geographic dimorphism in standardized crown height and crown acuteness of each tooth. Whereas no significant dimorphism was found between the two primary collection localities, the lower first anterior tooth was found to be significantly taller in males than females. This study allows TL estimations for *Pseudocarcharias* in the fossil record. If our regression equations for the anterior teeth are applied to previously described anterior teeth of *Pseudocarcharias* from the Miocene with preserved crowns, their TL estimates range up to 231 cm. This uppermost estimate is intriguing because it is about twice the size of the largest known extant *Pseudocarcharias*, providing new insights into the Neogene marine ecosystem.

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Introduction

The crocodile shark, *Pseudocarcharias kamoharai* (Matsubara, 1936) (Fig. 1A) is an extant lamniform shark found in tropical and subtropical oceans worldwide, occurring in surface waters to a depth of 590 m (Compagno 2001). It is the only living member of its family Pseudocarchariidae and the smallest living lamniform shark, with a maximum recorded size of 122 cm (Ebert 2016, Weigmann 2016). *Pseudocarcharias kamoharai* is rarely targeted by commercial or artisanal fisheries, and is primarily caught as a by-catch in longline tuna and swordfish fishing fleets (Fujita 1981, Long & Seigel 1997, Compagno 2001, Romanov et al. 2008, Ebert 2016). Although a number of recent studies have revealed details of this shark's biology, including reproductive biology, growth rate, and diet (Oliveira et al. 2010, Lessa et al. 2016, Estupiñán-Montaño & Galván-Magaña 2021, Calle-Morán et al. 2022, Calle-Morán & Aragón-Noriega 2023, Calle-Morán et al. 2025), many other biological aspects of the shark remain poorly known. This includes a limited understanding of the degree of intraspecific tooth variation present in the species (e.g. Bass et al. 1975, Cigala-Fulgosi 1992), although the general dental characteristics of the species are known (e.g. Long & Waggoner 1996, Shimada 2002a, 2005a).

Intraspecific tooth variations in elasmobranchs are well recognized in many forms, including tooth row counts and morphological characters (Applegate 1965, Cappetta 1986). These often take the form of ontogenetic shifts (Purdy & Francis 2007, Moyer & Bemis 2016, Cullen & Marshall 2019, Goodman et al. 2022), sexual dimorphism (Feduccia & Slaughter 1974, Gruber & Compagno 1981, Geniz et al. 2007), variation between populations (Lucifora et al. 2003), or a combination of multiple factors (Ellis & Shackley 1995, Straube et al. 2008, Powter et al. 2010, Underwood et al. 2015, French et al. 2017, Berio et al. 2020, Straube & Pollerspöck 2020). Understanding these variations is particularly important for the understanding of the evolution of sharks, because much of the fossil record of sharks is represented only by their teeth, since they have a poorly mineralized cartilaginous skeleton (e.g., Cappetta 2012). This is also true for the fossil record of *Pseudocarcharias*, where it is known only by isolated teeth in various Neogene marine deposits (Itoigawa et al. 1985, Cigala-Fulgosi 1992, Aguilera & Aguilera 2001, Antunes & Balbino 2003, Takakuwa 2007, Schultz 2013, Carrillo-Briceño et al. 2015, Aguilera et al. 2017, Landini et al. 2017, Höltke et al. 2020, 2022a, 2022b, Pollerspöck & Unger 2024).

Each side of the upper and lower jaws of *P. kamoharai* typically contain 13 and 12 rows of teeth, respectively (Shimada 2002a; see Fig. 1B). Each tooth consists of a crown and a root, but a tooth neck marked by a thin enameloid layer extends basally beyond the thicker enameloid of the crown (Fig. 1C). In this study, we examine the quantitative relationship between tooth size (specifically crown and enameloid heights) and total body length (TL), as well as the presence or absence of sexual dimorphism and geography-based differences in extant *P. kamoharai*. In addition, we review the fossil record of the genus *Pseudocarcharias*. We apply our quantitative data to fossil *Pseudocarcharias* and discuss its paleoecological implications.

Materials and Methods

Despite its widespread presence in circumtropical oceans, specimens of *Pseudocarcharias kamoharai* with measurable jaws, teeth, and recorded total lengths are rare. Nonetheless, we were able to examine 14 crocodile shark jaw samples from the central Pacific Ocean (Oahu, Hawaii, USA: n = 3), western Pacific Ocean (Okinawa, Japan: n = 9), and eastern Indian Ocean (Phuket, Thailand: n = 1), each with TL, sex, and locality data. They are now housed in the Ichthyology Collection of the California Academy of Science (CAS) in San Francisco, CA, USA.

Specimens examined are listed with catalog number, TL, upper jaw length UJL, sex, locality, and dental series from which measurements were taken: CAS 249132, 72 cm TL, 7.45 cm UJL, male, Okinawa, left dental series; CAS 249133, 74 cm TL, 7.45 UJL, male, Okinawa, right dental series; CAS 249134, 80 cm TL, 8.05 cm UJL, female, Okinawa, left dental series; CAS 249135, 82 cm TL, 7.6 cm UJL, female, Okinawa, right dental series; CAS 249136, 91 cm TL, 8.1 cm UJL, male, Okinawa, left dental series; CAS 249137, 98.5 cm TL, 7.95 cm UJL, male, Okinawa, right dental series; CAS 249138, 102 cm TL, 8.1 cm UJL, male, Okinawa, right dental series;

CAS 249139, 102.5 cm TL, 8.3 cm UJL, male, Oahu, left dental series; CAS 249140, 103 cm TL, 9.1 cm UJL, female, Okinawa, left dental series; CAS 249141, 104 cm TL, 9.1 cm UJL, female, Oahu, right dental series; CAS 249142, 104 cm TL, 8.9 cm UJL, female, Okinawa, right dental series; CAS 249143, 104.5 cm TL, 8.5 cm UJL, male, Oahu, left dental series; CAS 249144, 106 cm TL, 8.35 cm UJL, male, Okinawa, left dental series; and CAS 249145, 109 cm TL, 9.15 cm UJL, male, Phuket, left dental series. In summary, these specimens consist of 5 female and 9 male non-embryonic specimens, with total lengths ranging from 72 to 109 cm.

We follow Shimada's (2002a) dental terminology and tooth type identification for each of the samples. Three dental measurements were taken from the labial side of each tooth position: crown height (CH), the maximum vertical enameloid height; "enameloid height" (EH), the maximum vertical enameloid height including partial enamel coating below the tooth crown; and mid-crown width (MCW), the crown width measured at half the CH (Fig. 1C). A caliper was used to take dental measurements from the labialmost (first or functional) tooth

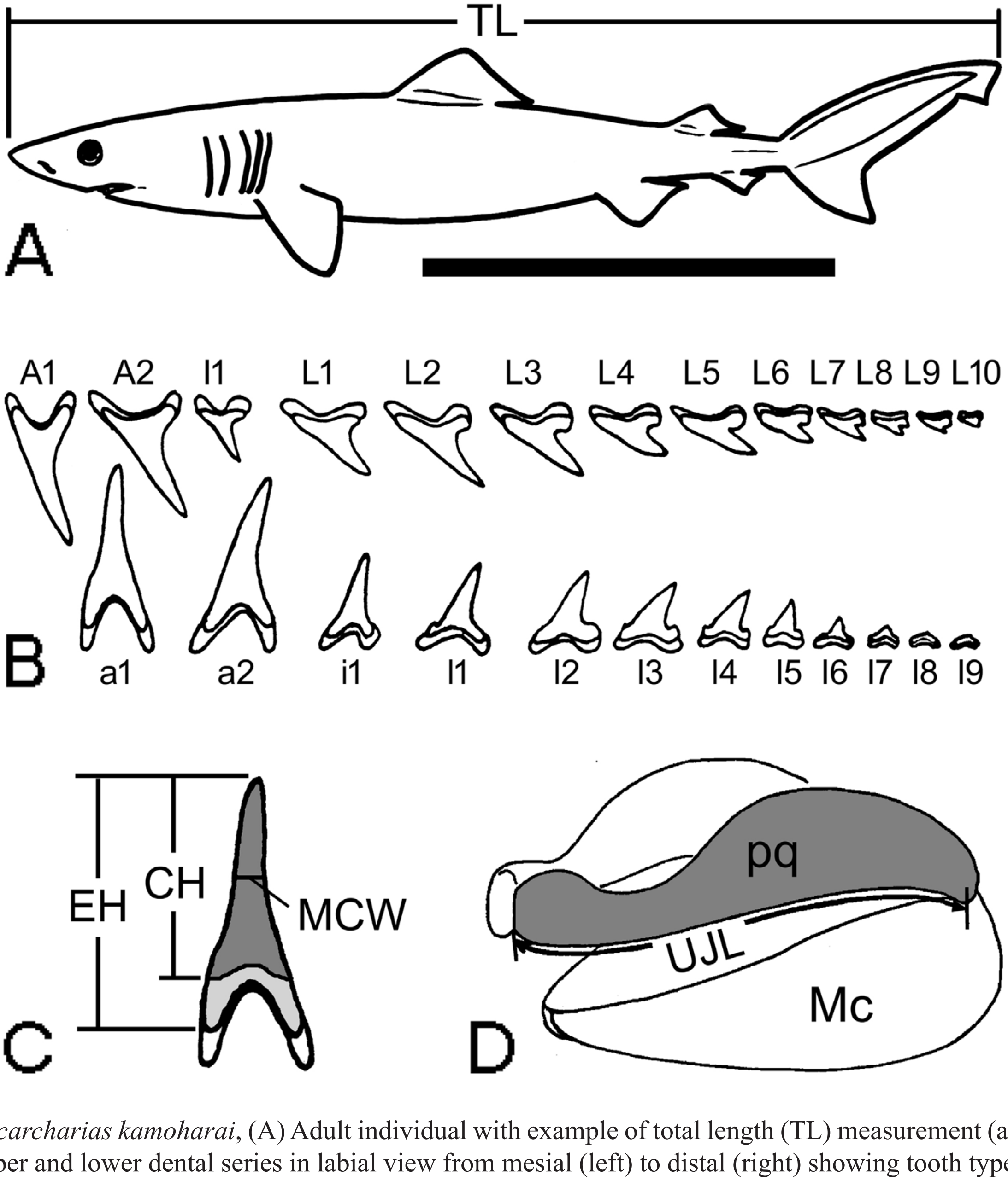

Figure 1. *Pseudocarcharias kamoharai*, (A) Adult individual with example of total length (TL) measurement (after Ebert et al. 2013). (B) Upper and lower dental series in labial view from mesial (left) to distal (right) showing tooth types (A, upper anterior tooth; a, lower anterior tooth; I, upper intermediate tooth; i, lower intermediate tooth; L, upper lateral tooth; l, lower lateral tooth; modified after Shimada (2002a; fig. 6). (C) Close-up view of lower first anterior tooth (a1) with example of crown height (CH), enameloid height (EH), and mid-crown width (MCW) measurements. (D) Close-up view of schematic lamniform shark jaw (abbreviations: pq, palatoquadrate; Mc, Meckel's cartilage) with example of upper jaw length (UJL) measurement, modified after Shimada (2002a; fig. 4A).

series in each tooth row from one side of each jaw specimen. When the first tooth series was not measurable, measurements were taken from the second tooth of the same tooth row or the corresponding tooth row on the opposite jaw side. In the case that no comparable tooth was available for measurement, an estimate was made based on the observable portion of the first tooth. In addition, the raw dental measurements were used to obtain two derived measurements: standardized crown height (SCH), which is the CH of each tooth divided by its upper jaw length (UJL), and crown acuteness (CA), which is one-half of the CH divided by its MCW. A tape measure was used to determine the UJL of each specimen, which is defined as the length of the palatoquadrate from the symphysis to the center of the lateral quadratomandibular joint (Fig. 1D).

The CH-TL and EH-TL relationship of each tooth position was examined using simple linear regression, i.e. the least squares method; $y=a+bx$, where $y=TL$ in cm, $x=CH$ in mm, a is the constant and b is the slope of the line; $\alpha=0.05$ (Zar 1996). The null hypothesis for each analysis was that the CH or EH cannot predict the TL. This analysis was repeated for a subset of the data limited to a single locality with the most samples (Okinawa) to minimize potential locality-based differences. In addition, a subset of the data was created by excluding juveniles to test for potential sexual dimorphism using a two-sample t-test. When data were determined to be abnormally distributed by a Shapiro-Wilk Normality test, a logarithm transformation of the data was attempted. If normality was not achieved by log transformation, a Mann-Whitney U-test was used on the original data in place of a t-test. This analysis was repeated for a subset of the data limited to a single locality (Okinawa). A final test was performed to determine potential differences between the two localities represented by multiple specimens (Okinawa and Oahu).

Results

Raw measurements of CH, EH, and MCW for each tooth in each specimen can be found in Supplemental Tables S1, S2, and S3, respectively. Assessments were categorized as ontogeny-based, sex-based, and geography-based. It should also be noted that multiple specimens were found to preserve prominent lateral cusplets, a feature which has been reported as highly variable intraspecifically in *P. kamoharai* (Matsubara 1936, Bass et al. 1975, Cigala-Fulgosi 1992, Pollerspöck & Unger 2024).

Ontogeny-based assessment. The results of the crown height (CH) regression analyses are presented in Table 1 and Supplemental Table S4. The probability of error (p) for each regression is variable, but generally increases from mesially located to distally located teeth for both the upper and lower tooth series. It is high for many teeth and low for others, ranging from 0.958 to <0.001 in the total dataset and from 0.618 to <0.001 in the Okinawa-specific dataset. The coefficient of determination (R2) is similarly variable, ranging from 0.769 to <0.001 in the total dataset and from 0.894 to 0.033 in the Okinawa-specific dataset. It also generally decreases from mesially located teeth to distally located teeth in both the upper and lower tooth series. The standard error (SE) for each regression is also variable, indicating significant scattering around the line for plots with low R2 values and less scattering for those with high values. The strongest correlations in the total dataset are found in the upper first anterior (A1: R2= 0.7687; $p < 0.0001$; SE = ± 6.407), the second upper anterior (A2: R2= 0.6179; p= 0.001; SE= ± 8.236), and the first lower anterior tooth positions (a1: R2= 0.7331; $p < 0.0001$; SE= ± 6.883).

The results of the enameloid height (EH) regression analyses are presented in Supplemental Tables S5 and S6. They generally have a lower R2 and higher p-value than the CH regressions at the corresponding tooth position. The R2 ranges from 0.673 to 0.001 in the total dataset and from 0.763 to 0.004 in the geography-based dataset, whereas p-values range from 0.980 to <0.001 in the total dataset and from 0.891 to 0.001 in the geography-based dataset.

Sex-based assessment. The results of the t-tests for sexual dimorphism are presented in Supplemental Tables S7 and S8, with notable results highlighted in Table 2. The majority of tooth measurements do not show significant differences between males and females in either dataset. Several measurements showed $p < 0.05$, indicating differences only in the geography-based dataset, but not the total dataset. Only the standardized crown height for the lower first anterior tooth (a1 SCH) demonstrated sexual dimorphism in both datasets, with males displaying a statistically greater SCH than females (1.344 ± 0.021 vs. 1.232 ± 0.016).

Geography-based assessment. The results of the t-tests for differences in tooth morphology by locality are presented in Supplemental Tables S9 and S10, with notable results highlighted in Table 3. The majority of measurements do not show significant differences between population localities. The three measurements that show a statistical difference between Okinawa and Oahu specimens are: a2 CA, l2 CA, and l8 SCH.

Discussion

Dental variations in extant *P. kamoharai*. Ontogenetic variation in dental morphology occurs in many elasmobranchs, including sharks (Purdy & Francis 2007, Moyer & Bemis 2016, Cullen & Marshall 2019, Goodman et al. 2022). The growth of teeth through replacement is also known to be correlated with the increase in body size through ontogenetic development in several lamniform species, in which the CH of all or nearly all tooth positions demonstrates statistically significant correlation to the TL (Shimada 2002b, 2002c, 2005b, Shimada & Seigel 2005, Shimada 2006, Chavez et al. 2012, Shimada 2019). A high R2 value and low p-value in several of our regression lines suggest that the CH of those tooth positions can be used to estimate the TL in *P. kamoharai* (Table 1). A positive correlation for the significant regression lines indicates that an increase in CH through replacement is generally proportional to increases in TL. However, a high p-value in other regression lines suggests that not all teeth are suitable for TL estimation, as the TL predictability from CH becomes less reliable. It is noteworthy that the CH is more variable in *P. kamoharai* relative to previously examined lamniform taxa. Similar R2 and p-values produced from both the total dataset and the Okinawa-specific dataset (Supplemental Table S4) support the reliability of TL estimates from CH across multiple populations. Generally, lower R2 values and higher p-values in regressions performed using the EH rather than CH indicate that EH is a less reliable measurement for TL estimates (Supplemental Table S5).

Sexual dimorphism in teeth is a commonly observed feature in elasmobranchs (Cappetta 1986, Feduccia & Slaughter 1974, Geniz et al. 2007, Underwood et al. 2015), including non-lamniform sharks (Ellis & Shackley 1995, Powter et al. 2010, Berio et al. 2020) and some lamniforms (Gruber & Compagno 1981, French et al. 2017). One notable pattern reported in sharks is mature males displaying significantly greater tooth height than females, especially in the anteriormost teeth, which has historically been described as an adaptation to assist males in biting behavior during copulation (Gruber & Compagno 1981, Ellis & Shackley 1995, Powter et al. 2010, Berio et al. 2020). In *P. kamoharai*, both the presence and absence of sexual dimorphism have been reported in the anterior teeth (Bass et al. 1975, Cigala-Fulgosi 1992). This study is the first quantitative analysis to test for the presence of dental sexual dimorphism in this species. Whereas several tooth positions demonstrated evidence of sexual dimorphism in the geography-based dataset, only the lower first anterior tooth (a1) was found to be dimorphic in both datasets (Supplemental Tables S7 and S8). Although this observation indicates a general absence of dimorphism in dental characteristics between males and females, the dimorphism demonstrated in the lower first anterior tooth is notable because males showed greater standardized crown heights than females (Table 2). We interpret this dimorphism as an adaptation to assist males in biting during mating. The reported presence of mating scars on gravid females of *P. kamoharai* is consistent with this behavior (Calle-Morán & Aragón-Noriega 2023).

Although tooth morphology is rarely used for taxonomic distinction in extant elasmobranchs (Guinot et al. 2018), intraspecific variation in dental characters between different geographic areas has been reported in one lamniform species, *Carcharias taurus* (Lucifora et al. 2003). Out of 39 total derived measurements tested in this present study (Supplemental Tables S1, S2, and S3), only three demonstrated significant differences between the Okinawa and Oahu populations of *P. kamoharai* (Supplemental Tables S9 and S10). Unlike the tests for sexual dimorphism (Supplemental Tables S7 and S8), there is no notable pattern to the measurements that showed geography-based differences (Supplemental Tables S9 and S10). This observation indicates that the two populations are generally homogenous in dental characteristics.

Paleobiological Application. Fossils assigned to the genus *Pseudocarcharias* have been described from Miocene deposits nearly worldwide. These include specimens identified as *P. kamoharai* from Italy and Germany; *P.* aff. *kamoharai* from Venezuela; *P.* cf. *kamoharai* from Brazil, Peru, Panama, and Portugal; *Pseudocarcharias* sp. from Japan; and *Pseudocarcharias rigida* (Probst, 1879) from Germany and Austria (Itoigawa et al. 1985, Cigala-Fulgosi 1992, Aguilera & Aguilera 2001, Antunes & Balbino 2003, Takakuwa 2007, Schultz 2013, Carrillo-

TABLE 1

Regression analyses between tooth crown height (CH) and total body length (TL) among specimens of *Pseudocarcharias kamoharai* (x= CH in mm, y= TL in cm)

R2= coefficient of determination; p= probability of error (* $p < 0.05$); SE= standard error of estimates

X	n	Regression equation	R2	SE	p
Upper Teeth					
A1	14	$y = -150.780 + 29.368x$	0.769	6.407	0.000*
A2	14	$y = -22.747 + 15.458x$	0.618	8.236	0.001*
I	14	$y = 61.619 + 9.579x$	0.216	11.80	0.095
L1	14	$y = 19.288 + 16.562x$	0.439	9.981	0.010*
L2	14	$y = 31.361 + 14.457x$	0.301	11.14	0.042*
L3	14	$y = 33.644 + 16.583x$	0.309	11.08	0.039*
L4	14	$y = 48.280 + 16.190x$	0.170	12.14	0.143
L5	14	$y = 60.286 + 16.447x$	0.206	11.88	0.104
L6	14	$y = 72.360 + 14.790x$	0.084	12.75	0.316
L7	14	$y = 47.700 + 36.320x$	0.120	12.50	0.224
L8	14	$y = 96.804 - 1.548x$	0.000	13.32	0.958
L9	14	$y = 77.640 + 20.040x$	0.055	12.95	0.418
L10	13	$y = 83.920 + 14.640x$	0.039	13.46	0.518
L11	7	$y = 65.250 + 45.000x$	0.258	11.55	0.245
Lower Teeth					
a1	14	$y = -103.518 + 18.193x$	0.733	6.883	0.000*
a2	14	$y = 23.303 + 7.326x$	0.195	11.95	0.114
i	14	$y = 9.397 + 15.771x$	0.373	10.55	0.020*
l1	14	$y = 27.550 + 14.580x$	0.239	11.63	0.076
l2	14	$y = 35.247 + 14.956x$	0.257	11.48	0.064
l3	14	$y = -16.450 + 34.230x$	0.490	9.514	0.005*
l4	14	$y = 24.750 + 27.280x$	0.371	10.57	0.021*
l5	14	$y = 72.840 + 11.850x$	0.089	12.72	0.301
l6	13	$y = 50.184 + 31.587x$	0.511	9.686	0.006*
l7	13	$y = 54.890 + 37.570x$	0.222	12.22	0.104
l8	13	$y = 47.830 + 54.120x$	0.510	9.698	0.006*
l9	12	$y = 47.150 + 71.660x$	0.603	9.042	0.003*
l10	6	$y = 84.830 + 15.890x$	0.067	14.67	0.621

Briceño et al. 2015, Aguilera et al. 2017, Landini et al. 2017, Höltke et al. 2020, 2022a, 2022b, Pollerspöck & Unger 2024). Although all are represented by isolated teeth, several of these previously described fossil teeth of *Pseudocarcharias* preserve complete crowns and have been reported as corresponding to the tooth positions found most anteriorly, the so-called "anterior teeth" (sensu Shimada 2002a), for which we find the most reliable regression equations (see above; Table 1). If we assume that the position assignments are correct, and that the CH of these fossil teeth have the same relationship to the TL as extant *P. kamoharai*, then a TL estimate is possible for each prehistoric individual based on these fossil teeth. When our regression equations for the homologous tooth rows are applied to these fossil teeth, their TL estimates range from 47 to 231 cm (Fig. 2; Supplemental Table S11). Whereas the smallest estimated individual was most likely a neonate based on prior size-at-birth estimates (Oliveira et al. 2010, Lessa et al. 2016, Calle-Morán & Aragón-Noriega 2023), the largest of these estimates (specimens described by Cigala-Fulgosi; Supplemental Table S11) are nearly double the longest recorded TL for extant *P. kamoharai* (122 cm; Lessa et al. 2016). This largest TL estimate is still considerably small for Cenozoic lamniforms (Welton 2013, Shimada et al. 2017, 2020), but nevertheless provides new insights into the Neogene marine ecosystem.

It is noteworthy that extant *P. kamoharai* is a specialist predator, feeding primarily on a limited number of squid species (Calle-Morán et al. 2022). The ocean waters of the Miocene Epoch are known to have been significantly warmer than present, including at localities where fossil teeth of *Pseudocarcharias* have been found (Sosdian et al. 2024). Elevated ocean temperatures have been found to contribute to increased developmental rate and abundance in squid populations in both wild and laboratory settings (Hatfield et al. 2001, Forsythe 2004, Chasco et al. 2022). The potentially greater squid populations of the warm Miocene oceans provide a plausible

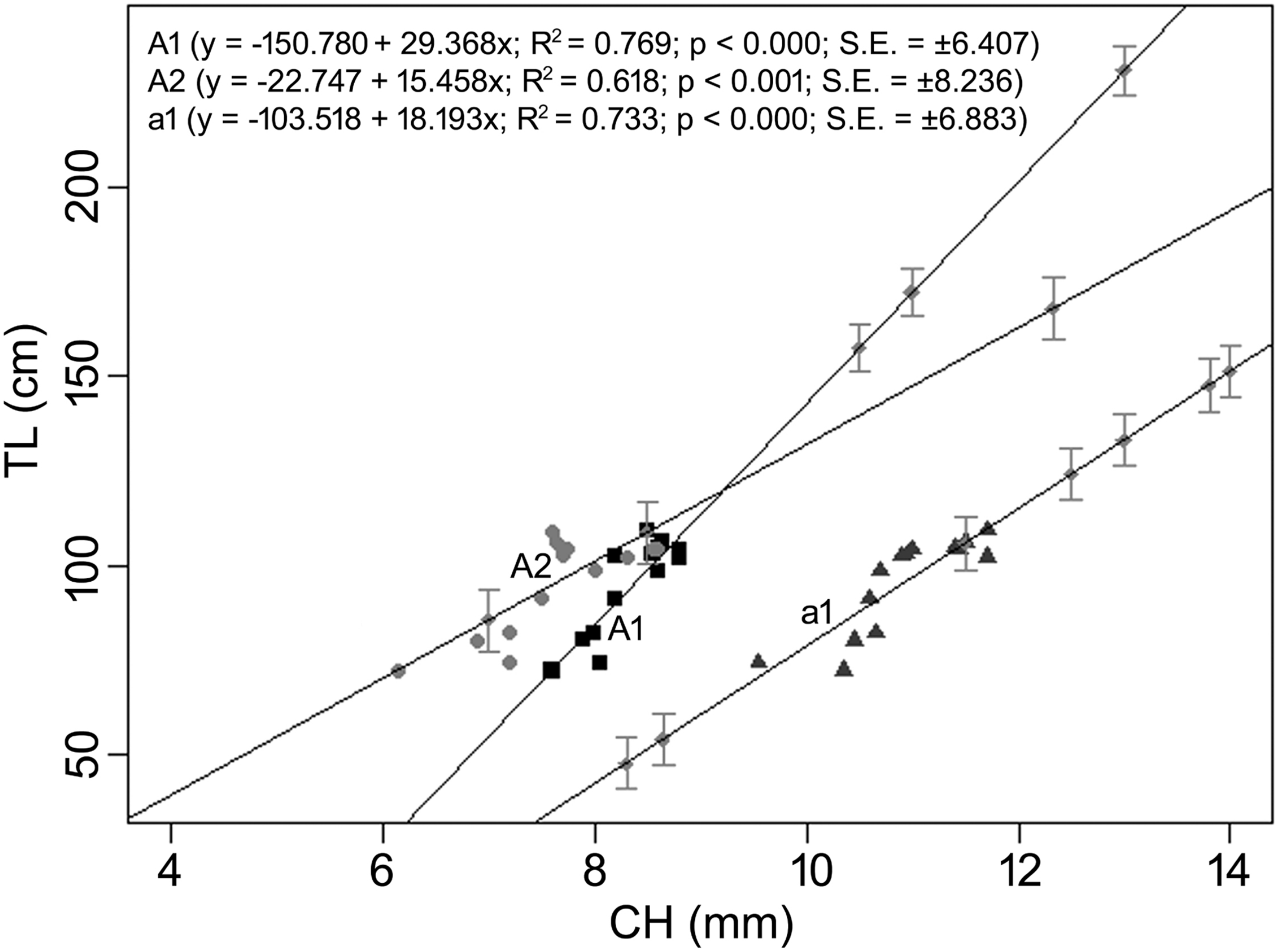

Figure 2. Bivariate scatter with regression line between tooth crown height (CH) and total body length (TL) for first upper anterior (A1: square), second upper anterior (A2: circle), and first lower anterior (a1: triangle) in *Pseudocarcharias kamoharai* (n= 14; for tooth types, see Fig. 1B; for statistics of regression lines, see Table 1). Diamonds with standard error bars represent TL estimated from CH of fossil teeth (Itoigawa et al. 1985, pl. 20, fig. 3, 4; Cigala-Fulgosi 1992, pl. 3, fig. 1, 2, 4–8; Schultz 2013, pl. 5, fig. 4; Carrillo-Briceño et al. 2015, fig. 4A, B; Landini et al. 2017, fig. 2L, M; Höltke et al, 2020, pl. 2, fig. 5, 2022a, fig. 3.7; Pollerspöck & Unger 2024, pl. 10, fig. 1, 2, 4).

TABLE 2

Significant differences between localities for adult *Pseudocarcharias kamoharai* specimens in standardized crown height (SCH) and crown acuteness (CA)

mean ± standard error of the mean; p = probability of error (* p <0.05).

Tooth Position	n	Males	n	Females	p
SCH					
All adults					
Lower teeth					
a1	7	1.344 ± 0.021	3	1.232 ± 0.016	0.011*
Okinawa Adults					
Upper teeth					
A1	4	1.054 ± 0.018	2	0.964 ± 0.025	0.044*
Lower teeth					
a1	4	1.369 ± 0.029	2	1.220 ± 0.016	0.028*
a2	4	1.262 ± 0.032	2	1.111 ± 0.023	0.038*
CA					
Okinawa Adults					
Upper teeth					
L1	4	1.838 ± 0.107	2	1.375 ± 0.014	0.045*
Lower teeth					
a2	4	3.083 ± 0.052	2	2.781 ± 0.105	0.040*

TABLE 3

Significant differences between localities for adult *Pseudocarcharias kamoharai* specimens in standardized crown height (SCH) and crown acuteness (CA)

mean ± standard error of the mean; p = probability of error (* p <0.05).

Tooth Position	n	Okinawa	n	Oahu	p
SCH					
Lower teeth					
l8	5	0.118 ± 0.004	3	0.099± 0.007	0.035*
CA					
Lower teeth					
a2	6	2.982 ± 0.077	3	2.681 ± 0.076	0.044*
l2	6	2.183 ± 0.167	3	1.534 ± 0.136	0.042*

mechanism for the enlarged body size (or 'gigantism' sensu lato) in the Miocene *Pseudocarcharias*, with a greater supply of prey fueling an increase in maximum body size.

Supplemental Information: Supplemental Tables 1–10 are archived at https://doi.org/10.5281/zenodo.18049231

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